THE EFFECT OF PRACTICE ON LEARNING AND TRANSFERRING GOAL DIRECTED ISOMETRIC CONTRACTIONS ACROSS IPSILATERAL UPPER AND LOWER LIMBS

A Thesis

by

NAVNEET KAUR

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

MASTER OF SCIENCE

May 2009

Major Subject: Kinesiology

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Approved by:

Chair of Committee,	Evangelos A. Christou
Committee Members,	David Wright
	Lisa Geraci
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ABSTRACT

The Effect of Practice on Learning and Transferring Goal Directed Isometric Contractions across Ipsilateral Upper and Lower Limbs. (May 2009)

Navneet Kaur, B.S. (PT), University of Delhi

Chair of Advisory Committee: Dr. Evangelos A. Christou

The purpose of this thesis was to determine whether practice-induced adjustments and retention of a goal directed isometric motor accuracy task were similar between ipsilateral upper and lower limb and whether there is an ipsilateral transfer between upper and lower limbs. In addition, this thesis project aimed to determine whether motor output variability and the activity of the involved agonist and antagonist muscles could predict any of the above stated changes. Sixteen young adults (8 men, 8 women; 22.1 ± 2.1 years) performed 80 trials of goal directed isometric contractions that involved accurately matching a target force of 25% MVC in 200 ms, either with the upper limb or the lower limb followed by the other limb. After an interval of 48 hours, 10 trials similar to the practice trials were performed to examine retention. Feedback of performance was provided in the form of a force-time trajectory along with numerical error values for force and time on each trial. End-point error was quantified as the absolute deviation from the targeted force and time. Motor output variability was quantified as the SD of force, SD of time to peak force and SD of force trajectory.

The practice-induced adjustments for force and time endpoint accuracy were similar for the two limbs, however, two days later, retention of the force accuracy was better with the upper limb compared with the lower limb. Practice-induced reduction and practice-to-retention

increase in force and time endpoint error were predicted by respective changes in peak force and time to peak force trial-to-trial variability for both limbs. In addition, the changes in accuracy were predicted by the changes in the activity of the involved agonist and antagonist muscles. Nonetheless, the changes in muscle activity differed between the two limbs. The adjustments in muscle activity were also different during the practice session despite the fact that the rate of improvement was similar for the two limbs. Finally, there was an asymmetric transfer of force accuracy from the lower limb to the ipsilateral upper limb, which was associated with the changes in motor output variability. The upper limb, which is inherently less variable as compared to the lower limb, may have retained the task better due to the formation of a stronger muscle synergy (or stronger internal model) to perform the contractions with accuracy. The lower limb, on the other hand may have formed a weaker internal model due to the greater interference from amplified signal-dependent noise (motor output variability) or an alternative motor plan, which may have been concerned primarily with the minimization of motor output variability instead of formation of a muscle synergy to perform the contractions accurately.

DEDICATION

I dedicate this thesis to my wonderful parents, Mr.Charan Singh and Mrs. Jasbir Kaur for their unconditional love and support over the years and for encouraging me to work hard towards achieving my academic and career goals.

I would also like to dedicate this to my friend, Mohit who kept my spirits high throughout and instilled in me the drive and determination to pursue my goals.

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I would like to thank my committee chair, Dr. Evangelos A. Christou for his continual guidance and support throughout the course of this research.

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TABLE OF CONTENTS

CHAPTER I

INTRODUCTION

Motor learning is defined as changes induced by practice or experience that lead to relatively permanent changes in the capability for movement (Schmidt and Lee 2005). Because the learning process can't be directly observed, changes in the performance of a motor task are used as an index of learning. Motor learning is associated with acute and long-term adaptations. Acute adaptations refer to the initial adjustments in the nervous system and motor output upon exposure to the novel task, whereas long-term adaptations refer to the ability to retain the initial adjustments and performance of the motor output. Finally, long-term adaptations improve the ability of an individual to transfer what was learnt to new conditions and variations of the practiced task. Transfer of learning refers to the gain or loss in the proficiency of performance on a new condition or variation of a task that was previously practiced. It is important to know how well a motor skill is retained and transferred to understand how well the skill was learnt. Learning-induced adaptations have been shown to induce changes in brain chemistry (Dunn 1980), changes in the cortical representation of the body parts involved in learning (Pascual-Leone et al. 1994), changes in the activity of higher centers (Floyer-Lea and Matthews 2005; Hikosaka et al. 2002) and changes in the activation of antagonist muscles (Christou et al. 2007).

Contralateral transfer between limbs

Motor learning improves performance not only of the practiced limb but also improves the performance (transfer) of the contralateral limb (Malfait and Ostry 2004). There is evidence

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that the transfer of learning across congruous contralateral limbs (hand to hand and foot to foot) is greater than the transfer of learning across incongruous contralateral limbs (hand to foot and vice versa) (Ammons et al. 1958; Cook 1936). A study on visuomotor task adaptations that required subjects to adapt to a 30^{o} counterclockwise rotation in the visual display during a center-out reaching task performed in eight directions showed that different movement features transferred in different directions across contralateral limbs. Subjects that practiced with the non-dominant arm first showed improved trajectory direction with the dominant arm, whereas subjects that practiced with dominant arm first showed improved final position accuracy (Sainburg and Wang 2002).

The transfer to contralateral limbs can be explained by the following three mechanisms: First, when a motor task has been learnt with one limb, the contralateral limb has already acquired the best technique or strategy to learn that motor task and thus, there is a transfer of learning across the two limbs. Second, the transfer of learning across two limbs can be explained using the concept of internal models. Skilled motor behavior depends on the acquisition of internal models, which are the representations of the sensorimotor transformations within the central nervous system that guide the actual transformations between sensory inputs and motor outputs to achieve a desired action (Wolpert et al. 2001). While the CNS uses the forward internal model to predict the sensory consequences of motor commands and estimate the state of the body and the environment, the inverse internal model helps the CNS transform the desired sensory consequences into the motor commands required to achieve them. When a motor task has been learnt by one limb, the forward and inverse internal models appropriate for that task have been acquired by that limb and these models are now available for use by the contralateral limb to perform the same task successfully. The third explanation comes from the

neuroanatomical and neurophysiological evidence that although the descending neural signals from the higher centers to the muscles are mainly contralateral, there is some overflow of these signals ipsilaterally that leads to stimulation of spinal motorneuron controlling the ipsilateral limbs as well (David 1942). The clinical relevance of contralateral limb transfer has been greatly explored in the rehabilitation of patients recovering from stroke where practice using the unaffected limb leads to improvement in performance with the affected contralateral limb.

Ipsilateral transfer between limbs

In contrast to the numerous studies that examined the ability of subjects to transfer motor learning to contralateral limbs, fewer studies have examined the transfer of learning across ipsilateral limbs. Subjects who practiced an interlimb multifrequency (2:1) coordination task with the upper limb moving twice as fast as the lower limb were able to transfer the same pattern to the contralateral side of the body. This pattern however did not transfer to the ipsilateral side of the body when subjects were asked to move the lower limb twice as fast as the upper limb (Vangheluwe et al. 2006). The authors proposed a dual layer movement representation model for their findings according to which the effector independent component (general movement goal of moving one limb twice as fast as the other) was thought to be represented at a higher level as compared to the effector specific component (muscle synergies acquired through practice), and hence a positive transfer to the contralateral side but not within the ipsilateral side. Seidler, Bloomberg and Stelmach (2001) found that the transfer of learning for goal directed pointing movements was symmetrical between the proximal and distal joints of the upper limb. The adaptations acquired were transferred from the wrist joint to the shoulder joint and vice versa. In the same study, arm and head pointing movements were also examined for transfer effects. There

was a high transfer from the arm to the head pointing movements and only little transfer from the head to the arm pointing movements (Seidler et al. 2001). These findings contradict those of many others that demonstrated a hierarchical nature of transfer between body segments, with the proximal segment always dominating the distal segment (Hay and Brouchon 1972; Krakauer et al. 2006; Putterman et al. 1969). Bloomberg and Stelmach (2001) proposed that different but dependent target representations exist for the arm and the head pointing movements, whereas a common representation exists for the arm segments.

A recent study examined the ability of individuals to transfer the force and time components of an isometric goal-directed task between the ipsilateral upper and lower limb submaximal isometric elbow flexion and dorsiflexion contractions (Christou and Rodriguez 2008). The authors demonstrated that time error and variability decreased significantly for the limb that performed the task second, while there was no transfer of force component across ipsilateral upper and lower limbs. The findings indicated that time and not force was transferred symmetrically between limbs. The authors proposed that planning of the timing (but not force) may be taking place at a common part of the brain for both the upper and the lower limb. They suggested that force did not transfer from one limb to the ipsilateral limb because of similar motor unit recruitment and discharge rate characteristics for the upper and the lower limb muscle, as the study used target force levels that were normalized to 25% of the maximum. In contrast, the time to peak force target was absolute at 200 ms.

Understanding of whether learning and transfer of learning is different between ipsilateral upper and lower limbs, two systems with inherently different motor output variability (Christou et al. 2003) within the same individual has both theoretical and clinical implications. Theoretically, it can help us understand how the central nervous system learns and transfers a

new task and the importance of the end effector in motor learning. For example, there is evidence that the lower limb exhibits greater motor output variability than the upper limb (Christou et al. 2003). According to the optimal feedback model (Scott 2004) greater noise in the nervous system will impair the formation of a strong internal model. This theory is supported by experimental evidence which demonstrates that practice improves the accuracy of the task by decreasing motor output variability within a trial (trajectory variability) and across trials (trial to trial variability) (Christou et al. 2007). These differences in motor performance may contribute to learning differences between the ipsilateral limbs. Clinically, it may enable the development of new training techniques to compensate for neurological impairments and promote neurological recovery.

Furthermore, it is important, both theoretically and clinically, to understand the associated changes in neuromuscular mechanisms that occur with motor learning. Because the activation of the motor unit is the last common pathway of the central nervous system to the periphery, the behavioral changes must be associated with acute and long-term adaptations in the activation of muscles involved in the task. Therefore, the differences in learning of a motor task between upper and lower limbs can also arise from the difference in the pattern of muscle activation involved in the learning process. Nonetheless, the literature on understanding the muscle activation with motor learning is limited. Such differences have been highlighted across young and old adults as they practiced a novel end-point isometric accuracy task (Christou et al. 2007). While young adults improved their force accuracy by adjusting the activity of both the agonist and antagonist muscle, old adults primarily adjusted the activity of the agonist muscle. In addition, an increase in the coactivation of agonist and antagonist muscles was reported at the elbow and shoulder joints with practice induced improvements in accuracy on a pointing task

(Gribble et al. 2003). These findings raise the possibility of a task-dependent nature of muscle activation with learning, which may be different for the upper and lower limb.

Overall, there is a need in the literature to further understand the relation between the practice-induced changes in performance across limbs, the ability to retain and transfer between ipsilateral upper and lower limbs, and the neuromuscular changes that occur at the level of the effector in a particular motor task. The overall purpose of this thesis project, therefore, was to determine whether the acute adjustments (rate of improvement with practice) and long-term adaptations (retention) to perform a novel motor task with accuracy are similar between the ipsilateral upper and lower limb and whether there is an ipsilateral transfer between upper and lower limbs. In addition, this thesis project attempted to determine whether the synergistic activation of the involved agonist and antagonist muscles in this task can predict such learning adaptations.

Research questions and hypotheses

This thesis project focused on addressing the following 4 research questions:

Question 1. Are there differences in motor performance between ipsilateral upper and lower limbs? If yes, can motor output variability and EMG measurements of the agonist and antagonist muscles predict the differences in the motor output between ipsilateral upper and lower limbs?
Hypothesis: Based on previous findings (Christou and Rodriguez 2008; Christou et al. 2003), it was hypothesized that the lower limb will be less accurate and more variable compared with the upper limb. The differences in performance will be due to differences in the synergistic activation of the agonist and antagonist muscles.

Question 2. Are the acute practice-induced adjustments different for the ipsilateral upper and lower limbs? If yes, can motor output variability and EMG measurements of the agonist and antagonist muscles predict the differences in the motor output between ipsilateral upper and lower limbs?

Hypothesis: Based on previous findings (Christou and Rodriguez 2008), it was hypothesized that the relative acute adjustments (rate of improvement with practice) will be similar for the upper and lower ipsilateral limbs.

Question 3. Is there any transfer of learning between ipsilateral upper and lower limb? If yes, which components (force or time) of the motor task are transferred between ipsilateral upper limb and lower limb as a result of practice? Can motor output variability and EMG measurements of the agonist and antagonist muscles predict such transfer?

Hypothesis: Based on previous findings (Christou and Rodriguez 2008), it was hypothesized that time but not force will transfer symmetrically between the ipsilateral upper and lower limbs. The transfer of timing between the two limbs will be due to transfer in the timing of activation between the agonist and antagonist muscles.

Question 4. Is the retention of the practiced motor task 48 hours after practice different for the ipsilateral upper and lower limb? If yes, which components (force or time) of the motor task are retained better as a result of practice? Can motor output variability and EMG measurements of the agonist and antagonist muscles predict the differences in retention?

Hypothesis: Because time was transferred between ipsilateral upper and lower limbs in previous findings (Christou and Rodriguez 2008), it was hypothesized that time but not force will be

retained. The retention will be similar for the ipsilateral upper and lower limbs. The retention of timing between the two limbs will be due to retention in the timing of activation between the agonist and antagonist muscles.

CHAPTER II

METHODS

Subjects

Sixteen young adults (eight men, eight women; 22.1 $\pm$ 2.1 years) participated in this study. All participants reported being physically healthy and moderately active and all of them were right limb dominant for both the leg and the arm according to the Edinburgh Handedness Inventory (Oldfield 1971). The experimental protocol for the study was approved by the Institutional Review Board at Texas A&M University. Subjects provided a written informed consent prior to participation in the study.

Experimental arrangement

An isokinetic dynamometer (KIN-COM 125A; Chattanooga Corporation, Chattanooga, TN) was used to measure the force exerted during goal-directed isometric contractions with the non-dominant upper and lower limb. The signal from the force transducer of the Isokinetic dynamometer was collected with an external A/D board (iWorx 118, iWorx CB Sciences Inc., Dover, New Hampshire, USA) and visual feedback was provided on a 51'' screen 1.8m in front of the subject via Matlab custom-made software. Each subject was seated on the chair of the dynamometer and affirmed that could see both the target and force-time trajectories. For the upper limb contraction, the left shoulder and the left elbow were positioned at 90^{o} of flexion and the forearm was fully supinated. The upper limb goal-directed contraction primarily involved elbow flexion (Figure 1A). For the lower limb contraction, the left hip was positioned at 110^{o} of flexion with neutral rotation and the left knee was positioned at 100^{o} of flexion. The ankle joint

was positioned so that the foot and the shank formed an angle of 90^{o}. The lower-limb goal-directed contraction primarily involved dorsiflexion (Figure 1B). Stabilizing trunk and thigh straps were used to avoid accessory joint movements that could confound the findings.

