

MOTOR LEARNING AND ITS TRANSFER DURING BILATERAL ARM REACHING

A Thesis
Presented to
The Academic Faculty

by

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In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy in the
School of Applied Physiology

Georgia Institute of Technology
August 2011

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“I can do all things through Christ who gives me strength.”

Philippians 4:13

ACKNOWLEDGEMENTS

I give all of the glory to my Lord and Savior Jesus Christ, who in His grace and mercy has blessed me with the talent, intellect, and wisdom to pursue my dreams and has provided me with an amazing support system that has allowed me to accomplish the research and writing of this thesis.

I would like to especially thank my parents, Ron and June Harley, who taught me that working hard will get me far in life and that the rest is in the hands of the Lord Jesus Christ who listens to my heart and knows what I need before I even do. Without my parents' guidance, support and love I would not be here. I would also like to thank the rest of my family, those locally and abroad, for their encouragement and support.

I would like to thank my advisor, Dr. Boris Prilutsky, who has guided me through this process and took time to listen to my concerns and helped me at every turn of this journey, and my thesis committee, Dr. Andrew Butler, Dr. Richard Nichols, Dr. Teresa Snow and Dr. Steven Wolf, for their insightful comments, support and encouragement.

The motivation from my colleagues at the Georgia Tech Research Institute to *get 'er done* is gratefully acknowledged. I would especially like to thank Dr. Douglas Britton who has been instrumental in my career and supportive of my research pursuits.

I would like to thank, Ms. Rina Du Plooy, my high school music and piano teacher, who instilled in me many of the motor learning principals that have served as the motivational factor for me in pursuing this line of research, and to my fellow graduate students, Brad Farrel, Ricky Mehta, Gregory Phillips and Gary Schwaiger, for their

support and time in aiding me with this research.

Lastly, I would like to thank all of the individuals who volunteered for this study, with out whom I would not have been able to accomplish my research goals.

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SUMMARY

Have you ever attempted to rub your abdomen with one hand while tapping your head with the other? Separately these movements are easy to perform but doing them together (bilateral task) requires motor adaptation. Motor adaptation is the process through which the Central Nervous System improves upon performance. Transfer of learning is the process through which learning a motor task in one condition improves performance in another condition. The purpose of this study was to determine whether transfer of learning occurs during bilateral goal-directed reaching tasks. It was hypothesized that transfer of learning would occur from the non-dominant to the dominant arm during bilateral tasks and that position and load feedback from the arms would affect the rate of adaptation and transfer of learning. During the experiments, subjects reached with one or both their index finger(s) to eight targets while a velocity dependent force perturbation (force environment) was applied to the arm(s). Three groups of bilateral tasks were examined: (1) *unilateral reaching*, where one arm learned to reach in a force environment, while the other arm remained stationary and therefore did not provide movement related position or load feedback; (2) *bilateral reaching single load*, where both arms performed reaching movements but only one arm learned a force environment and therefore the other arm provided movement related position feedback but not load feedback; (3) *bilateral reaching two loads*, where both arms performed reaching movements and both learned a force environment, while providing movement related position and load feedback. The rate of adaptation of the force environment was quantified as the speed at which the perturbed index finger trajectory became straight over the course of repeated task performance. The rate of adaptation was significantly slower for the dominant

arm during the *unilateral reaching* tasks than during the *bilateral reaching single load* tasks ($p < 0.05$). This indicates that the movement related position feedback from the non-dominant arm improved significantly the motor adaptation of the dominant arm; therefore transfer of learning occurred from the non-dominant to the dominant arm. The rate of adaptation for the non-dominant arm did not differ significantly ($p > 0.05$) between the *unilateral reaching* and *bilateral reaching single load* tasks. Results also indicated that the rate of adaptation was significantly ($p < 0.05$) faster for both the non-dominant and the dominant arms during the *bilateral reaching two loads* tasks than during the *bilateral reaching single load* tasks. The latter results indicate that transfer of learning occurred in both directions - from the dominant to the non-dominant arm and from the non-dominant to the dominant arm - when position and load feedback was available from both arms, but only when the force environment acted in the same joint direction. This study demonstrated that transfer of learning does occur during bilateral reaching tasks and that the direction and degree of transfer of learning may be modulated by the position and load feedback that is available to the central nervous system. This information may be used by physical therapists in order to improve rehabilitation strategies for the upper extremity.

CHAPTER I

BACKGROUND AND SIGNIFICANCE

1.1 Introduction

A piece of music written for the piano, such as the *Sonata in C Major* by Wolfgang Amadeus Mozart [108] has an intricate part for each arm and may take an average pianist up to a year to master. While another piano piece such as *Twinkle Twinkle Little Star* [176] consists of a single melody for the right arm and may be mastered in a matter of minutes. The difference in the time to master each piece of music may be attributed to the complexity of moving two arms and ten digits simultaneously in perfect rhythm for the *Sonata in C Major*, versus moving one arm and five digits to play *Twinkle Twinkle Little Star*. By increasing the number of joints and therefore the degrees of freedom that must be controlled by the Central Nervous System (CNS) the complexity increases and therefore the time to learn the intricate movements also increase.

Have you ever attempted to rub your abdomen with one hand while tapping your head with the other? Separately these movements are easy to perform but their simultaneous executions require interlimb coordination that is learned over time. Motor adaptation is the process through which the CNS improves upon performance. Transfer of learning is the process through which learning a motor task in one condition improves performance in another condition. Studies on motor adaptation have predominantly focused on the movement of one arm (unilateral tasks) [38, 41, 48, 49, 155]. A few studies have considered what happens when both arms learn to move at the same time (bilateral tasks) [2, 36, 34, 55, 59, 64, 65, 81, 80, 188]. What remains unclear is how one arm may influence the motor adaptation of the other arm during

bilateral goal-directed reaching tasks. The **long term goal** of this research is to understand the mechanisms of bilateral motor control and motor adaptation and to investigate transfer of learning during bilateral tasks.

1.2 Motor adaptation and learning

Thorndike proposed the empirical law of effect which states that in order for learning to have occurred positive reinforcement is required [179]: rewarding a required response leads to a repetition of the response, while punishing incorrect responses leads to their elimination. The process of acquiring a correct motor behavior has been suggested to lead to the behavior becoming automatic, that is the contribution of conscious movement control becomes smaller [12]. Today the process of acquiring a novel motor behavior is attributed to neural plasticity in the Central Nervous System (CNS). Not only are humans able to acquire specific movements in novel conditions during motor adaptation, but this process of adapting to one condition can improve performance in another condition, which is called transfer of learning.

Richard Schmidt formally defined motor learning as “a set of processes associated with practice or experience leading to relatively permanent changes in the capability for responding” [148]. This is also referred to as skill acquisition, which is different from motor adaptation. During skill acquisition a movement may be learned that does not dissipate with time, such as riding a bicycle. In contrast, effects of motor adaptation do not last over time and may be dependent on the constraints that are placed on the motor task to be accomplished [156]. It is thought that during motor adaptation the CNS generates voluntary motor commands that activate targeted muscles thereby causing movement to occur. Sensory organs (e.g., Golgi tendon organs, muscle spindles, eyes, etc) detects movement and provides sensory feedback to the CNS regarding the actual movement. If the actual movement differs from the intended one, the CNS detects this movement error and changes the motor commands

in order to reduce the movement error. During this process of trial and error, the CNS chooses and retains the motor commands that are appropriate for the given motor task and environment, thereby forming the motor program. Over the years various models have been proposed to explain the process of motor adaptation.

1.2.1 Models of motor adaptation and learning

In 1917, Lashley demonstrated that rats were able to execute a learned maze navigation behavior after sensory feedback had been removed. This led to the formulation of the *open-loop system hypothesis* of learned motor behavior [90]. Lashley theorized that the CNS does not rely on sensory feedback to execute a learned task. This led to a theory of the *feedforward model*, which states that the motor program is defined prior to the onset of the movement, with sensory feedback only coming into play at the termination of movement [79].

In 1971, Adams proposed the *closed-loop model* of motor control, which stated that the CNS does rely on sensory feedback during the execution of skilled tasks [1]. Adams incorporated the detection of movement error and correction of motor behavior into the motor control model. This line of research led to the development of the *feedback model*, which is conceptually the opposite of the *feedforward model*. The *feedback model* states, that the motor program is not defined prior to the movement, but rather evolves during the movement. The motor commands are generated during movement by comparing the current location of the arm against the target location, through the movement error [69].

The *hybrid model* incorporates the *feedforward* and *feedback models*, in that a motor program may be defined prior to the onset of movement, however it may be constantly updated through sensory feedback [32]. This *hybrid model* has been shown to be consistent with experimental evidence obtained for upper extremity reaching tasks [72, 140]. Further developments of the *hybrid model* have led to the current

generally accepted understanding of the processes underlying motor control during upper extremity goal-directed reaching.

The CNS is intimately involved in motor adaptation (Fig. 1, page 5). The intention to generate a movement starts in the motor association areas of the supplementary motor cortex and premotor cortex where the motor program (controller, Fig. 1, page 5) is formed [143]. The motor association areas use information from the somato-sensory areas and posterior parietal cortex to update the motor program [56, 86, 143, 185]. The neural signals forming the motor program are transmitted to the primary motor area [143]. From there motor commands descend via the corticospinal tract to spinal interneurons and motor neurons and activate the contralateral muscles [21]. It is commonly believed that the motor commands are formed in the contralateral hemisphere to the arm that is being controlled. Only less than 15% of the fibers in the corticospinal tract do not cross over to the contralateral side at the pyramidal decussation [15, 16, 17]. Movement is thought to be constantly monitored by body sensors (e.g. eyes, muscle spindles, golgi tendon organs, etc) which transduce sensory information back to the CNS. The CNS compares this sensory feedback against the predicted feedback and evaluates the movement (movement evaluation, Fig. 1, page 5) [135]. Many researchers believe that the cerebellum may receive an efference copy of the motor commands from the primary motor cortex via the superior colliculus-cerebellar-brainstem pathway loop [121, 120, 154]. Studies have shown that the cerebellum plays a role in generating the predicted feedback, based on a history of motor commands that form an internal model [112, 159, 171, 193]. Due to noise that may be present in the system and external environment (produced by perturbations), there are often differences between the predicted and actual sensory feedback. The parietal cortex is thought to compare the predictive feedback against the proprioceptive and visual sensory feedback in order to update the estimated state of the system (i.e., arm location in space) and sends this information to the primary motor cortex