Force and EMG measurements

The force exerted by upper limb muscles was recorded with a force transducer at the wrist joint. The force exerted by lower limb muscles was recorded with a force transducer at the dorsal aspect of the left foot. The force signal was low pass filtered at 20 Hz and digitized at 1000 samples/s with a data acquisition system (iWorx 118, iWorx CB Sciences Inc., Dover, New Hampshire, USA) and stored on a personal computer.

The Electromyographic (EMG) activity of the primary agonist and antagonist muscles involved in the upper limb and lower limb contractions was measured with narrow pad Ag-AgCl bipolar surface EMG electrodes (model BL –AE- N, B&L Engineering, Tustin, CA, USA). The interelectrode distance or the distance between the conductive areas of the two electrodes in the bipolar electrode arrangement electrodes was less than ¼ of the muscle-fiber length for all muscles. The electrodes had an in-built amplifier that had a gain of 330 times, input impedance greater than 100 M Ω and a bandwidth of 10Hz to approximately 3.12 kHz. The placement of the electrodes on the muscles followed the guidelines proposed by the European initiative, Surface Electromyography for Noninvasive Assessment of Muscles (Hermens and Freriks 1997). For the upper limb contractions the EMG activity of the biceps, short and long heads; triceps long and lateral heads and the brachioradialis muscles was quantified; whereas, for the lower limb contractions the EMG activity of the Tibialis anterior, Peroneus longus, medial Gastrocnemius, lateral Gastrocnemius and Soleus muscles was quantified. The reference electrode was placed on

the styloid process of ulna. The interference EMG signals were band-passed filtered with a fourth order Butterworth digital filter from 10-500 Hz. To quantify the burst of activity from each muscle, the interference EMG signal was rectified and low pass filtered at 6 Hz using a fourth-order Butterworth digital filter. The EMG of all the muscles was sampled at 1000 samples/s with a data acquisition system (iWorx 118, iWorx CB Sciences Inc., Dover, New Hampshire, USA) and stored on a personal computer. The interference EMG signals were observed online by the investigator using the LabScribe2 Data Recording and Analysis software (iWorx LabScribe2, iWorx CB Sciences Inc., Dover, New Hampshire, USA) and a custom made MATLAB program.

Experimental procedures

Testing was conducted in two different days (sessions) with an interval of 48 hours between the two sessions (Figure 2). During the first testing session, the following were performed: 1) Brief familiarization of the equipment and task. 2) Five maximal voluntary isometric contractions (MVC). 3) Practice: Eight blocks of 10 practice trials (80 trials) of goal-directed submaximal isometric contractions performed either with the upper limb or lower limb. Contractions were repeated every 3 s and at the end of each block subjects received 1 minute rest. 4) Five MVCs as performed earlier to assess whether the repeated submaximal contractions induced any muscle fatigue. The same sequence of tasks was performed with the other limb after 20 minutes of rest. The order of the ipsilateral upper and lower limbs was counterbalanced among subjects.

The second testing session was conducted after an interval of 48 hours from the first testing session. During the second testing session, the following were performed: 1) Five MVC

trials. 2) Retention trials: One block of 10 trials of isometric goal-directed contractions at the same force and time target levels as the first session to examine retention of the task practiced during the first session; 3) Random trials: Eight blocks of 12 trials (96 trials) of goal directed isometric contractions at four different force and time targets. Each block was followed by a 1 minute rest period before the next block of trials and the trials within a block were separated by 3s rest periods. 4) Five MVCs as performed earlier to determine whether the protocol induced any muscle fatigue. The same sequence of movements was performed with the other limb after a break of 20 minutes. The order of limbs was the same as session 1 and was counterbalanced among subjects.

MVC TASK. Subjects were instructed to exert their maximal force as fast as they could during elbow-flexion, elbow-extension, dorsiflexion and plantarflexion isometric contractions. The maximum force value was considered as the MVC for the task performed. The MVC was used to normalize the force during practice (25% MVC) and random trials (12% and 50% MVC). In addition MVC was used to normalize the EMG amplitude for various muscles during the two experimental sessions. Finally, MVC was used at the beginning and end of trials for each limb to determine whether the repeated submaximal contractions induced any muscle fatigue.

ENDPOINT ACCURACY TASK. The task was to match the peak of the force-time trajectory exerted by the upper or lower limb to the center of the target box (Figure 3). The center of the target had both time (X-axis) and force (Y-axis) coordinates. The size of the target box was 20% of the targeted parameters. For the practice and retention trials the target coordinates were 200 ms (time target) and 25% MVC (force target). The same contraction was repeated for 80 practice trials (8 blocks of ten trials per limb) and ten retention trials (one block of ten trials per limb). For the random trials the target coordinates were: 1) 200 ms and 12.5%

MVC; 2) 200 ms and 50% MVC; 3) 100 ms and 25% MVC; 4) 400 ms and 25% MVC. The order of appearance for each target occurred randomly in eight blocks of 12 trials (4 targets x 3 random trials for each target). A custom-written program in Matlab® (Math Works™ Inc., Natick, Massachusetts, USA) manipulated the targeted force level and time and provided visual feedback regarding the errors.

The subjects were instructed to perform the contraction when they saw the target box change color from red to green. The red color target lasted 1s and was used to prepare the subject for the upcoming contraction ("GET READY" phase), whereas the green target was an indication to the subject that could initiate the contraction ("CONTRACT" phase). To avoid reaction time effects, the subjects were told to perform the movement at any point of time as long as the green box continued to be displayed on the screen. Feedback of performance was provided to the subjects in the form of a force-time trajectory along with numerical error values for force and time on each trial (Figure 4). There is evidence (Christou et al. 2007; Newell 1976) that when knowledge of results is provided by this kind of feedback, it improves performance in subsequent trials. The same knowledge of results was provided to the subjects during the retention and transfer trials. The screen with the target and the feedback was projected on a wall 1.8m in front of the subject at eye level. The screen was 46' long, 35' wide and 58' diagonally across. The length of the target box (along the x-axis) was 20% of the length of the x-axis of the screen and the width of the target box (along the y-axis) was 20% of the length of the y-axis of the screen.

Data analysis

Data were acquired and analyzed off-line with custom-written program in Matlab® (Math Works™ Inc., Natick, Massachusetts, USA). The force and surface EMG signals were analyzed from the start to the peak of the force trajectory. The start of the force trajectory was considered when the contraction value exceeded the resting value by 3% of the peak force in each trial. The force signal was low-pass filtered at 20 Hz with a fourth order Butterworth digital filter and digitized at 1000 samples/s. The interference EMG signals were band-pass filtered with a fourth order Butterworth digital filter from 10-500 Hz and subsequently rectified and low-pass filtered at 6 Hz to identify the burst of EMG activity in each muscle and contraction.

MOTOR OUTPUT. For each contraction the following parameters were recorded: 1) peak force; 2) time to peak force; 3) force endpoint error - quantified as the absolute difference between the targeted peak force and the exerted peak force for every trial; 4) time endpoint error - quantified as the absolute difference between the targeted time-to-peak force and the exerted time-to-peak force for every trial; 5) trajectory variability – quantified as the SD of force in the detrended force trajectory (start of force to peak force). This was achieved by removing the linear trend from the force data. In addition, the trial-to-trial variability for each block of trials was quantified for the following: 1) SD of peak force; 2) (CV; (SD / mean force) x 100); 3) SD of time to peak force; 4) CV of time to peak force.

EMG BURSTS. The EMG bursts of the involved agonist and the antagonist muscles was quantified with the following parameters: 1) EMG amplitude – peak of the EMG burst normalized to the peak EMG value of the MVC; 2) EMG onset – start of EMG activity quantified when EMG burst was > 5% of the peak EMG; 3) EMG offset – end of EMG activity quantified when EMG burst was < 5% of the peak EMG following the peak EMG burst; 4) EMG

duration - time between the onset and the offset of the EMG burst; 5) Time to peak EMG: duration of time from the onset of the EMG burst to the time of peak EMG amplitude; 6) Antagonist-Agonist EMG delay - time between the peak EMG amplitude of the major antagonist muscle (Triceps brachii or Soleus) relative to that of the major agonist muscle (Biceps brachii or Tibialis anterior) (7) Time of EMG overlap between the agonist and antagonist muscles. The trial to trial variability of the above listed parameters was quantified as the SD of each parameter for every block of trials.

To determine the changes in EMG activity of the involved muscles with practice, the change in EMG burst parameters was quantified as the difference in the EMG parameters recorded during the last practice block from the EMG parameters recorded during the first practice block. To determine the transfer of changes in the EMG activity of the involved muscles between ipsilateral upper and lower limb, the change in EMG burst parameters was quantified separately for the order where the upper limb contractions were performed first and the order where they were performed second. For the order where the upper limb contractions were performed first, the change in EMG parameters was quantified as the difference in the EMG parameters averaged over the 8 practice blocks with upper limb contractions from the EMG parameters averaged over 8 practice blocks with lower limb contractions. For the order where the upper limb contractions were performed second, the change in EMG parameters was quantified as the difference in the EMG parameters averaged over 8 practice blocks with lower limb contractions from the EMG parameters averaged over 8 practice blocks with upper limb contractions. To determine the changes in EMG activity of the involved muscles with retention following practice, the change in EMG burst parameters was quantified as the difference in the

EMG parameters recorded during the last practice block from the EMG parameters recorded during the retention block.

Statistical analysis

To examine the performance differences with practice and any potential transfer between the upper and the lower limb after one session of practice, a mixed three way ANOVA (2 limbs x 8 blocks of practice trials x 2 orders) with repeated measures on limbs and blocks of trials was used (SPSS version 16.0). To examine the performance differences between the last practice block (10 trials) and the retention block (10 trials), a mixed two way ANOVA (2 limbs x 2 times) with repeated measures on the limbs and the times was used.

Multiple linear regression models were used to establish statistical models that could predict 1) the change in force and time endpoint error (criterion variables) during a single practice session for the ipsilateral upper and lower limb from the change in peak-force variability, time-to-peak force variability, force trajectory variability, and agonist and antagonist muscle EMG activity parameters (predictor variables); 2) the change in force and time endpoint error (criterion variables) with transfer between ipsilateral upper and lower limb from the change in peak-force variability, time-to-peak force variability and force trajectory variability; and 3) the change in force and time endpoint error (criterion variable) with retention 48 hours after practice for ipsilateral upper and lower limb from the change in peak-force variability, time-to-peak force variability, force trajectory variability, and agonist and antagonist muscle EMG activity parameters (predictor variables). Only those predictor variables were included in the multiple regression models, that were significantly associated (bivariate regressions) with the force and time endpoint error (criterion variables).

The squared multiple correlation (R^2) and the adjusted squared multiple correlation (adjusted R^2) were used to give the goodness-of-fit of the model, to indicate how well the linear combination of the variables predicted the force and time endpoint error. Since the adjusted R^2 can overestimate the percentage of the variance in the criterion variable that can be accounted for by the linear combination of the predictor variables, especially with small sample size and a large number of predictors (Green and Salkind 2002), it is reported as the adjusted R^2. Part correlations (part *r*), were used to estimate the relative importance of the predictors as they provide the correlation between a predictor and the criterion after accounting for the effect of all other predictors in the regression equation (Green and Salkind 2002). A positive sign of the part correlation indicates a direct relation between the predictor and the criterion variable, whereas a negative sign indicates an inverse relation between the predictor and the criterion variable.

The alpha level was 0.05 for all statistical tests. Data are reported as means ± confidence intervals within the text and figures.

CHAPTER III

RESULTS

The purpose of this thesis project was achieved by examining the following: 1) Whether performance and practice-induced adjustments during a single practice session were similar with the ipsilateral upper and lower limb. 2) Whether any transfer of learning occurred between the ipsilateral upper and lower limb following a single practice session. 3) Whether retention 48 hours after practice of the goal-directed task was similar for the ipsilateral upper and lower limb. In addition, there was an interest of whether motor output variability and EMG of the involved agonist and antagonist muscles could predict any of the above potential differences in behavior.

Fatigue

To examine the level of fatigue in the muscles, a paired-samples T test was conducted to determine the difference in the MVC force before and after the testing session for the elbow flexion and dorsiflexion contractions. There was no significant difference in the means of the MVC forces between the pre and post test values for both upper ($t = 2.229$, $P = 0.09$) and lower limb ($t = 1.855$, $P = 0.08$). Therefore, the changes observed as a result of practice are not related to muscle fatigue in the contracting muscles.

Practice and limb motor performance

ENDPOINT ACCURACY. The end-point accuracy was quantified in the force and time domains. The force end-point error was the shortest distance between the exerted peak force and the targeted force, whereas the time end-point error was the shortest distance from the exerted

time to peak force and targeted time. Because the absolute amount of force was different between the upper and lower limb, the force error was normalized to the targeted force.

For the force end-point error, there was a significant limb ($F(1,14) = 7.205$, $P = 0.018$) and block ($F(7,98) = 12.118$, $P = 0.000$) main effect (Figure 5A). The limb main effect indicated that the upper limb exhibited greater force endpoint accuracy compared with the lower limb. The block main effect indicated that the rate of decline in force endpoint error with practice was similar for the upper and lower limb. The interaction between limb and block was not significant ($F(1,98) = 0.733$, $P = 0.644$). For the time endpoint error, there was only a significant block ($F(7,98) = 2.853$, $P = 0.009$) main effect (Figure 5B), which indicated that the rate of decline in time endpoint error with practice was similar for the upper and lower limb. The limb main effect ($F(1,14) = 2.246$, $P = 0.156$) and limb x block interaction ($F(1,98) = 0.674$, $P = 0.694$) were not significant.

MOTOR OUTPUT VARIABILITY. The motor output variability was quantified as the trial-to-trial variability (SD) of the peak force and time to peak force. In addition, the trajectory variability was quantified for each trial as the SD of the detrended force from the onset of force to the peak force.