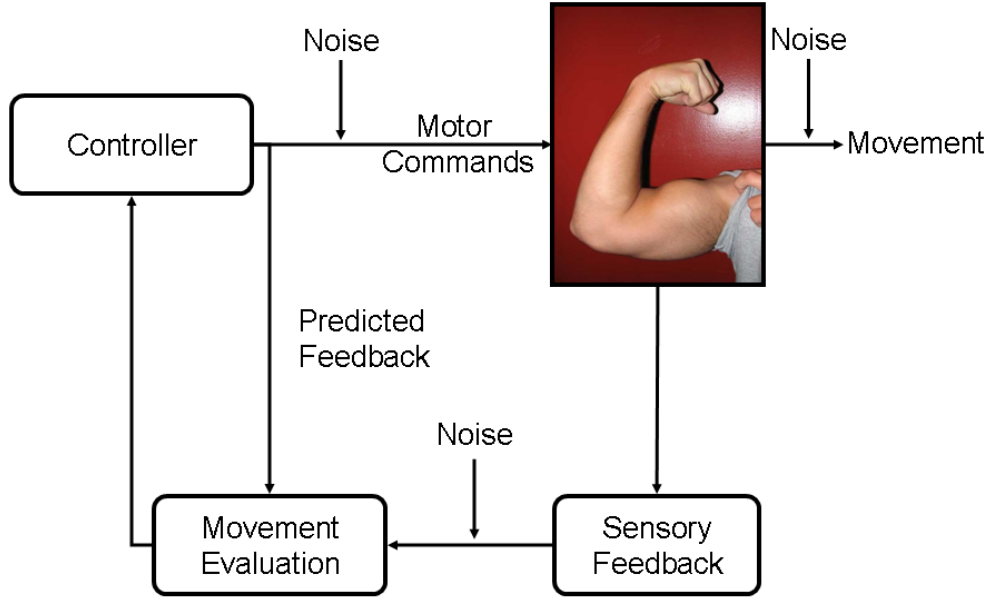


Figure 1: General motor control and motor learning model.

via supplementary motor areas to generate new motor commands [33, 60, 156, 193]. It has been shown that if the parietal cortex is injured or stimulated via transcranial magnetic stimulation in humans, the individuals are not able to update the direction of their movement if the target location changes during goal-directed reaching [33, 60]. Therefore, it is believed that the parietal cortex is responsible for comparing the predicted feedback and sensory feedback. This model accounts for motor adaptation, in that through movement evaluation the movement error is reduced over time.

To illustrate how motor adaptation may occur in a unilateral reaching task, the following example is presented (Fig. 2, page 7). Subjects sat in a Kinarm robot and performed reaches with their unilateral right dominant arm towards eight targets (Fig. 2.a). Initially subjects performed target reaching with a straight line index finger tip trajectory in the neutral environment (Fig. 2.b). If the Kinarm robot generates an index finger tip velocity dependent force \mathbf{F} applied to the arm, the index finger tip

trajectory becomes curved (Fig. 2.d). The force vector \mathbf{F} is a function of the index finger velocity vector \mathbf{V} ,

$$\mathbf{F} = \mathbf{B} * \mathbf{V} \quad (1)$$

where, \mathbf{F} is the force vector $\mathbf{F} = [Fx, Fy]$ applied to the index finger tip (in Newton), \mathbf{V} is the finger tip velocity vector $\mathbf{V} = [Vx, Vy]$ (in meter/second), and \mathbf{B} is the viscosity matrix (in Newton*seconds/meter):

$$\mathbf{B} = \begin{bmatrix} 0 & 10 \\ -10 & 0 \end{bmatrix} \quad (2)$$

As a result, the force environment \mathbf{F} is directed clockwise and perpendicular to the index finger tip trajectory (Fig. 2.c). Upon initial exposure to the force environment, the finger tip trajectories have large deviations from the straight line (perpendicular displacements) therefore large movement errors are observed (Fig. 2.d). Perpendicular displacement is defined as the maximum perpendicular distance of the finger tip trajectory from a straight line connecting two targets. After training, the finger tip trajectories straighten out and the movement errors become smaller (Fig. 2.e). The speed at which this transition from large to small perpendicular displacements occur is termed the rate of adaptation. Then during a catch trial, when the force environment is unexpectedly turned off, there are large movement errors once more which are in the opposite direction compared to the case when the arm was initially exposed to the force environment (Fig. 2.f). The difference in the movement error between the catch trial conditions (Fig. 2.f) and the learned environment (Fig. 2.e) is often referred to as the aftereffect and has been shown to be a measure of how well the subject has learned the force environment in unilateral reaching studies [155]. The process of adaptation to the force environment is likely to take place in accordance with the mechanisms described above in this section. The sensory feedback signals

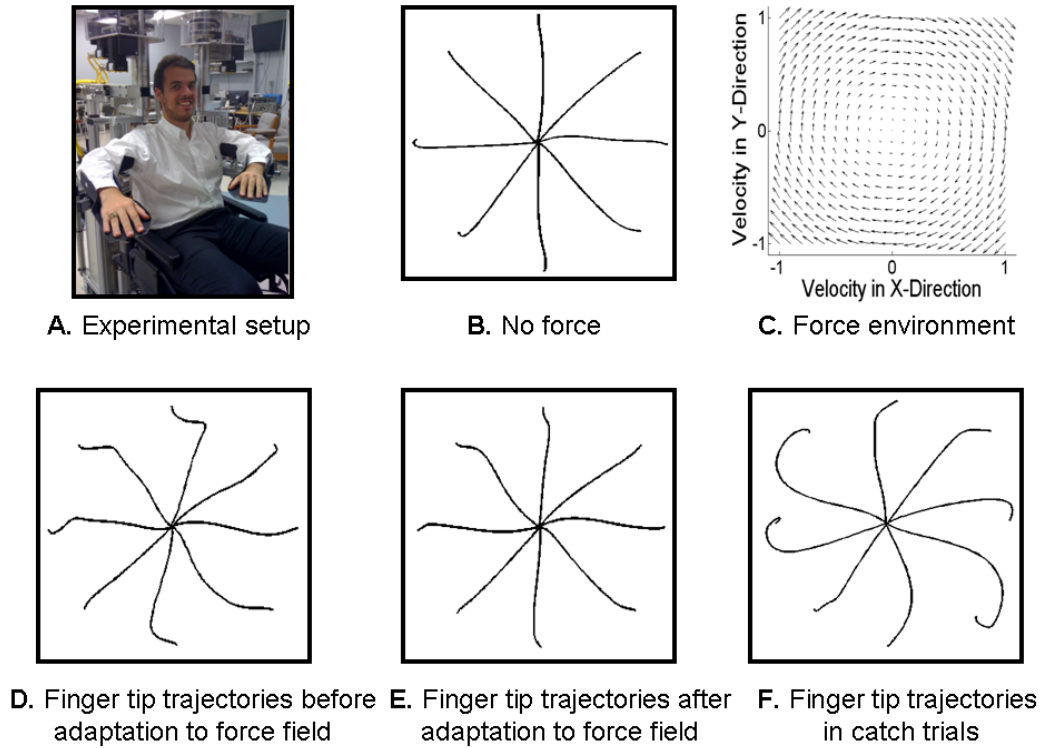


Figure 2: An example of motor adaptation of the unilateral right dominant arm. (a) Subject sits in the Kinarm. (b) Averaged finger tip trajectories of the right dominant arm in the neutral environment. (c) Depiction of the clockwise force environment applied during the unilateral right dominant arm reaching. (d) Initial finger tip trajectories when the force environment is first turned on. (e) Finger tip trajectories after adaptation to the force environment. (f) Finger tip trajectories during the catch trials when the force environment is randomly removed.

from the moving arm are the essential part of these mechanisms.

1.2.2 Sensory feedback during goal-directed arm reaching

Muscle, joint and skin receptors provide proprioceptive feedback to the CNS. Such muscle receptors as Golgi tendon organs and muscle spindles are sensitive to muscle force and muscle length, respectively. The Golgi tendon organs are located at the muscle-tendon junctions and innervated by group Ib afferents. The Ib afferents are activated when the muscle is producing force, thus encoding the muscle force output. The group Ib fibers synapse onto interneurons in the spinal cord that relay information

to motoneurone of synergists and antagonists at the spinal cord and also projects to the cortical regions. The primary and secondary muscle spindle afferents innervate the intrafusal muscle fibers in the spindles, muscle length sensors. The muscle spindles lie in parallel to the extrafusal muscle fibers, and therefore are able to detect the changes in the length of the muscle when it is stretched. The primary muscle spindle afferents are able to detect the velocity at which the muscle fibers are stretched. The primary muscle spindle afferents synapse directly onto α -motor neurons of the muscle and its synergists; they also project to motor neurons of the antagonists via Ia-interneurons. The secondary muscle spindle afferents tend to detect the actual changes in muscle fiber length and synapse onto interneurons that transmit length related information further to α -motor neurons and the cortical areas. The skin also contains sensors: (1) Merkel discs are able to detect light touch and texture, (2) Pacinian corpuscles sense deep pressure, stretch, and vibration, and (3) Ruffini corpuscles sense heavy touch, pressure and stretching of the skin and are also located in the joints and therefore can sense joint movements [143]. Goal-directed arm movements tend to be long enough in duration to allow for proprioceptive sensory feedback to play a key role in updating any movement errors that may occur. It is thought that reflex pathways allow for fast and immediate updates of the neural commands during a single reach [180]. These command corrections are mediated by the neural pathways from muscle afferents [156]. During fast reaching tasks, updating motor commands during the reach may take longer than task requirements allow due to a feedback delay. However, it has been suggested that in this case the system may rely on a *feedforward model* of control [6, 52, 101] which allows the CNS to predict what the sensory feedback would be, based on a history of motor commands that form the internal model of the musculoskeletal system and the external environment.

In the current study the sensory feedback produced by the muscles are manipulated in order to elicit different responses from the arm(s) during bilateral tasks.

When the arm is stationary it produces presumably constant force and length feedback. When the arm(s) move but a force environment is not applied, the arm(s) muscle afferents produce changes in muscle force and length feedback. These changes are related to changes of the arm position due to movement and therefore for the purpose of this study are termed *movement related position feedback*. When the arm(s) move in a force environment, there is presumably larger changes in the muscle forces and thus activity of group Ib afferents. These changes directly relate to the force environment and therefore are termed *external load feedback*. By altering movement related position feedback and external load feedback from the two arms it may be possible to determine how sensory information affects motor adaptation.

A typical way in which motor adaptation has been studied is by applying perturbations (such as visual rotations of the observed arm or changing the force environment) and observing the changes in the performance. Studies have demonstrated that individuals are able to adapt to visual perturbations [84, 86, 97, 98, 104]. Other studies have used applications of novel force environments [155] or force pulses [49] as perturbations to the moving arm in order to quantify the rate of adaptation and understand the motor behavior of the arm. When considering bilateral tasks, there are multiple combinations of how the force environment may be applied to the arms. One question is, does motor adaptation depend on whether one or both arms experience the force environment? This question will be addressed in Chapter 4, page 63.

It is difficult to make general conclusions about motor adaptation because experimental findings are often dependent on the nature of the task [95, 94, 31, 170]. Unilateral studies of motor adaptation and learning have considered, wrist movement [4, 41], elbow flexion [51, 111, 145], thumb and finger pinching [58], key pressing [59], finger tapping [178], drawing [27, 83, 140, 139, 183], and reaching [10, 26, 30, 32, 38, 49, 56, 57, 68, 76, 84, 86, 99, 105, 129, 137, 155]. Studies on bilateral tasks have considered, finger tapping [77, 85, 88], cyclical movement [41, 53, 66, 70], pinching index

finger to thumb [13], flexing of index finger [14] and reaching [34, 35]. Most of these bilateral task studies looked at rhythmic movements, the role of sensory feedback and the coordination between the limbs. Bilateral goal-directed reaching is interesting, because the movements are discrete, and yet may require a high degree of coordination especially if the movements are out-of-phase. There are several possible models to describe bilateral motor control which will be explored next.

1.3 Bilateral motor control

Bernstein has been credited with introducing the concept of coordination between the limbs and asking the question of how the motor system is able to control so many degrees of freedom at once [12]. This question has been the pursuit of many studies that have led to the formulation of several possible models that may predict bilateral motor behavior. Four of these models will be discussed next: (1) The Generalized Motor Program (GMP), (2) Intermanual Crosstalk, (3) Hierarchical Model and (4) The Optimal Feedback Control (OFC) model.