For the SD of peak force, there was a significant limb ($F(1,14) = 8.054$, $P = 0.013$) and block ($F(7,98) = 8.879$, $P = 0.000$) main effect (Figure 6A). The limb main effect indicated that the lower limb exhibited greater variability in peak force compared with the upper limb. The block main effect indicated that the rate of decline in peak force variability with practice was similar for the upper and lower limb. The interaction between limb and block was not significant ($F(1,98) = 1.572$, $P = 0.153$). For the SD of time to peak force, the limb main effect ($F(1,14) = 0.240$, $P = 0.632$), block main effect ($F(7,98) = 1.276$, $P = 0.270$) and limb x block interaction

($F(1,98) = 0.867$, $P = 0.536$) were not significant. The results were similar for the CV of peak force and the CV of time to peak force. For the SD of force trajectory, there was a significant limb ($F(1,14) = 8.042$, $P = 0.013$) main effect (Figure 6B). The limb main effect indicated that the lower limb exhibited greater variability in force trajectory compared with the upper limb. The block ($F(7,98) = 0.794$, $P = 0.594$) main effect and the interaction between limb and block ($F(1,98) = 1.064$, $P = 0.393$) were not significant.

Prediction of the change in endpoint accuracy with practice

A single practice session of 80 trials improved the ability of the participants to perform accurate contractions (in force and time) with the upper and lower limb. Therefore, we wanted to determine whether the practice-induced adjustments for the upper and lower limb (change from block 1 to block 8) were associated with changes in: a) motor output variability (peak force variability, time-to-peak force variability, and force trajectory variability); and b) changes in the activation of the involved agonist and antagonist muscles.

MOTOR OUTPUT VARIABILITY. The change in force endpoint error with practice for the upper limb was predicted ($R^2 = 0.379$; adjusted $R^2 = 0.334$; $P = 0.011$; Figure 7A) from the change in the variability of peak force but not from the change in the variability of time to peak force or the change in the variability of force trajectory. Similarly, the change in force endpoint error with practice for the lower limb was predicted ($R^2 = 0.345$; adjusted $R^2 = 0.298$; $P = 0.017$; Figure 7A) from the change in the variability of peak force but not from the change in the variability of time to peak force or the change in the variability of force trajectory. The change in time endpoint error with practice for the upper limb was predicted ($R^2 = 0.779$; adjusted $R^2 = 0.763$; $P = 0.000$; Figure 7B) from the change in the variability of time-to-peak force but not

from the change in the variability of peak force or the change in the variability of force trajectory. Similarly, the change in time endpoint error with practice for the lower limb was predicted ($R^2 = 0.469$; adjusted $R^2 = 0.431$; $P = 0.003$; Figure 7B) from the change in the variability of time-to-peak force but not from the change in variability of peak force or the change in the variability of force trajectory. This analysis indicates that the improvements in force endpoint accuracy with practice for both limbs were moderately predicted from a decrease in the variability of peak force, whereas the improvements in time endpoint accuracy with practice for both limbs were moderately predicted from a decrease in the variability of time to peak force. The individual associations between the change in endpoint accuracy and motor-output variability measures with practice are reported in Table 1.

EMG. A similar analysis examined the adjustments in the agonist–antagonist EMG activity that accompanied improvements in accuracy with practice for ipsilateral upper and lower limbs. The change in force endpoint error with practice for the upper limb was predicted ($R^2 = 0.764$; adjusted $R^2 = 0.679$; $P = 0.002$; Figure 8A) from the change in the EMG delay between Biceps brachii (long head) and triceps brachii (lateral head) muscles (part $r = -0.377$), the change in the variability of the EMG delay between the Biceps brachii (long head) and triceps brachii (lateral head) muscles (part $r = 0.559$), the change in the EMG amplitude of Biceps brachii (short head) muscle (part $r = -0.457$) and the change in the time-to-peak EMG of the Biceps brachii (short head) muscle (part $r = 0.346$). The change in force endpoint error with practice for the lower limb was predicted ($R^2 = 0.480$; adjusted $R^2 = 0.400$; $P = 0.014$; Figure 8A) from the change in the EMG amplitude of the Soleus muscle (part $r = 0.348$) and the change in the duration of EMG activity of the Gastrocnemius Medialis muscle (part $r = 0.536$). The change in time endpoint error with practice for the upper limb could not be predicted from the changes in

the agonist–antagonist EMG activity. The change in time endpoint error with practice for the lower limb was predicted ($R^2 = 0.803$; adjusted $R^2 = 0.753$; P = 0.000; Figure 8B) from the change in the variability of time-to-peak EMG of the Soleus muscle (part r = 0.250), the change in the amplitude of the Peroneus Longus muscle (part r = -0.224) and the change in the variability of duration of the Tibialis anterior muscle (part r = 0.367). This analysis indicates that improvements in force endpoint accuracy with practice for the upper limb were predicted from a decrease in the agonist-antagonist EMG delay, decrease in the EMG amplitude of the agonist (Biceps brachii, short head) muscle, increase in the variability of agonist-antagonist EMG delay and increase in the time to peak EMG of agonist (Biceps brachii, short head), whereas the improvements in force endpoint accuracy with practice for the lower limb were predicted from the increase in the EMG amplitude of the antagonist (Soleus) muscle and increase in the EMG duration of the antagonist (Gastrocnemius medialis) muscle. The improvements in time endpoint accuracy with practice for the upper limb were not predicted from the changes in the agonist-antagonist EMG activity, whereas the improvements in time endpoint accuracy with practice for the lower limb were predicted from an increase in the variability of time to peak EMG of the antagonist (Soleus) muscle, decrease in the EMG amplitude of the agonist (Peroneus longus) muscle and increase in the variability of EMG duration of the agonist (Tibialis anterior) muscle.

Transfer between ipsilateral upper and lower limbs

ENDPOINT ACCURACY. For the force end-point error, the limb x order x block interaction ((F(1,98) = 1.929; P = 0.073; Figure 9) was not statistically significant. However, this interaction exhibited a trend towards a decrease in the endpoint force error for the upper limb when the upper limb contractions were preceded by the lower limb contractions compared with

when the upper limb contractions were performed first. Furthermore, this interaction indicated that the lower limb contractions were not influenced by the order of performance. For the time endpoint error, there was no significant limb x order x block interaction ($F(1,98) = 0.940$; $P = 0.479$). This indicated that the change in time endpoint error was not influenced by the order of performance. Therefore, only force endpoint accuracy and not time endpoint accuracy exhibited a trend towards transfer between ipsilateral upper and lower limbs. This occurred from the lower limb to the ipsilateral upper limb and not from the upper limb to the ipsilateral lower limb.

MOTOR OUTPUT VARIABILITY. For the SD of peak force ($F(1,98) = 0.282$; $P = 0.267$) and the SD of time to peak force ($F(1,98) = 1.956$; $P = 0.069$), there was no significant limb x order x block interaction. The results were similar for the CV of peak force and the CV of time to peak force. For the SD of force trajectory, there was a significant limb x order x block interaction $F(1,98) = 3.152$; $P = 0.005$; Figure 10). This indicated that the change in the variability of force trajectory was lower when the upper limb contractions were preceded by the lower limb contractions compared with when the upper limb contractions were performed first. Therefore, only force trajectory variability got transferred between ipsilateral upper and lower limbs and this occurred form the lower limb to the ipsilateral upper limb.

Prediction of ipsilateral transfer of force endpoint accuracy

Only the peak force endpoint error showed a trend towards transfer from the lower limb to the upper limb. Therefore, we wanted to determine whether the transfer of force endpoint accuracy from the lower limb to the ipsilateral upper limb was associated with changes in the motor output variability (peak force variability, time-to-peak force variability, and force trajectory variability).

MOTOR OUTPUT VARIABILITY. The change in force endpoint error across limbs for the order where the upper limb contractions preceded the lower limb contractions and the order where the lower limb contractions preceded the upper limb contractions was predicted (R^2 = 0.812; adjusted R^2 = 0.798; P = 0.000; Figure. 11) from the change in variability of peak force but not from the change in the variability of time to peak force or the change in the variability of force trajectory. This analysis indicates that the ipsilateral transfer of force endpoint accuracy from the lower limb to the ipsilateral upper limb (but not from the upper limb to the ipsilateral lower limb) was predicted by a decrease in the variability of peak force. The individual associations between the transfer of force endpoint accuracy and motor-output variability measures are reported in Table 2.

Retention of practiced task for the ipsilateral upper and lower limbs

ENDPOINT ACCURACY. For the force end-point error, there was a significant limb ($F(1,14) = 22.732$; P = 0.000) and time ($F(1,14) = 32.967$; P = 0.000) main effect (Figure 12A). The limb main effect indicated that, on average, the lower limb compared with the upper limb exhibited a greater force endpoint error for the last practice block and the retention block. The time main effect indicated that the average force endpoint error for both limbs on the retention block was greater than the last practice block. The interaction between limb and time was significant ($F(1,14) = 5.611$; P = 0.033) for the force endpoint error, which indicated that the upper limb retained peak force endpoint accuracy better than the lower limb. For the time endpoint error, there was a significant time ($F(1,14) = 9.163$; P = 0.009) main effect (Figure 12B). The time main effect indicated that the average time endpoint error for both limbs on the retention block was greater than the last practice block. The limb main effect ($F(1,14) = 1.615$; P

= 0.225) and the interaction between limb and time (F(1,14) = 0.757; P = 0.399) were not significant. Therefore, the average force and time endpoint errors were greater on the retention block than the last practice block for both limbs. The upper limb exhibited greater force endpoint accuracy than the lower limb and better retention after 48 hours.

MOTOR OUTPUT VARIABILITY. For the SD of peak force, there was a significant limb (F(1,14) = 21.120; P = 0.000) and time (F(1,14) = 32.281; P = 0.000) main effect (Figure 13A). The limb main effect indicated that lower limb had greater variability in peak force as compared to the upper limb. The time main effect indicated that, on average, there was an increase in the variability of peak force from the last practice block to the retention block for both the limbs. The interaction between limb and time was significant (F(1,14) = 11.274, P = 0.005). This interaction indicated that the retention of peak force variability was better with the upper limb than the lower limb. For the SD of time to peak force, there was a significant time main effect (F(1,14) = 6.808, P = 0.021; Figure 13B). The time main effect indicated that, on average, there was an increase in the variability of time to peak force from the last practice block to the retention block for both the limbs. The limb main effect (F(1,14) = 1.720; P = 0.211) and the limb x time interaction (F(1,14) = 0.001, P = 0.982) were not significant. The results were similar for the CV of peak force and the CV of time to peak force. For the SD of force trajectory, there was a significant limb (F(1,14) = 12.236, P = 0.004; Figure 13C) main effect. The limb main effect indicated that the lower limb had a greater variability in force trajectory as compared to the upper limb. The time main effect (F(1,14) = 0.764, P = 0.397) and the interaction between limb and time (F(1,14) = 3.864, P = 0.069) were not significant.

Prediction of the practice-to-retention change in endpoint accuracy

After two days, retention performance for force and time endpoint accuracy was impaired relative to the last practiced block for both limbs. The upper limb exhibited lesser impairment in force endpoint accuracy as compared to the ipsilateral lower limb, indicating that the upper limb retained peak force accuracy better than the ipsilateral lower limb. Therefore, we wanted to determine whether the practice-to-retention changes for the upper and lower limb (change from the last practice block to the retention block) were associated with changes in: a) motor output variability (peak force variability, time-to-peak force variability and force trajectory variability) and b) changes in the activation of the involved agonist and antagonist muscles.

MOTOR OUTPUT VARIABILITY. The change in force endpoint error from the last practice block to the retention block for the upper limb was predicted ($R^2 = 0.531$; adjusted $R^2 = 0.498$; $P = 0.001$; Figure 14A) from the change in variability of peak force but not from the change in variability of time to peak force or variability of force trajectory. Similarly, the change in force endpoint error from the last practice block to the retention block for the lower limb was predicted ($R^2 = 0.870$; adjusted $R^2 = 0.861$; $P = 0.000$; Figure 14A) from the change in the variability of peak force but not from the change in variability of time to peak force or the change in the variability of force trajectory. The change in time endpoint error from the last practice block to the retention block for the upper limb was predicted ($R^2 = 0.747$; adjusted $R^2 = 0.729$; $P = 0.000$; Figure 14B) from the change in variability of time-to-peak force but not from the change in the variability of peak force or the change in the variability of force trajectory. Similarly, the change in time endpoint error from the last practice block to the retention block for the lower limb was predicted ($R^2 = 0.422$; adjusted $R^2 = 0.381$; $P = 0.006$; Figure 14B) from the change in the variability of time-to-peak force but not from the change in the variability of peak

force or the change in the variability of force trajectory. This analysis indicates that the decline in force endpoint accuracy from the last practice block to the retention block for both limbs was predicted by an increase in the variability of peak force, whereas the decline in time endpoint accuracy for both limbs was predicted by an increase in the variability of time-to-peak force. The individual associations between the change in endpoint accuracy and motor-output variability measures from the last practice block to the retention block are reported in Table 3.

EMG. A similar analysis examined the adjustments in the agonist–antagonist EMG activity that accompanied the practice-to-retention changes in force and time endpoint accuracy for ipsilateral upper and lower limbs. The change in force endpoint error from the last practice block to the retention block for the upper limb was predicted ($R^2 = 0.556$; adjusted $R^2 = 0.445$; $P = 0.018$; Fig. 15A) from the change in variability of the EMG amplitude of the Triceps brachii (long head) muscle (part r = 0.282), the change in the EMG duration of the Triceps brachii (lateral head) muscle (part r = -0.501) and the change in the EMG amplitude of the Biceps brachii (long head) muscle (part r = 0.321), whereas the change in force endpoint error from the last practice block to the retention block for the lower limb predicted ($R^2 = 0.525$; adjusted $R^2 = 0.406$; $P = 0.026$; Fig. 15A) from the change in time to peak EMG of the Gastrocnemius medialis muscle (part r = 0.353), the change in the EMG duration of the Tibialis anterior muscle (part r = -0.386) and the change in the EMG amplitude of the Gastrocnemius medialis muscle (part r = 0.256). The change in time endpoint error from the last practice block to the retention block for the upper limb was predicted ($R^2 = 0.750$; adjusted $R^2 = 0.688$; $P = 0.001$; Fig. 15B) from the change in variability of the EMG amplitude of the Brachioradialis muscle (part r = 0.415), the change in the variability of the time to peak EMG of the Biceps brachii (long head) muscle (part r = 0.284) and the change in the time to peak EMG of the Brachioradialis muscle (part r =

0.436), whereas the change in time endpoint error from the last practice block to the retention block for the lower limb was predicted ($R^2 = 0.867$; adjusted $R^2 = 0.818$; P = 0.000; Fig. 15B) from the change in the variability of time to peak EMG of the Soleus muscle (part r = 0.460), the change in the EMG amplitude of the Tibialis anterior muscle (part r = 0.318), the change in the EMG delay between Tibialis anterior and Soleus muscles (part r = -0.319) and the change in the time to peak EMG of the Soleus muscle (part r = -0.163). This analysis indicates that practice-to-retention change in force endpoint accuracy for the upper limb was predicted from an increase in the variability of the EMG amplitude of an antagonist (Triceps brachii (long head)) muscle, decrease in the EMG duration of an antagonist (Triceps brachii (lateral head)) muscle and increase in the EMG amplitude of an agonist (Biceps brachii (long head)) muscle, whereas the practice-to-retention change in force endpoint accuracy for the lower limb was predicted from an increase in the time to peak EMG of an antagonist (Gastrocnemius medialis) muscle, decrease in the EMG duration of an agonist (Tibialis anterior) muscle and increase in the EMG amplitude of an antagonist (Gastrocnemius medialis) muscle. The practice-to-retention change in time endpoint accuracy for the upper limb was predicted from an increase in the variability of the EMG amplitude of an agonist (Brachioradialis) muscle, increase in the variability of time to peak EMG of an agonist (Biceps brachii (long head)) and increase in the time to peak EMG of an agonist muscle (Brachioradialis), whereas the practice-to-retention change in time endpoint accuracy for the lower limb was predicted from an increase in the variability of time to peak EMG of the Soleus muscle, increase in the EMG amplitude of the Tibialis anterior muscle, decrease in the EMG delay between Tibialis anterior and Soleus muscles and decrease in the time to peak EMG of the Soleus muscle.