1.3.1 Generalized Motor Program

The *Generalized Motor Program* incorporates the notion that there is a single motor program that controls both arms during bilateral tasks [59, 188]. This motor program specifies all of the movement parameters (velocity, direction, threshold, gain, etc) necessary to complete the task prior to the initiation of movement, similar to the *feedforward model*. Studies have shown that typically the temporal aspects (speed, time, etc) are common parameters that may be specified by the motor program, while force is thought to be coded differently for each arm [149]. When the *Generalized Motor Program* refers to a single motor program, this does not mean that there is a single region in the brain where the motor program is formed. Instead it is suggested that all of the brain regions play an intricate role that work together to produce a single motor program that controls the motor behavior of each arm during bilateral

tasks [31]. Studies have shown that there are several regions in both hemispheres that are active during bilateral movements. These include the primary motor cortex, somatosensory areas [39], supplementary motor areas [136, 166], basal ganglia [132] and the cerebellum [103].

1.3.2 Crosstalk between arm controllers (Intermanual Crosstalk)

The concept of *Intermanual Crosstalk* incorporates the notion that there are two motor controllers generating motor commands, one for each arm [7, 96, 31]. Interference and transfer of learning between the arms are thought to occur because of an interaction of the motor commands and/or feedback signals between the arms (crosstalk), and may be important during motor adaptation of bilateral tasks [55]. Potential neural pathways that may mediate crosstalk between the limbs' control systems include (1) ipsilateral pathways, (2) bilateral corticomotoneuronal projections in the spinal cord, as well as (3) the corpus callosum (carsoon2005).

- Ipsilateral pathways: Less than 15% of the neurons that originate in the primary motor cortex do not cross the midline at the pyramidal decussation but project onto ipsilateral spinal interneurons and motoneurons [128]. These uncrossed fibers may be responsible for activity in the ipsilateral homologous muscles when only the contralateral limb is intended to move [21].
- Spinal cord: Branched corticospinal projections may occur at the spinal cord level and may be an alternative pathway for mediation of bilateral mirror movements [21, 102].
- Corpus callosum: The corpus callosum may be the primary structure responsible for the cross-talk between the hemispheres. Studies have indicated that the corpus callosum plays a vital role in coordination [9, 43, 54, 110] and synchronicity [44, 153] between the arms during bilateral tasks. Specifically, it has

been reported that the anterior corpus callosum influenced the difference in reaction time and movement time between the arms during bilateral movements [130], and the posterior corpus callosum affected differences in coordination [43] and synchronicity [44, 153] between the arms. Other studies have demonstrated the importance of the corpus callosum for accomplishing coordinated bilateral tasks [9, 54, 110].

If this model is used it is predicted that during bilateral tasks, information is transferred from one hemisphere to the other. However, it does not specify what type of information is being transferred or the direction of information transfer between the hemispheres. One assumption that is made of the *Intermanual Crosstalk* model is that each arm has its own motor controller generating a motor program, and that information is transferred between the two motor controllers via the neural pathways indicated above [21, 96, 31].

1.3.3 Hierarchical Model

There is a possibility that the *Generalized Motor Program* and the *Intermanual Crosstalk models* may be combined to form the *Hierarchical Model*. In accordance with the *Hierarchical Model* a motor command is generated with common movement parameters for both arms (*Generalized Motor Program*), whereas some arm specific aspects of the motor commands and/or feedback signals from the arms interact with the opposite motor controller (*crosstalk*).

1.3.4 Optimal Feedback Control

Thorndike proposed the empirical law of effect which states that in order for adaptation to occur, positive reinforcement is required [179]. One expects to receive a reward at the end of the movement while paying a cost. This reward versus cost may affect how quickly and accurately one adapts to a new motor task, and how one responds to the sensory feedback [154]. The *Optical Feedback Control* (OFC) theory

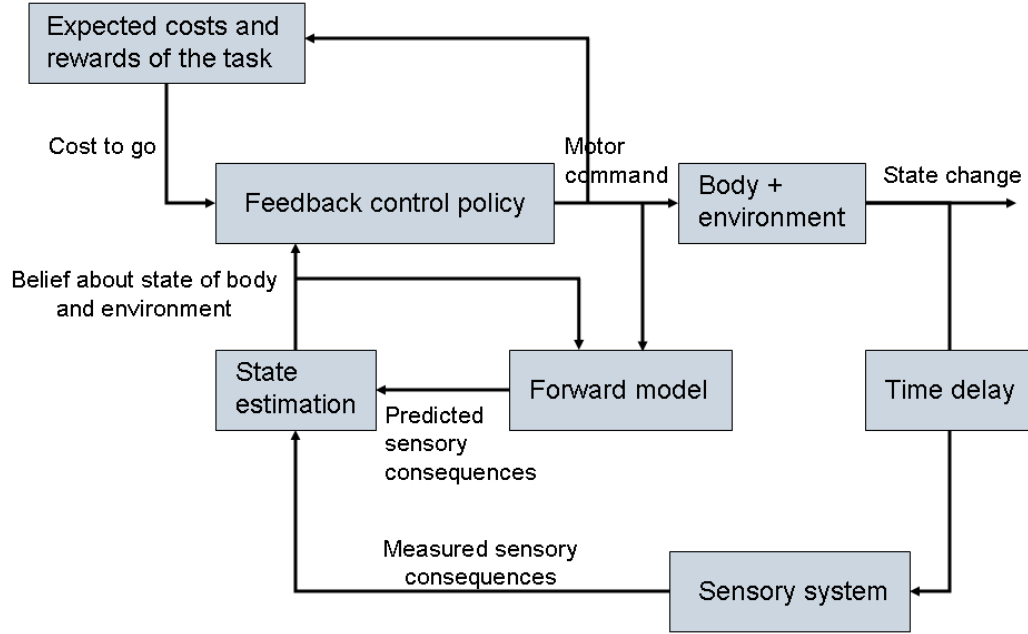


Figure 3: A schematic for goal directed movements as suggested by the *Optimal Feedback Control* theory. Adopted from [154].

has been suggested to explain how movement evaluation, i.e. comparing between the predicted and actual sensory feedback, takes place (Fig. 3, page 13) [181, 154].