CHAPTER IV

CONCLUSION

The purpose of this thesis project was to determine whether the ability of individuals to perform and learn with the ipsilateral upper and lower limb is similar. An additional interest of this project was to examine whether transfer could occur between ipsilateral upper and lower limbs. As expected from previous studies (Christou and Rodriguez 2008; Christou et al. 2003), the lower limb was less accurate and more variable from trial-to-trial than the upper limb. This impairment in performance was evident for the force but not the time component of the task. The practice-induced adjustments for force and time endpoint accuracy were similar for the two limbs, however, two days later the retention of the force accuracy was better with the upper limb compared with the lower limb. Finally, there was a trend for asymmetric transfer of force endpoint accuracy from the lower limb to the ipsilateral upper limb. The practice-induced adjustments for both limbs and the differential transfer between the upper and lower limbs were predicted by trial-to-trial motor output variability and activation of the involved agonist and antagonist muscles.

Limb performance and practice-induced adjustments

One of the main reasons for comparing the upper and lower limb in this learning paradigm was the expected differences in endpoint accuracy and motor output variability. Previous studies have demonstrated that the lower limb is less accurate and more variable than the upper limb. For example, Christou & Rodriguez (2008) demonstrated recently that the upper limb is more accurate than the lower limb during goal-directed isometric contractions. In

addition, there is evidence that independent of the joint used in the upper and lower limb, the lower limb will be more variable across trials compared with the upper limb during goal-directed isometric contractions (Christou et al. 2003). According to the minimum variance theory, the central nervous system learns to perform new tasks with accuracy by minimizing the signal-dependent noise, which is exhibited as endpoint variability across trials (Harris and Wolpert 1998). In addition, according to the optimal feedback control model (Scott 2004), this noise can impair the ability of individuals to form an internal model and thus retain the task. These performance differences between limbs, therefore, present a good model to determine whether within the same individual, an effector (limb) with greater inherent variability will impair learning and transfer of a goal-directed isometric task.

Consistent with the previous findings (Christou and Rodriguez 2008; Christou et al. 2003) the results of this project demonstrate that the upper limb was more accurate and less variable than the lower limb. Specifically, force endpoint error and peak force variability was greater for the dorsiflexion contractions (lower limb) compared with the elbow-flexion contractions (upper limb). In contrast, the time endpoint error and time to peak force variability were not significantly different between the two limbs. This finding contrasts the time findings of previous studies (Christou and Rodriguez 2008; Christou et al. 2003). This difference may be due to methodological differences. For example, for the Christou et al. (2003) study, subjects had to match a parabola with their force output, whereas in this project, subjects aimed to place their endpoint force in a target. The Christou & Rodriguez (2008) methods, however, were similar with this project except that the screen for the target presentation was not directly in front of the subjects but 20 degrees to their left. This setup may have influenced the accurate perception of the contraction time during the previous study.

The lower limb exhibits greater motor output variability and lower endpoint accuracy as compared to the upper limb. This can be explained by the greater number of synapses that occur to activate the lower limb muscles compared with the upper limb muscles or a smaller cortical representation for the lower limb muscles as compared to the upper limb muscles. Another possible explanation could be that the upper limb movements are practiced more than the lower limb movements in normal daily routines. It has been shown that the hand and arm muscles were active for 18% of the recording time, whereas leg muscles were active for only 10% of the recording time during a 10-hour recording session, and that the upper-limb muscles, on average were activated 67% more often than the lower-limb muscles (Kern et al. 2001). Thus, the more practiced upper limb movements are more extensively represented in the primary motor cortex as compared with the less practiced lower limb movements (Ungerleider et al. 2002), which leads to a more accurate and less variable upper limb performance as compared with the lower limb performance, as the upper limb can draw from a more diverse repertoire of internal models.

Despite the differences in accuracy and motor output variability between the two limbs, the practice-induced adjustments (improvements) in accuracy and variability were similar for the two limbs. In support of the proponents of the minimum variance theory (Hamilton et al. 2004; Harris and Wolpert 1998; van Beers et al. 2004) and previous studies performed with the upper limb (Christou et al. 2007; Christou and Rodriguez 2008), the improvement in force and time endpoint accuracy with practice was associated with a decline in motor output variability. For both limbs, approximately 35% of the improvement in force accuracy was predicted by the decline in peak force variability. Approximately 78% and 47% of the improvement in time endpoint accuracy was predicted by the decline in time to peak force variability for the upper and lower limb respectively. These findings are consistent with results from previous studies which

showed that force and time endpoint accuracy improved with practice and such improvements were associated with a decline in motor output variability during isometric contractions (Christou and Rodriguez 2008; Floyer-Lea and Matthews 2005) and movements (Corcos et al. 1993; Darling and Cooke 1987; Gottlieb et al. 1988; Muller and Sternad 2004).

The predictions of the minimum variance theory (Hamilton et al. 2004; Harris and Wolpert 1998; van Beers et al. 2004), therefore, are supported by the parallel improvement in endpoint accuracy and motor output variability. Nonetheless, the reduction of signal-dependent noise (motor output variability) can only partially explain the endpoint accuracy improvements. It is possible, therefore, that improvements in motor performance with practice come from two major adjustments in muscle activity. Such muscle adjustments may lead to: a) a reduction in the motor output variability and b) improvement in the position of the endpoint relative to the target. The results of this project, demonstrate that this occurs for both the upper and lower limb. For the upper limb, practice-induced adjustments were strongly predicted ($R^2 = 0.76$) by longer delay between the agonist and antagonist muscles, reduction in the variability of the delay between the agonist and antagonist muscles, an increase in the amplitude of the agonist activity, and a decrease in the rate of the EMG development for the agonist muscle. For the lower limb, practice-induced adjustments were moderately predicted ($R^2 = 0.48$) by a decrease in the amplitude of the major antagonist muscle and a decrease in the duration of another antagonist muscle. These synergistic muscle adaptations, therefore, may be related to the formation of an internal model while learning to perform this task accurately (Scott 2004). Consequently, the formation of an internal model appears to be stronger for the upper limb compared with the lower limb during practice.

Task retention

The main interest of this proposal was to determine whether retention of the goal-directed task would be similar for the upper and lower limb due to the differential amount of inherent variability. The findings clearly demonstrate that 48 hours after the practice session, performance (force and time endpoint accuracy) declines compared with the last block of practice. Nonetheless, the upper limb better retained the force component of the goal-directed task compared with the lower limb. This finding supports the prediction by Harris and Wolpert (1998) and Scott (2005) that greater signal-dependent noise may impair the formation of a strong internal model and consequently learning of a motor task with accuracy. For example, the upper limb compared with the lower limb, exhibited lower trial-to-trial variability in peak force but not time to peak force. Consistent with the predictions, only retention of the force endpoint accuracy was impaired for the lower limb compared with the upper limb. Retention of time endpoint accuracy was similar for the two limbs because the time to peak force trial-to-trial variability was also similar for the two limbs. For the upper limb contractions, approximately 50% of the impairment in force accuracy 2 days after the practice session was predicted by the amplified peak force variability. For the lower limb contractions, however, approximately 86% of the impairment in force accuracy 2 days after the practice session was predicted by the amplified peak force variability. Therefore, it appears that constraining the peak force trial-to-trial variability 2 days after practice was harder to do with the lower limb than the upper limb. This suggests that the formation of the internal model with the upper limb may have been better to reduce peak force variability, which consequently helped subjects retain the task better. Interestingly, the impairment in retention was also predicted by different EMG parameters for the upper and lower limb. Specifically, the impaired force endpoint accuracy in the upper limb

during the retention task relative to the last practice block, was predicted ($R^2 = 0.556$) from an increase in the variability of the antagonist EMG amplitude, a decrease in the EMG duration of the antagonist muscle, and an increase in the agonist EMG amplitude. In contrast, the impaired force endpoint accuracy in the lower limb during the retention task relative to the last practice block, was predicted ($R^2 = 0.525$) from an increase in the time to reach peak EMG of the antagonist muscle (slower rate), a decrease in the EMG duration of the agonist muscle, and an increase in the antagonist EMG amplitude.

It is possible, therefore, that 2 days after the practice session different muscle activation schemes were forgotten by the nervous system to accurately control the upper and lower limb. This comes in addition to the different muscle activation adaptations that occurred with practice, which may also point to the possibility that different parameters were controlled at the last block of practice for the upper and lower limb. Potentially, the differences in muscle activation adaptation with practice and during the retention period may reflect differential acquisition of internal models. Internal models are thought to be representations of the sensorimotor transformations within the central nervous system that guide the actual transformations between sensory inputs and motor outputs to achieve a desired action (Wolpert et al. 2001). Possibly, practice with lower inherent motor output variability, as occurred with the upper limb, may have caused less interference with the formation of an internal model. Therefore, it is possible that a stronger internal model was formed for the upper limb than the lower limb, which consequently allowed the subjects to retain the task better. Another possible explanation could be that the motor plan of the goal-directed contraction for the upper and lower limbs was different. For instance, the motor plan formed by the higher centers for the lower limb could have been more concerned with minimization of motor output variability simply because the lower limb was

inherently more noisy due to the greater number of synapses that occur to activate the muscles or the smaller cortical area that is dedicated to the lower limb. In contrast, the motor plan for the upper limb goal-directed contractions could have been less concerned with minimization of the motor output variability and more concerned with the formation of a synergy between the antagonist muscles to improve the endpoint of the force. Consequently it led to greater retention of the force component of the task.

Ipsilateral transfer

Only force endpoint accuracy showed a trend towards being transferred between the ipsilateral upper and lower limb. The transfer occurred in a distal to proximal direction from the lower limb to the ipsilateral upper limb but not vice versa. There was no transfer of motor output variability (except force trajectory variability) across the ipsilateral upper and lower limb. This is in contrast to the findings of Christou & Rodriguez (2008) where only the time components of the goal-directed task got transferred symmetrically between the ipsilateral upper and lower limb. The differences in findings may be due to methodological differences. For example, for the Christou & Rodriguez (2008) study, the elbow flexion was performed while the forearm was in neutral position, whereas in this study, we used a supinated position of the forearm (relatively harder). In addition, as described above, the feedback of the goal-directed contractions was provided to the left of the subject, whereas in this study, the feedback was provided right in front of the subject. Potentially, this off center view of the feedback may have made it more difficult for the Christou & Rodriguez (2008) subjects to perceive time feedback. Finally, the number of subjects in each group was almost twice as many in this project compared with the previous

study. Whatever the methodological differences, this type of study needs to be repeated to determine whether transfer can occur ipsilaterally between upper and lower limbs.

Independent of the dissimilar findings between the study by Christou and Rodriguez (2008) and this project, there was an improvement in the force endpoint accuracy in the upper limb contractions when they were preceded by lower limb contractions but not vice versa. Interestingly, this transfer was also associated with trial-to-trial variability. Specifically, the improvement in force endpoint accuracy for the upper limb contractions when they were preceded by lower limb contractions was strongly associated with reductions in peak force trial-to-trial variability. Therefore, one possible explanation is that subjects who performed with the lower limb first experienced more variability in the force-time feedback environment and thus had more experience with performing adjustments in their muscle activation to reduce the motor output variability. Another possible explanation is that practice with the lower limb occurred in a more variable environment due to the inherently greater variability of the lower limb compared with the upper limb. Previous studies show that variability of practice improves the ability of subjects to transfer to new variations of the task (Shea et al.1990; Shea and Morgan 1979; Wulf and Lee 1993). Nonetheless, this is the first study to show that this transfer may occur between a more variable to a less variable effector system.

Furthermore, this study supports previous findings that transfer ipsilaterally can occur from distal to proximal segments. For example, Seidler, Bloomberg and Stelmach (2001) found that the transfer of learning for goal directed pointing movements was symmetrical between the proximal and distal joints of the upper limb. The adaptations acquired were transferred from the wrist joint to the shoulder joint and vice versa. In the same study, arm and head pointing movements were also examined for transfer effects. There was a high transfer from the arm to

the head pointing movements and only little transfer from the head to the arm pointing movements.

Based on the literature review, this may be the first study that compares the ability of humans to learn and retain goal-directed contractions with the upper and lower limb. The findings clearly demonstrate that although the rate of learning is similar for the two limbs, the upper limb, which is inherently less variable than the lower limb, better retains the force accuracy of goal-directed isometric contractions. Based on the changes observed in motor output variability and activation of the antagonist muscles, it is hypothesized that the upper limb formed a stronger internal model than the lower limb. The formation of a weaker internal model for the lower limb compared with the upper limb may have been due to: a) greater interference from amplified signal-dependent noise (greater motor output variability) or b) an alternative motor plan, which may have been concerned primarily with minimization of motor output variability instead of the formation of a strong muscle synergy to execute the contraction accurately. Future studies should further explore the influence of inherent motor output variability in learning and transferring motor tasks with accuracy. Such studies may include comparisons between young and older adults or between neurological patients and healthy controls. In addition, the findings of this project should be extended to goal-directed movements and more complex tasks.