The OFC theory incorporates the notion that in order for movement to occur three problems need to be solved: (1) system identification: the CNS needs to predict what the sensory consequences will be when the planned movement is executed, (2) state estimation: the CNS needs to compare the predicted feedback against the actual sensory feedback in order to update the current system state estimation (arms mechanical state in the world) and (3) optimal change of motor command: the CNS needs to use this updated state of the arms to modify the motor program, based on the expected costs and rewards for the task, in order to improve movement outcome. Neurophysiological studies have identified anatomical structures in the cortical areas that may mediate system identification, state estimation and optimal control. Studies

have suggested that the cerebellum is involved with system identification, the parietal cortex allows for state estimation, while the basal ganglia is involved with the optimal change of motor command [154, 181].

The cerebellum receives input from the primary motor cortex (M1), which is thought to be an efference copy of the motor command, i.e., the descending input via the corticospinal tract to the interneurons and motoneurons activating muscles. The cerebellum uses the efference copy to build an internal model that predicts the sensory feedback of the intended movement. Nowak et al. [112] conducted an experiment where a ball was dropped into a basket that subjects held. The performance variable that was considered was the time it took between the start of ball movement and the onset of tightening subject's grip on the basket. In healthy subjects it was found that the response time was much faster when the subject dropped the ball in the basket than when the experimenter dropped it. When the subject dropped the ball, he/she was able to predict in advance what the sensory feedback should be, and thus would tighten their grip sooner. Nowak et al. compared the results of the healthy subjects, against a patient that had no cerebellum due to a rare developmental condition; however sensory feedback of the patient appeared to be intact. There was no difference in response time between the conditions of dropping the ball by experimenter or the patient. Therefore, it has been suggested that the cerebellum is involved with predicting the sensory consequences of motor commands [112, 154, 193].

There have been several studies on the posterior parietal cortex that demonstrated that this cortical area is involved with state estimation. A lesion study on monkeys reaching with their arms while the lights were turned on and off, demonstrated that the inferior parietal lobe interprets visual feedback while the superior parietal lobe interprets proprioceptive feedback [135]. Other studies have supported the notion that the posterior parietal cortex evaluates visual and proprioceptive sensory feedback against the predicted feedback in order to update the current state estimation of the

arm in the world [33, 60]. The posterior parietal cortex receives the sensory and predicted feedback via the thalamus which acts as a relay between the primary motor cortex (M1), cerebellum, basal ganglia and other cortical regions.

According to the *OFC* theory, the basal ganglia is thought to be involved with optimal change or selection of motor commands, by weighing the cost versus reward for a specific movement. The basal ganglia receives inputs from nearly all the cortical regions, including a branching of the corticostriatal neurons which is thought to contain another efference copy of the descending motor command. The basal ganglia has two outputs, first is the direct pathway which disinhibits neurons in the thalamus, superior colliculus and the brainstem. The other indirect pathway inhibits these regions. Packard and McGuagh [122] conducted a study where rats were placed in a pool of water and had to swim to a platform in order to get out of the water. Two platforms were placed in the water, a large platform was marked with a red flag and a small platform was marked with a green flag. Healthy rats gradually learned to swim to the red flag, while rats with a lesion to their basal ganglia took longer to learn this. These rats were probably not able to associate the reward stimuli of standing on the large platform with the red flag. Other studies on Parkinson’s disease patients have also come to the conclusion that the basal ganglia is possibly involved with comparing the cost versus the reward of performing movements [100].

1.4 Transfer of learning

Transfer of learning has been defined as the process through which learning a motor task in one condition improves performance in another condition. Transfer of learning has been shown to occur between arms when one arm has undergone motor adaptation and the opposite non-trained arm was tested and demonstrated signs of adaptation [11, 38, 76, 99]. Transfer of learning has also been demonstrated to occur when a unilateral motor task was trained, but a bilateral task was tested [113, 114]. The

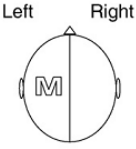
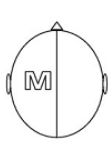
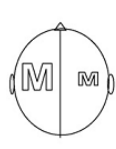

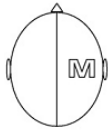
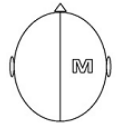
	Callosal	Proficiency	Cross-Activation
Training with Right Dominant Arm			
Testing with Left Non-dominant Arm			
Unilateral Studies	NDom \rightarrow Dom	NDom = Dom	Dom \rightarrow NDom
Bilateral Prediction	NDom influences Dom	No difference between arms	Dom influence NDom
References	Taylor and Heilman 1980	Laszlo 1970	Parlowe and Kinsbourne 1989

Figure 4: Overview of the three transfer of learning models: (1) Callosal Model, (2) Proficiency Model and (3) Cross-Activation Model. These models predict the direction in which transfer of learning may occur during a bilateral task between the dominant (Dom) and the non-dominant (NDom) arms. (Images taken from [5]).

opposite has also been shown to occur where subjects trained a bilateral motor task but was tested on a unilateral task [71, 158]. One key question that has not yet been addressed in the literature is: Does transfer of learning occur during bilateral tasks? This question will be addressed in Chapter 3, page 42.