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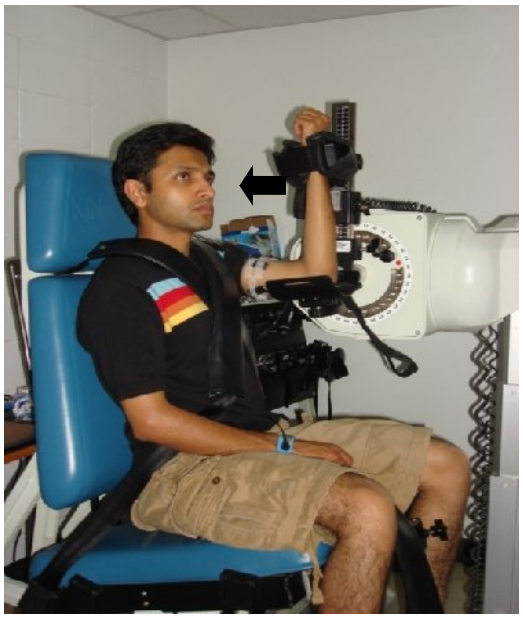
APPENDIX A

FIGURES

Figure 1

A



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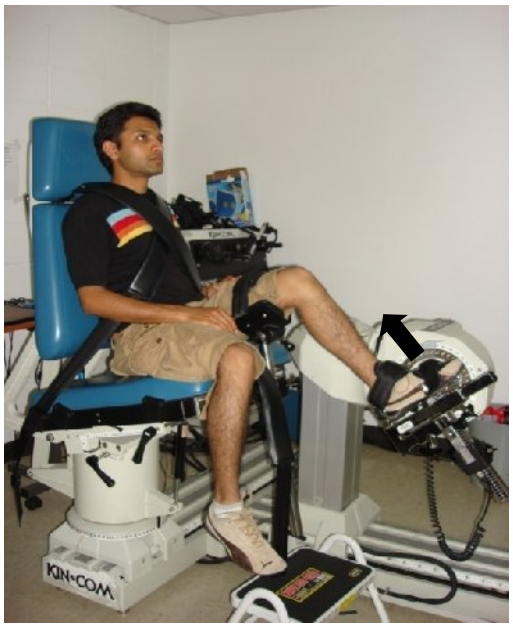


Figure 2

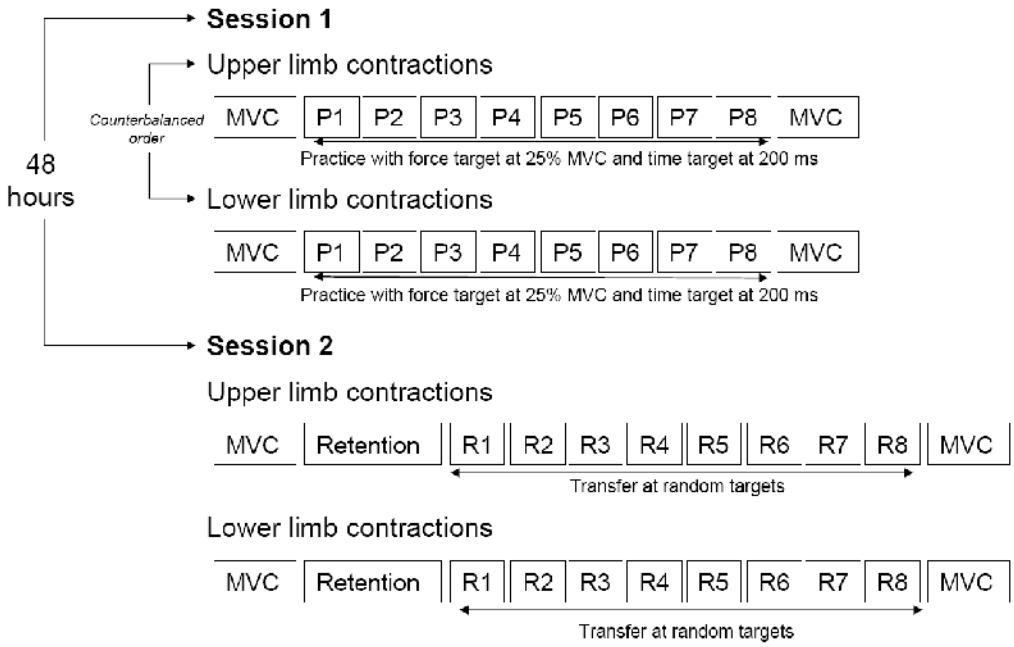

Session 1
Upper limb contractions
Counterbalanced order
MVC P1 P2 P3 P4 P5 P6 P7 P8 MVC
Practice with force target at 25% MVC and time target at 200 ms
48 hours
Lower limb contractions
MVC P1 P2 P3 P4 P5 P6 P7 P8 MVC
Practice with force target at 25% MVC and time target at 200 ms
Session 2
Upper limb contractions
MVC Retention R1 R2 R3 R4 R5 R6 R7 R8 MVC
Transfer at random targets
Lower limb contractions
MVC Retention R1 R2 R3 R4 R5 R6 R7 R8 MVC
Transfer at random targets

Figure 3

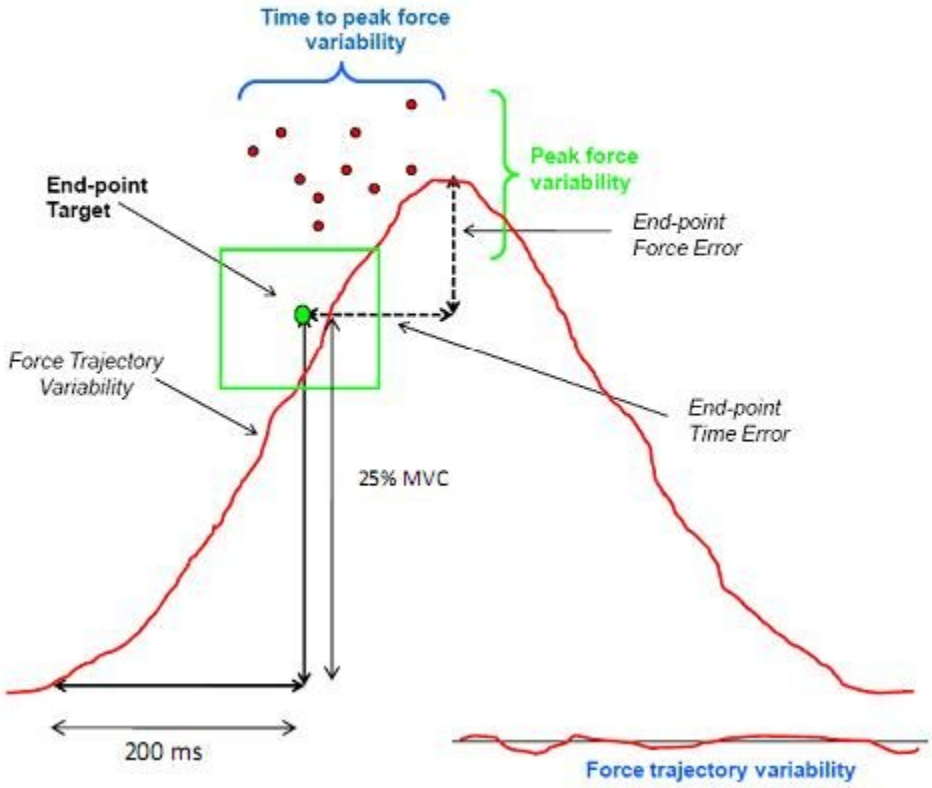

Time to peak force variability
Peak force variability
End-point Target
End-point Force Error
Force Trajectory Variability
End-point Time Error
25% MVC
200 ms
Force trajectory variability

Figure 4

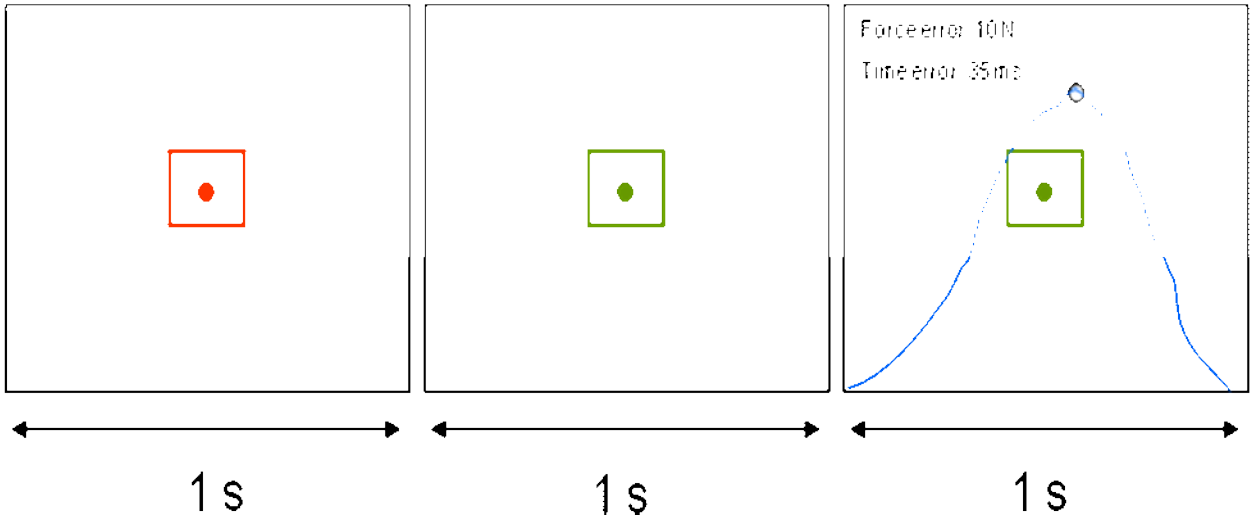
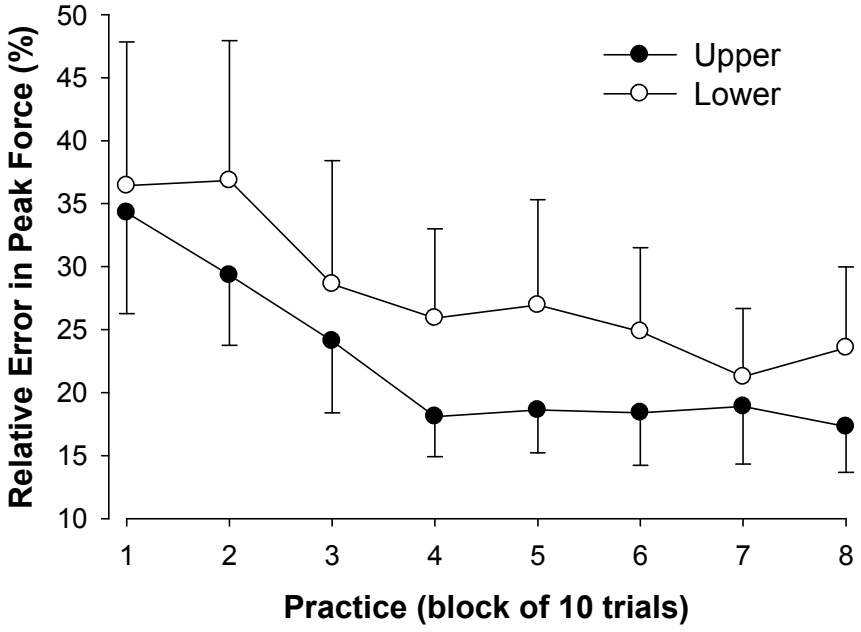


Figure 5

A


Relative Error in Peak Force (%)
50
45
40
35
30
25
20
15
10
Upper
Lower
1
2
3
4
5
6
7
8
Practice (block of 10 trials)

B

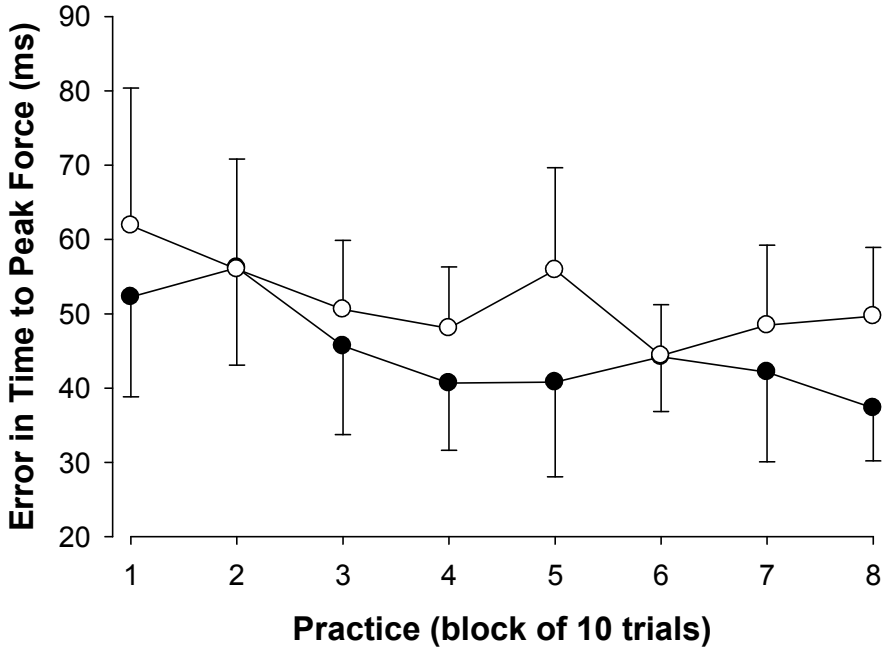
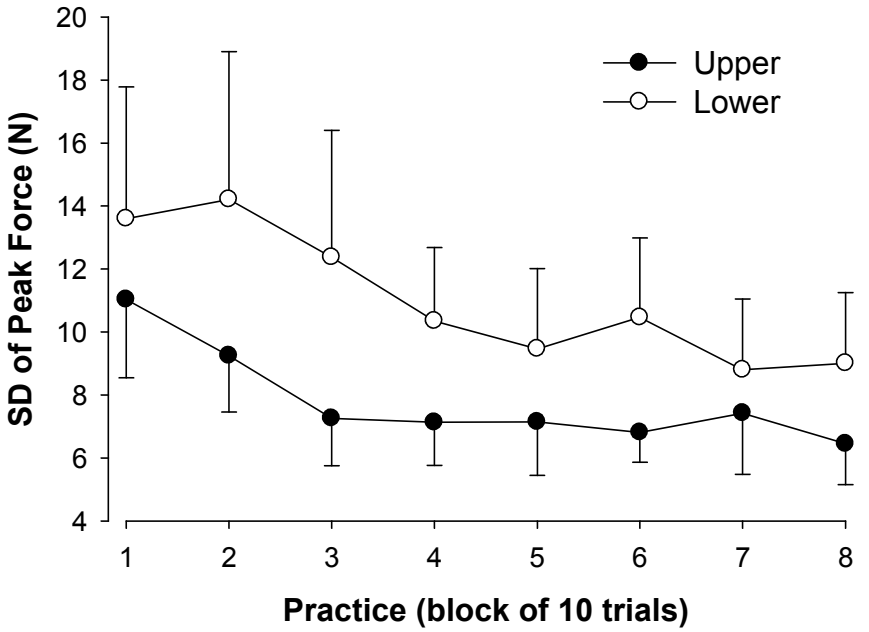

Error in Time to Peak Force (ms)
90
80
70
60
50
40
30
20
1
2
3
4
5
6
7
8
Practice (block of 10 trials)

Figure 6

A


20
18
16
14
12
10
8
6
4
SD of Peak Force (N)
Upper
Lower
1
2
3
4
5
6
7
8
Practice (block of 10 trials)

B

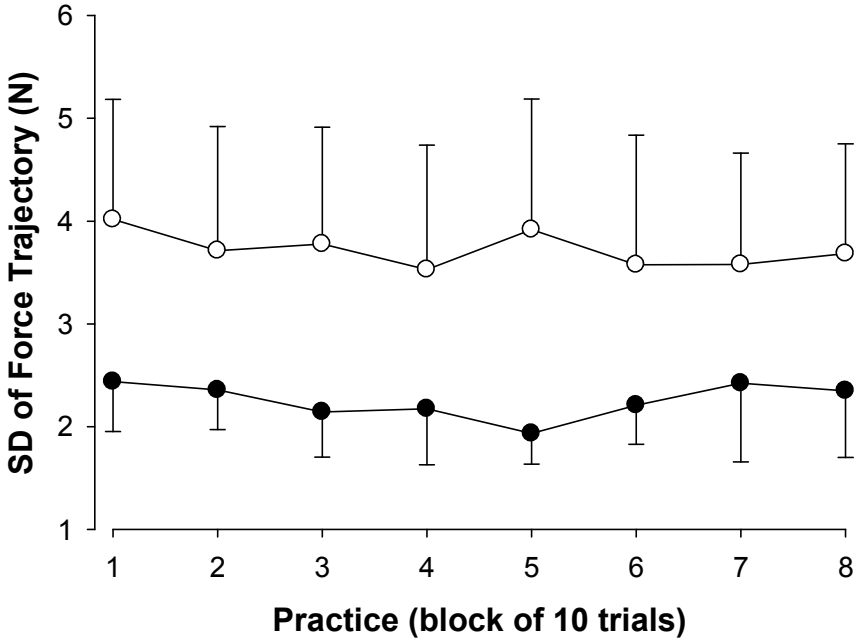
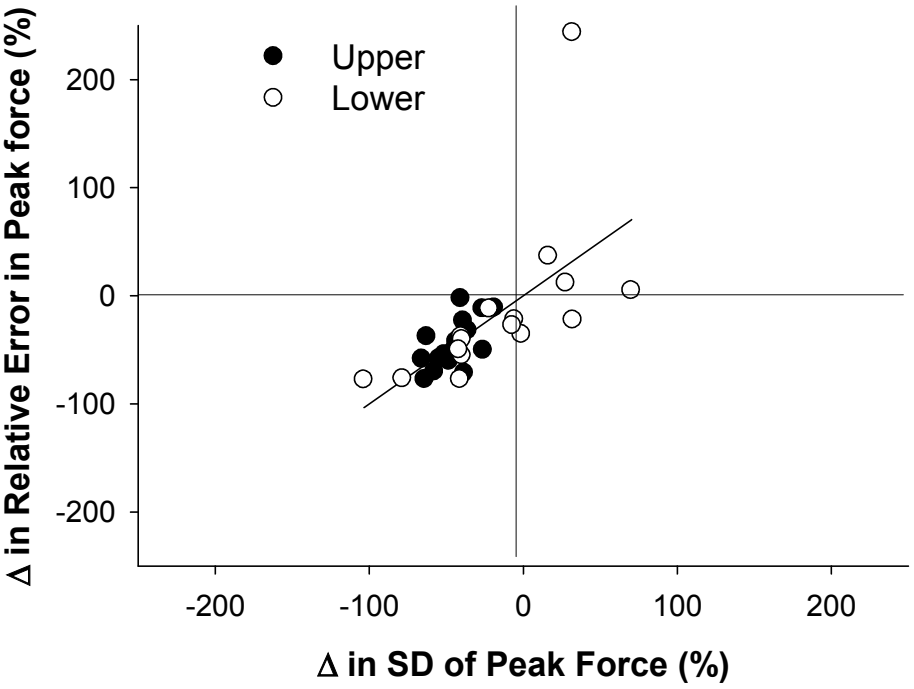

6
5
4
3
2
1
SD of Force Trajectory (N)
1
2
3
4
5
6
7
8
Practice (block of 10 trials)

Figure 7

A


Upper
Lower
200
100
0
-100
-200
-200
-100
0
100
200
Δ in Relative Error in Peak force (%)
Δ in SD of Peak Force (%)

B

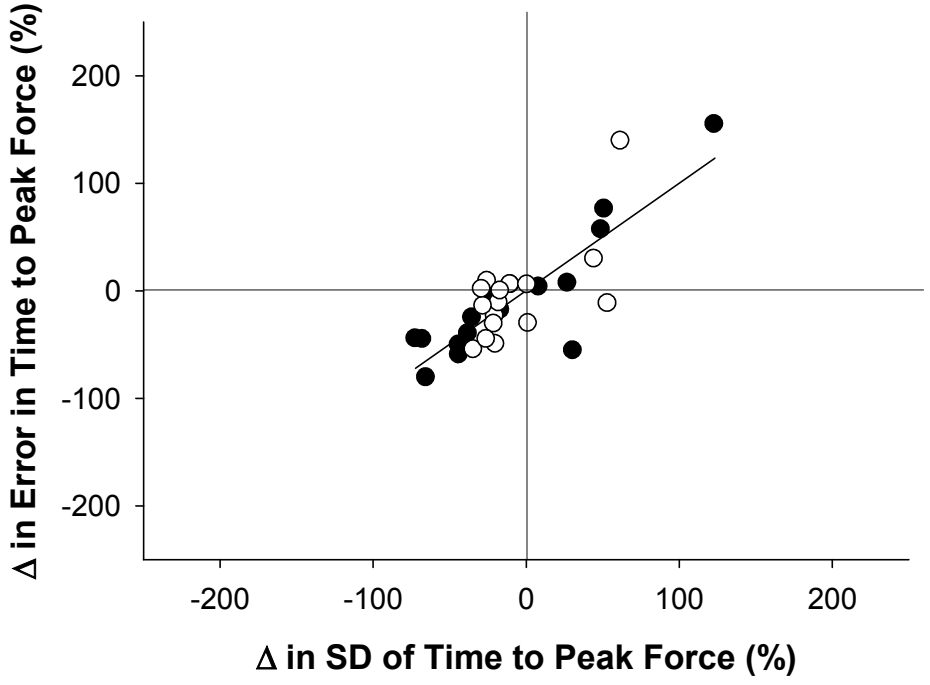
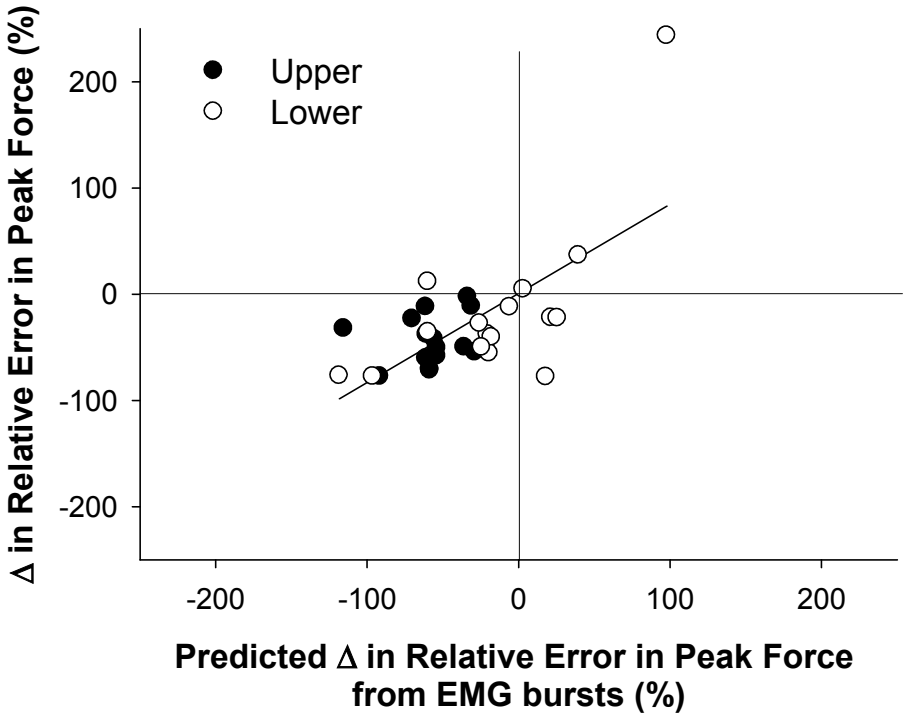

200
100
0
-100
-200
-200
-100
0
100
200
Δ in Error in Time to Peak Force (%)
Δ in SD of Time to Peak Force (%)

Figure 8

A


Upper
Lower
200
100
0
-100
-200
-200
-100
0
100
200
Δ in Relative Error in Peak Force (%)
Predicted Δ in Relative Error in Peak Force
from EMG bursts (%)

B

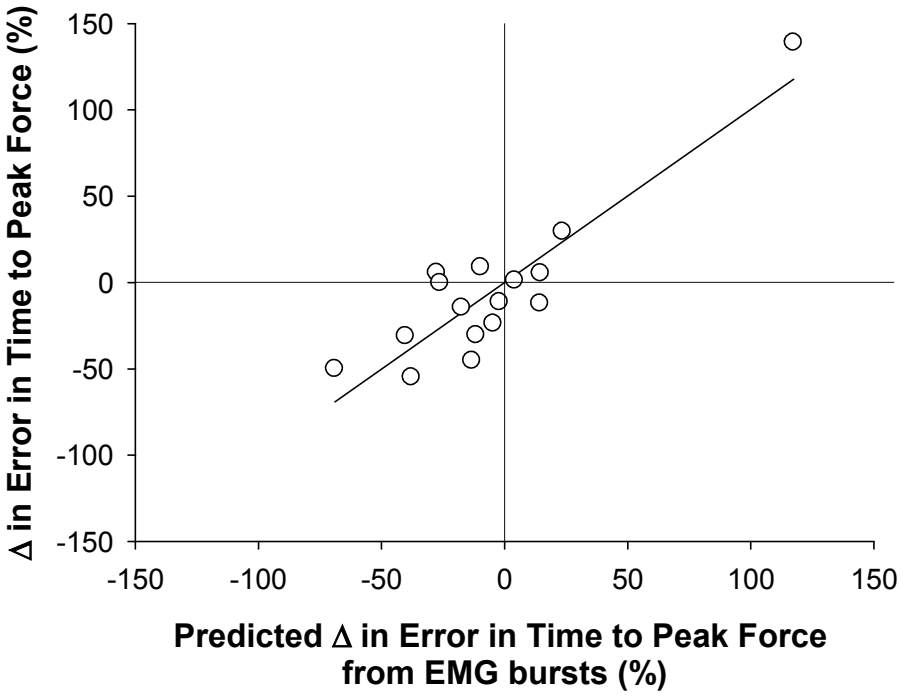

150
100
50
0
-50
-100
-150
-150
-100
-50
0
50
100
150
Δ in Error in Time to Peak Force (%)
Predicted Δ in Error in Time to Peak Force
from EMG bursts (%)

Figure 9

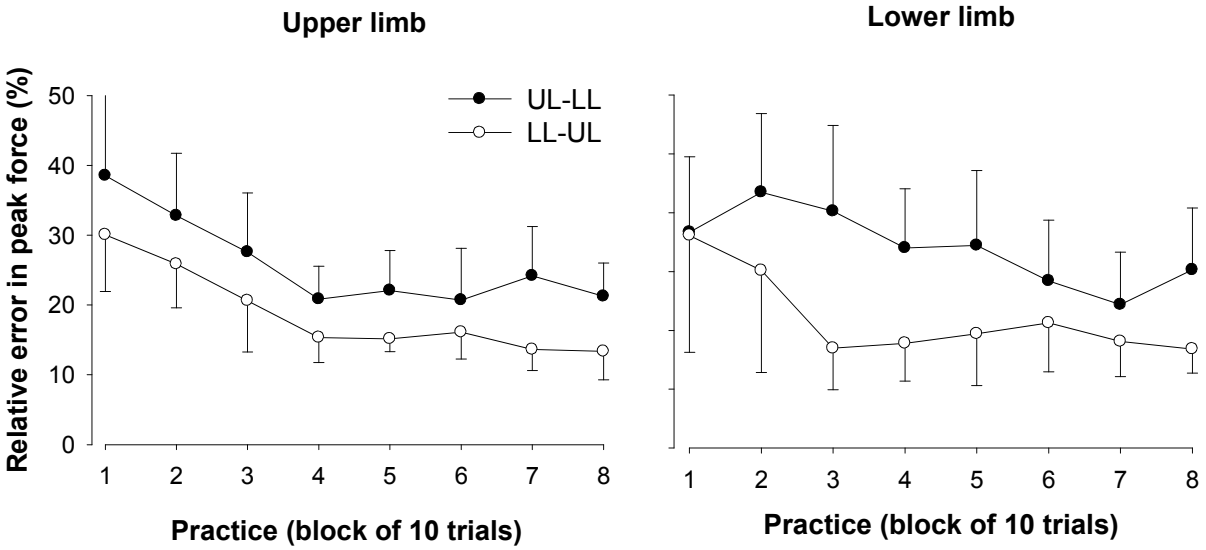

Upper limb
Lower limb
Relative error in peak force (%)
UL-LL
LL-UL
0
10
20
30
40
50
1
2
3
4
5
6
7
8
Practice (block of 10 trials)
Practice (block of 10 trials)