This section will review: (1) Three current models (*callosal*, *proficiency* and *cross-activation*) that have been proposed to explain how transfer of learning may occur (Fig. 4, page 16), (2) The role that handedness may play in transfer of learning as explained by the *dynamic dominance hypothesis*, (3) A description of cortical areas that may be associated with transfer of learning, and (4) The effect that the external environment may have on transfer of learning.

1.4.1 Models of transfer of learning

1.4.1.1 *Callosal Model*

According to the *callosal model*, a single motor program, located in the left dominant hemisphere, controls the motor behavior of both the arms. The right dominant arm has direct access to this motor program, whereas the left non-dominant arm only has access to it via the corpus callosum [175]. Therefore, the dominant arm should benefit more from the motor learning of the non-dominant arm than vice versa [150]. Several studies have supported this expectation and shown that transfer of learning is greater from the non-dominant arm to the dominant arm than from the dominant arm to the non-dominant arm [58, 67, 175]. The *Generalized Motor Program model* is consistent with the callosal model, in that it also suggests that a single motor program controls the movement of both the arms. If the *callosal model* is applied to bilateral reaching tasks, it is predicted that the non-dominant arm would influence the motor behavior of the dominant arm.

1.4.1.2 *Proficiency Model*

The *proficiency model* incorporates the notion that there are two motor programs, one for each arm, which are stored in the contralateral hemisphere to the arm being trained. In accordance with this model, each arm can benefit from motor learning of the other arm [177]. Laszlo et al. in 1970 demonstrated that sensory feedback influences the direction of transfer of learning between the arms [91]. When subjects were trained with reduced feedback (removing visual, audio and tactile sensing) and then tested in normal feedback conditions on the other arm, transfer of learning occurred only from the dominant to the non-dominant arm. However, when the other arm was tested in the reduced feedback condition, transfer of learning occurred only from the non-dominant to the dominant arm. Other studies have indicated that there is no difference in the direction of transfer of learning [177]. Thus, there may be an

equal update of the two motor programs via motion dependent feedback independent of which arm is being trained. If the *proficiency model* is applied to bilateral reaching tasks, it is predicted that there will be no difference in the amount of influence that one arm has on the other.

1.4.1.3 *Cross-Activation Model*

The *cross-activation model* incorporates the notion that there is a motor program in each hemisphere for the corresponding arm, and these programs are able to interact with one another in a way similar to that proposed for the *Intermanual cross-talk model* [124]. In a study where the cerebral hemispheres were surgically disconnected (callosotomy), it was found that transfer of learning did not occur for unilateral tasks [160]. With the *Cross-Activation model*, arm dominance comes into play in that the non-dominant hemisphere/arm system receives information from the dominant hemisphere/arm system, but not vice versa. When the dominant arm is trained it forms a dominant motor program in the dominant hemisphere and a less complete motor program in the non-dominant hemisphere. When the non-dominant arm performs the task for which the dominant arm was trained, the non-dominant arm has access to this lesser motor program in the non-dominant hemisphere. However, when the non-dominant arm is trained, it only forms a motor program in the non-dominant hemisphere that does not affect the dominant motor program. Therefore according to the *cross-activation model*, transfer of learning is expected to occur from the dominant arm to the non-dominant arm [62, 91, 124, 150, 182, 189].

Haaland and Harrington (1996) conducted a series of experiments demonstrating that in patients with unilateral brain damage to the dominant hemisphere, there were deficits in the motor behavior of the non-dominant arm. However, the dominant hemisphere did not experience any deficits when there was damage to the non-dominant hemisphere [61]. This supports the idea of the *cross-activation model*, in that the

dominant hemisphere potentially contains key circuitry that affects the motor behavior of the non-dominant arm. In one of the few studies that looked at transfer of learning during a bilateral task, it was found that transfer occurred from the right dominant arm to the left non-dominant arm, thereby supporting the *cross-activation model* [182]. Subjects were trained to trace a star with their right hand and a straight line with their left. During testing the left hand traced the star and the right hand traced the straight line. Transfer of learning did occur for a bilateral task, from the dominant arm to the non-dominant arm. Viviani et al. (1998) conducted a study that considered hemispheric asymmetries with respect to handedness [185]. Subjects performed a bilateral task that involved tracing elliptical trajectories with both their hands. Subjects performed this cyclical bilateral task while a positron emission tomography (PET) scanner was recording brain activity. The results of the study indicated that for both right- and left-arm dominant individuals, the dominant arm led the non-dominant arm. Also, the dominant hemisphere had consistently greater neural activity in the motor and premotor areas than the non-dominant hemisphere, which supports the *cross-activation model*. Therefore, it was concluded that the asymmetric motor behavior of the arms were related to the asymmetric neural activations in the hemispheres. If the *cross-activation model* is applied to bilateral reaching tasks, it is predicted that the dominant arm would influence the motor behavior of the non-dominant arm, but not vice versa.

1.4.2 Dynamic Dominance Hypothesis

The *dynamic dominance hypothesis* [137] incorporates the notion that the right dominant arm is more proficient in coordinating dynamical intersegmental interactions than the left non-dominant arm and therefore should be better in controlling arm endpoint trajectory in terms of trajectory direction and shape. At the same time, the left non-dominant arm is more capable of performing static stabilizing tasks and

thus is more proficient in specifying the final arm endpoint position. Sainburg and colleagues conducted a series of experiments in order to understand the asymmetric behavior of the arms due to handedness [141, 138, 190]. Subjects performed goal-directed unilateral reaching with either visual or inertial perturbations. The results demonstrated that when the arms were exposed to inertial forces, the dominant arm produced significantly smaller muscle torques than the non-dominant arm in order to accomplish the same task [137]. This suggested that the dominant arm is better in controlling limb dynamics. Other studies have demonstrated that the final position of the non-dominant arm is often more accurately achieved than that of the dominant arm [7, 8, 137, 141].