Figure 10

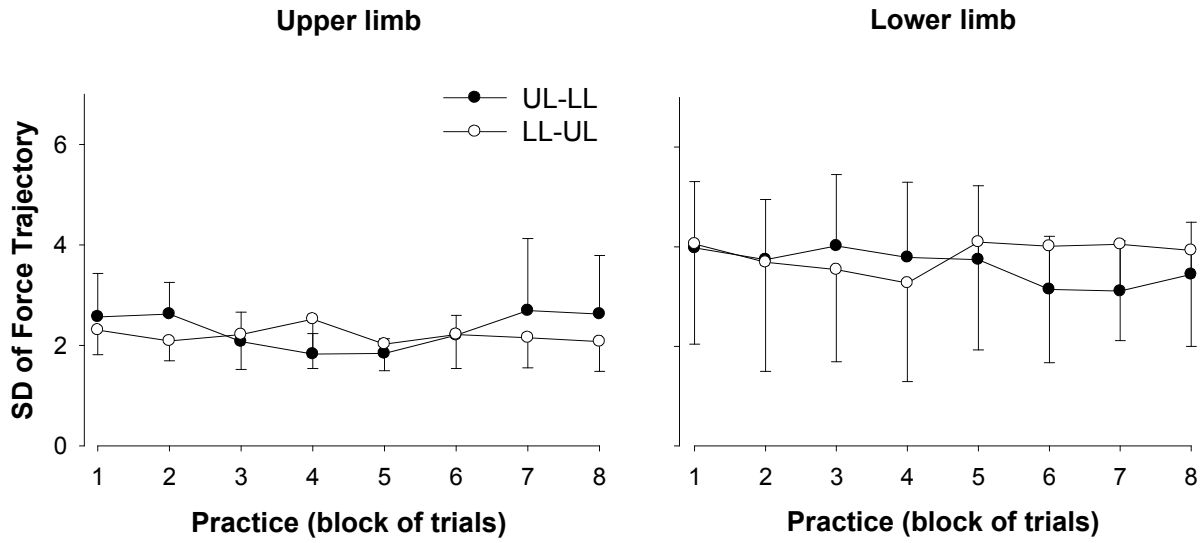

Upper limb
Lower limb
UL-LL
LL-UL
SD of Force Trajectory
0
2
4
6
1
2
3
4
5
6
7
8
Practice (block of trials)
Practice (block of trials)

Figure 11

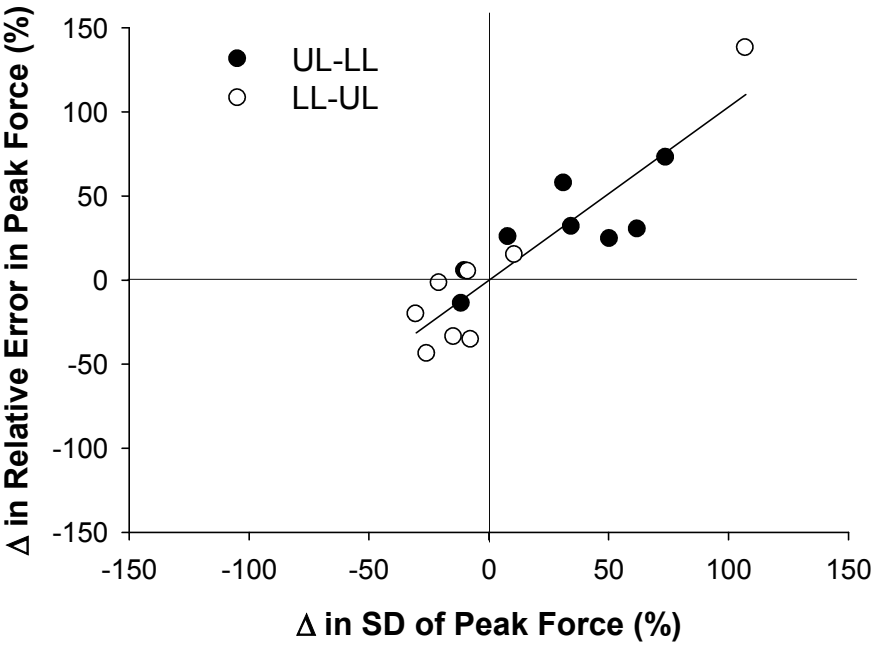
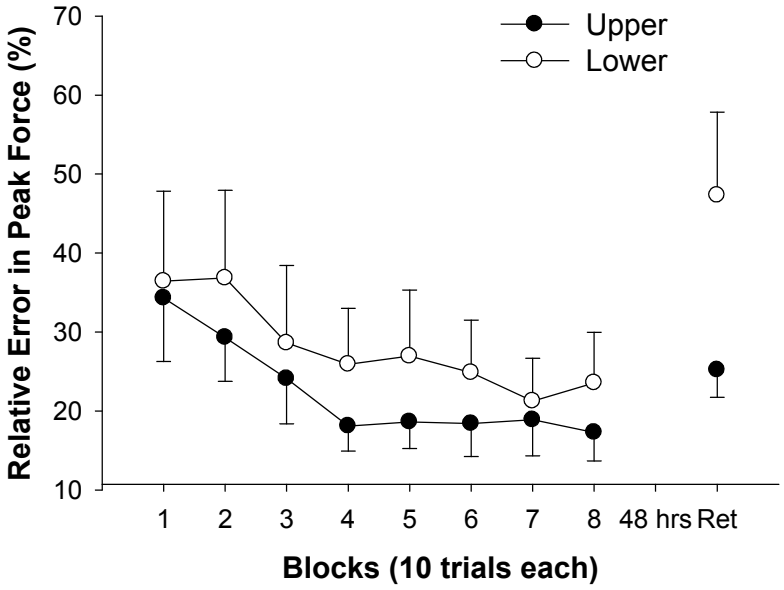

UL-LL
LL-UL
Δ in Relative Error in Peak Force (%)
Δ in SD of Peak Force (%)
150
100
50
0
-50
-100
-150
-150
-100
-50
0
50
100
150

Figure 12

A


Upper
Lower
Relative Error in Peak Force (%)
70
60
50
40
30
20
10
1
2
3
4
5
6
7
8
48 hrs
Ret
Blocks (10 trials each)

B

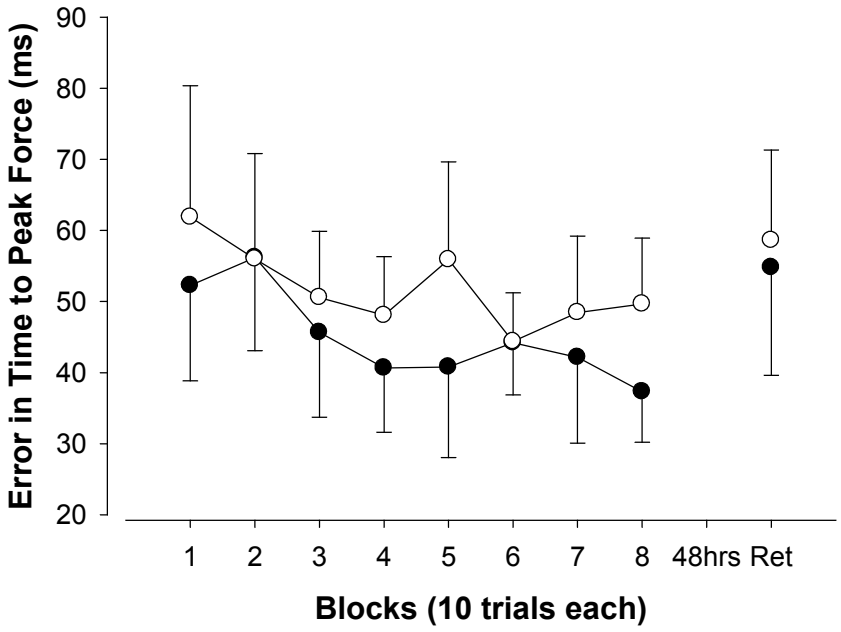
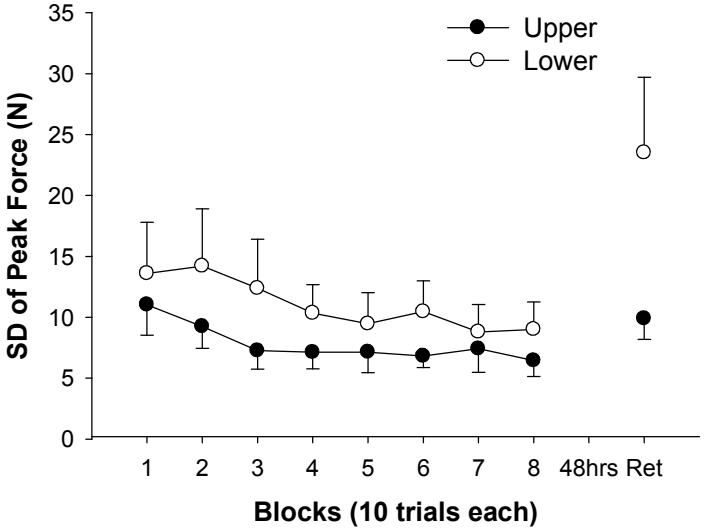
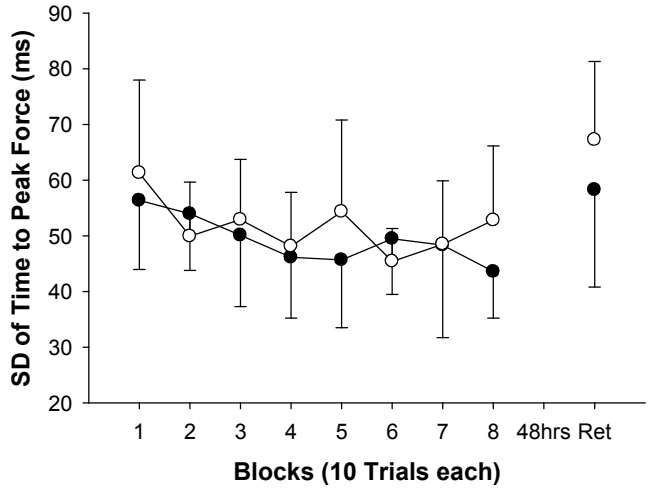

Error in Time to Peak Force (ms)
90
80
70
60
50
40
30
20
1
2
3
4
5
6
7
8
48hrs
Ret
Blocks (10 trials each)

Figure 13

A



B



C

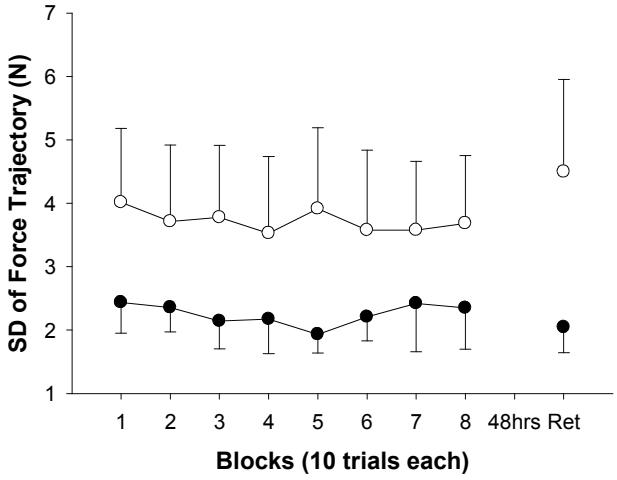
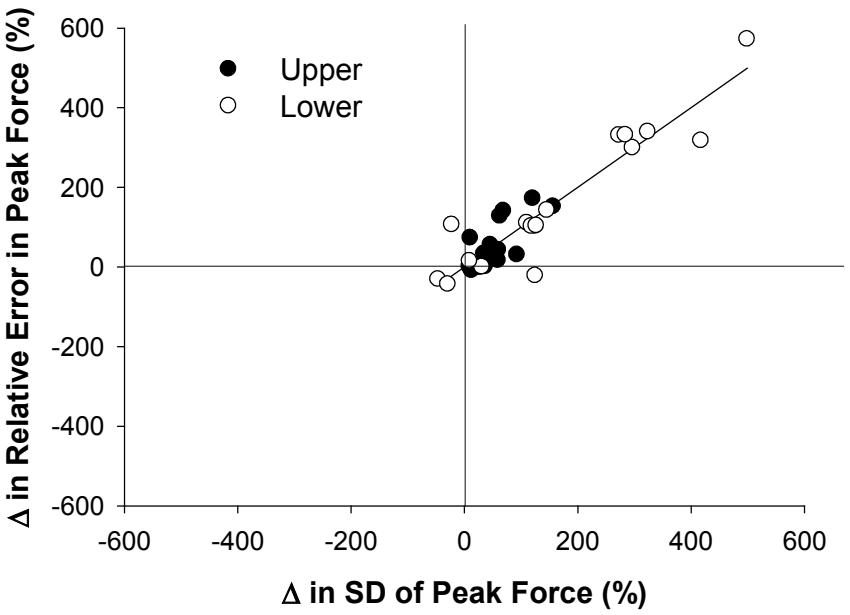


Figure 14

A


Upper
Lower
Δ in Relative Error in Peak Force (%)
Δ in SD of Peak Force (%)
600
400
200
0
-200
-400
-600
-600
-400
-200
0
200
400
600

B

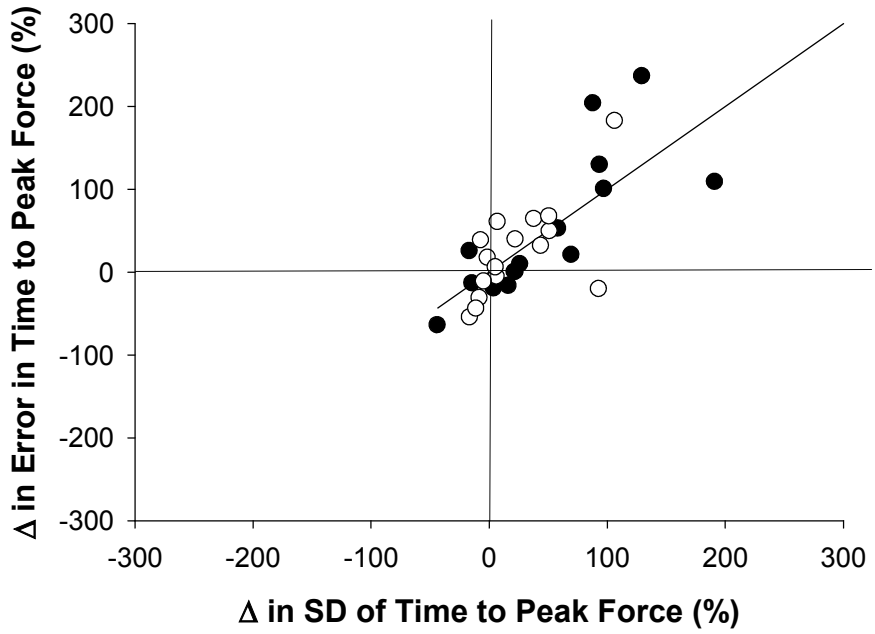
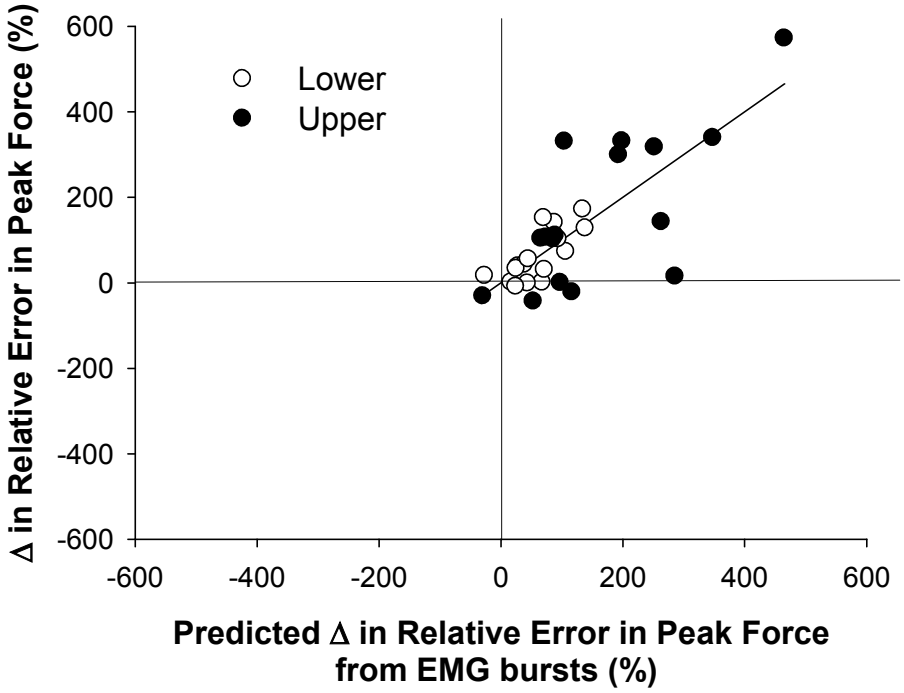
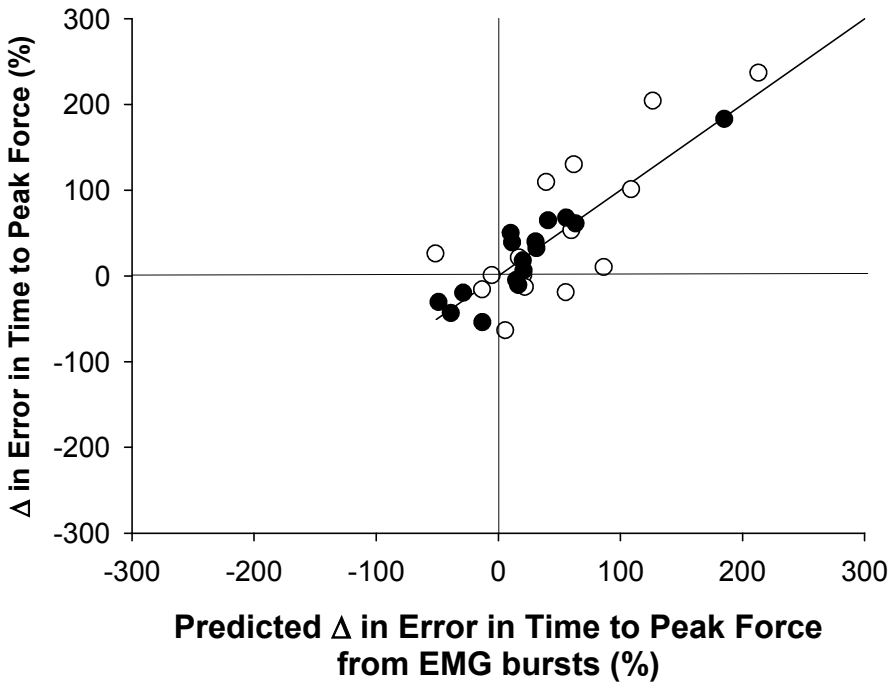

Δ in Error in Time to Peak Force (%)
Δ in SD of Time to Peak Force (%)
300
200
100
0
-100
-200
-300
-300
-200
-100
0
100
200
300

Figure 15

A


Lower
Upper
Δ in Relative Error in Peak Force (%)
600
400
200
0
-200
-400
-600
-600
-400
-200
0
200
400
600
Predicted Δ in Relative Error in Peak Force
from EMG bursts (%)

B


Δ in Error in Time to Peak Force (%)
300
200
100
0
-100
-200
-300
-300
-200
-100
0
100
200
300
Predicted Δ in Error in Time to Peak Force
from EMG bursts (%)

APPENDIX B

TABLES

Table 1. Pearson correlations between the change in end-point accuracy and the change in motor-output variability with practice in ipsilateral upper and lower limbs

Δ in Motor Output Variability	Upper Limb force endpoint error	Upper Limb time endpoint error	Lower limb force endpoint error	Lower limb time endpoint error
SD peak force	**0.615**	-0.035	**0.588**	**-0.488**
SD time to peak force	-0.106	**0.883**	-0.376	**0.685**
SD force trajectory	0.371	0.079	-0.214	10.107

Bold numbers indicate significant Pearson correlation ($P < 0.05$).

Table 2. Pearson correlations between the change in end-point accuracy and the change in motor-output variability with transfer of peak force accuracy across ipsilateral upper and lower limbs.

Δ in Motor Output Variability	Upper Limb force endpoint error
SD peak force	**0.901**
SD time to peak force	-0.260
SD force trajectory	0.386

Bold numbers indicate significant Pearson correlation ($P < 0.05$).

Table 3. Pearson correlations between the practice-to-retention change in end-point accuracy and the practice-to-retention change in motor-output variability with practice in ipsilateral upper and lower limbs

Δ in Motor Output Variability	Upper Limb force endpoint error	Upper Limb time endpoint error	Lower limb force endpoint error	Lower limb time endpoint error
SD peak force	**0.729**	0.182	**0.933**	-0.068
SD time to peak force	0.066	**0.864**	-0.141	**0.650**
SD force trajectory	0.135	0.247	**0.540**	-0.030

Bold numbers indicate significant Pearson correlation ($P < 0.05$).

APPENDIX C

LEGENDS FOR FIGURES

Figure 1. Experimental apparatus setup for the upper limb and the lower limb: subject was seated on the chair of an isokinetic dynamometer and affirmed that could see both the target and force-time trajectories. (A) For the upper limb contraction, the left shoulder and the left elbow were positioned at 90^{o} of flexion and the forearm was fully supinated. The upper limb goal-directed contraction primarily involved elbow flexion. (B) For the lower limb contraction, the left hip was positioned at 110^{o} of flexion with neutral rotation and the left knee was positioned at 100^{o} of flexion. The ankle joint was positioned so that the foot and the shank formed an angle of 90^{o}. The lower-limb goal-directed contraction primarily involved dorsiflexion.

Figure 2. Sequence of events for the testing sessions: Testing was conducted in two sessions separated by an interval of 48 hours. Each testing session started with a brief familiarization of the equipment and the task but no practice trials were given. During the first testing session, the following were performed: 1) Five maximal voluntary isometric contractions (MVC). 2) Eight blocks of 10 practice trials (block P1 to block P8) performed with force target at 25%MVC and time target at 200ms either with the upper limb or lower limb 4) Five MVCs as performed earlier. The same sequence of tasks was performed with the other limb after 20 minutes of rest. During the second testing session, the following were performed: 1) Five MVC trials. 2) Retention trials: One block of 10 trials performed at the same force and time target levels as the first session. 3) Random trials: Eight blocks of 12 trials performed at four different

force and time targets. (block R1 to block R8) 4) Five MVCs as performed earlier. The same sequence of movements was performed with the other limb after a break of 20 minutes.

Figure 3. Goal-directed end-point accuracy task: target was the center of a box displayed on a white background. The center of the target had both time (X-axis) and force (Y-axis) coordinates. Subjects were instructed to match the peak of the force-time trajectory exerted by the upper or lower limb to the target. Force and time end-point errors were quantified as the absolute error to the targeted force and time. Force trajectory variability was quantified as the SD of force in the detrended force trajectory (start of force to peak force). The trial-to-trial peak force variability for each block of trials was quantified as the SD of peak force and the coefficient of variation of peak force (CV; (SD / mean force) x 100); and the trial-to-trial time to peak force variability was quantified as the SD and CV of time to peak force.

Figure 4. Presentation of the target and the feedback to the subjects: subjects were instructed to perform the contraction when they saw the target box change color from red (A) to green (B). (A) The red color target lasted 1s and was used to prepare the subject for the upcoming contraction ("GET READY" phase). (B) the green target lasted 1s and was an indication to the subject they could initiate the contraction ("CONTRACT" phase) at any point of time as long as the green box continued to be displayed on the screen. (C) feedback of performance was provided to the subjects in the form of a force-time trajectory along with numerical error values for force and time on each trial.

Figure 5. Average peak force and time endpoint error for blocks of 10 trials across the 8 block practice protocol. (A) practice improved force endpoint error similarly in the upper and lower limb. Similarly, the lower limb exhibited greater force endpoint error as compared to the upper limb (B) practice improved time endpoint error similarly in the upper and lower limb. The rate of improvement with practice was similar for both upper and lower limbs.

Figure 6. Variability (SD) of peak force and variability (SD) of force trajectory for blocks of 10 trials across the 8 block protocol. (A) The rate of decline in variability of peak force with practice was similar for the upper and lower limb. The lower limb exhibited greater variability in peak force compared to the upper limb. (B) The lower limb exhibited greater variability in force trajectory as compared to the upper limb.

Figure 7. Prediction of the change in force and time endpoint error with practice from changes in motor output variability. (A) the decrease in force endpoint error with practice was predicted from a decrease in the peak force variability for both limbs. (B) the decrease in time endpoint error with practice was predicted from a decrease in time-to-peak force variability for both limbs.

Figure 8. Prediction of the change in force and time endpoint error with practice from changes in agonist-antagonist EMG. (A) The improvements in force endpoint accuracy with practice for the upper limb were predicted from a decrease in the agonist-antagonist EMG delay, decrease in the EMG amplitude of the agonist (Biceps short head) muscle, increase in the variability of agonist-antagonist EMG delay and increase in the variability of agonist-antagonist

EMG delay, whereas the improvements in force endpoint accuracy with practice for the lower limb were predicted from the increase in the EMG amplitude of the antagonist (Soleus) muscle and increase in the EMG duration of the antagonist (Gastrocnemius medial head) muscle. (B)The improvements in time endpoint accuracy with practice for the upper limb were not predicted from the changes in the agonist-antagonist EMG activity, whereas the improvements in time endpoint accuracy with practice for the lower limb were predicted from an increase in the variability of time to peak EMG of the antagonist (Soleus) muscle, decrease in the EMG amplitude of the Peroneus longus (agonist) muscle and increase in the variability of EMG duration of the agonist (Tibialis anterior) muscle.

Figure 9. Transfer of endpoint force error across upper (UL) and lower limb (LL) for blocks of 10 trials across the 8 block protocol. The upper limb contractions exhibited lower peak force endpoint error when they were preceded by lower limb contractions (LL-UL) compared with when they were practiced first (UL-LL). The lower limb contractions exhibited similar peak force endpoint error under both conditions (UL-LL and LL-UL). This indicated an asymmetric transfer of peak force accuracy from the lower limb to the upper limb and not from the upper limb to the lower limb.

Figure 10. Transfer of variability (SD) of force trajectory across upper (UL) and lower (LL) limb for blocks of 10 trials across the 8 block protocol. The upper limb contractions exhibited lower peak force endpoint error when they were preceded by lower limb contractions (LL-UL) compared with when they were practiced first (UL-LL). The lower limb contractions exhibited similar peak force endpoint error under both conditions (UL-LL and LL-UL). This

indicated an asymmetric transfer of force trajectory variability from the lower limb to the upper limb and not from the upper limb to the lower limb.

Figure 11. Prediction of the transfer of change in force endpoint error across limbs from changes in motor output variability. The transfer of endpoint force accuracy across ipsilateral upper (UL) and lower limbs (LL) was predicted ($R^2 = 0.812$) by changes in peak force variability across limbs.

Figure 12. Retention of average force and time endpoint error after 48 hours (48 hrs) of rest. (A) force endpoint error increased from the last practice block to the retention block (Ret) for both upper and lower limb. Lower limb exhibited a greater endpoint force error than the upper limb from the last practice block to the retention block (Ret). The rate of increase of force endpoint error was greater for the lower limb than the upper limb. (B) time endpoint error increased from the last practice block to the retention block (Ret) for both upper and lower limb. The rate of increase of time endpoint error from the last practice block to the retention block (Ret) was similar for the upper and lower limb.

Figure 13. Retention of variability (SD) in peak force, time-to-peak force and force trajectory. (A) peak force variability increased from the last practice block to the retention block (Ret) for both upper and lower limb. Lower limb exhibited greater peak force variability and a greater rate of increase in peak force variability than the upper limb from the last practice block to the retention block (Ret). (B) variability of time to peak force increased from the last practice block to the retention block (Ret) at a similar rate for both limbs. (C) lower limb exhibited

greater force trajectory variability than the upper limb from the last practice block to the retention block (Ret).

Figure 14. Prediction of retention of force and time endpoint accuracy from changes in motor output variability. (A) the decline in force endpoint accuracy from the last practice block to the retention block for both limbs was predicted by an increase in the variability of peak force. (B) the decline in time endpoint accuracy for both limbs was predicted by an increase in the variability of time-to-peak force.

Figure 15. Prediction of retention of force and time endpoint accuracy from changes in agonist-antagonist EMG. (A) The practice-to-retention change in force endpoint error for the upper limb was predicted from an increase in the variability of the EMG amplitude of an antagonist (Triceps brachii (long head)) muscle, decrease in the EMG duration of an antagonist (Triceps brachii (lateral head)) muscle and increase in the EMG amplitude of an agonist (Biceps brachii (long head)) muscle, whereas the practice-to-retention change in force endpoint accuracy for the lower limb was predicted from an increase in the time to peak EMG of an antagonist (Gastrocnemius medialis) muscle, decrease in the EMG duration of an agonist (Tibialis anterior) muscle and increase in the EMG amplitude of an antagonist (Gastrocnemius medialis) muscle. (B) The practice-to-retention change in time endpoint accuracy for the upper limb was predicted from an increase in the variability of an agonist (Brachioradialis) muscle, increase in the variability of time to peak EMG of an agonist (Biceps brachii (long head)) and increase in the time to peak EMG of an agonist muscle (Brachioradialis), whereas the practice-to-retention change in time endpoint accuracy for the lower limb was predicted from an increase in the

variability of time to peak EMG of an antagonist (Soleus) muscle, increase in the EMG amplitude of an agonist (Tibialis anterior) muscle, decrease in the EMG delay between agonist (Tibialis anterior) and antagonist (Soleus) muscles and decrease in the time to peak EMG of an antagonist (Soleus) muscle.

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