The *dynamic dominance hypothesis* also incorporates the notion that the type of information that is transferred between the arms depends on the properties of the arms' motor programs and the inherent task of each arm [138]. Sainburg and Wang (2002) demonstrated that for a visuomotor perturbation, the information transferred between the arms was specific to each arm [137]. Subjects adapted to a 30° counter clockwise visual rotation of the targets with the right- and left-arm separately. After adaptation the other arm was tested to evaluate whether transfer of learning occurred. The results showed improvement in the initial movement direction (trajectory information) of the right dominant arm after the left arm was trained due to the motor adaptation of the left non-dominant arm. The non-dominant arm improved in final position accuracy after the right dominant arm was trained due to the motor adaptation of the right dominant arm. Therefore it was suggested that final position information was transferred from the dominant to the non-dominant arm, while the trajectory information was transferred from the non-dominant to the dominant arm. These findings supported the *dynamic dominance hypothesis*, in that each arm utilizes the information available to it in order to improve specific kinematic features of its performance in accordance with the arm specialization. Therefore it may be

predicted that for bilateral tasks, that trajectory information will transfer from the non-dominant to the dominant arm while final position information will transfer from the dominant to the non-dominant arm.

1.4.3 Cortical areas associated with transfer of learning

The direction in which transfer of learning occurs may be dependent on hemispheric dominance [137] and on the strategies developed by the subjects during training [164]. Researchers have debated over the direction of transfer of learning between the arms, which have led to the development of the before mentioned transfer of learning models. A few studies have examined what the underlying neural mechanisms may be for transfer of learning by employing positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) technologies [45, 5]. In a series of PET studies conducted on monkeys performing reaching tasks, brain activity during transfer of learning were examined [115, 116]. Results of these studies indicated that during learning bilateral activation of the prefrontal cortex (PFC) and intraparietal sulcus (IPS) occurred. Contralateral cerebellar activity was also observed for the arm being used. Obayashi suggested that transfer of learning is mediated by the fronto-parietal-cerebellar pathway, and that information is shared between the frontal cortices via the anterior corpus callosum [45]. Perez et al. (2007) conducted a study using fMRI on transfer of learning of a finger tapping sequence task [127]. The right hand trained a 12-item finger tapping sequence and then the left hand was tested in a mirror image sequence, random sequence and a different unlearned sequence. Results of this study indicated that greater transfer of learning from the right hand to the left hand resulted in greater activity of the supplementary motor area (SMA). When transcranial magnetic stimulation was applied to the SMA, transfer of learning did not occur. The conclusion of that study was that the SMA is responsible for intermanual transfer of learning. Anguera et al. examined how the brain activity

during learning a unilateral task may support the transfer of learning models [5]. Subjects participated in a visuomotor adaptation unilateral task, where the right dominant arm was trained and the left non-dominant arm was tested. During transfer of learning to the left non-dominant arm, the fMRI data revealed brain activity in the non-dominant hemisphere, especially in the temporal cortex, medial frontal gyrus, middle occipital gyrus. Neural activity was also observed in the temporal cortex of the dominant hemisphere. Therefore during transfer of learning there was neural activity in both hemispheres which would support the *cross-activation model*, but not the *callosal model* or the *proficiency model*. However, these results may be dependent on the experimental design in that the right dominant arm was trained and the left non-dominant arm was tested. It is unknown whether these results would support the *cross-activation model* if the left non-dominant arm is trained and the right dominant arm is tested.

Currently there are various hypotheses that have been proposed regarding the neural mechanisms for transfer of learning of unilateral tasks. As has been demonstrated there are various pathways and neural structures that may be involved with transfer of learning: PFC, IPS, cerebellar, corpus callosum, SMA, temporal cortex, middle occipital gyrus. Further research in this area is needed, in order to understand the neural mechanisms involved with transfer of learning. All of these studies considered transfer of learning of unilateral tasks, and thus it is unclear what neural pathways and structures may be involved during transfer of learning in bilateral tasks.

1.4.4 Environment

The force environment in which transfer of learning occurs has been shown to play a role in motor adaptation and transfer of learning. Burgess et al. demonstrated that transfer occurred from a bilateral to a unilateral reaching task when the same extrinsic force environment (coordinate frame is external to the body, e.g. both arms

experience a clockwise force environment) were applied to the arms [19]. Malfait and Ostry showed that transfer occurs in an extrinsic coordinate frame only if the force environment is applied abruptly but not if it gradually increases [95]. It has also been shown that during unilateral reaching [28], transfer of learning occurs from the dominant to the non-dominant arm only in the extrinsic coordinate frame and not in the intrinsic coordinate frame (coordinate frame is with respect to the joints in the body, e.g. the right arm experienced a clockwise force environment which tends to extend the right arm joints, while the left arm is experiencing a counter clockwise force environment which also tends to extend the left arm joints). This results supports the *cross-activation model*. Therefore, it is plausible that transfer of learning may depend on the direction of the force environment (i.e., extrinsic or intrinsic coordinate frame). The question becomes, does the direction of the force affect bilateral motor adaptation? This question is addressed in Chapter 5, page 73.

1.5 Motor behavior of the arm

The human body has more kinematic degrees of freedom than is strictly necessary to perform a movement. As a result, the arm endpoint can be positioned in a specific location with many different combinations of angles at the shoulder, elbow and wrist. Despite this kinematic redundancy healthy individuals tend to utilize limited specific motor patterns, which are called kinematic invariant characteristics. These include (1) straight-line finger tip trajectory, (2) bell-shaped hand velocity profile, (3) power law and (4) Fitt's law. Straight-line finger tip trajectory is observed when the finger tip moves in a nearly straight line from one target to another (Fig. 2.b, page 7). Joint angles during these reaching tasks are variable and may have complex non-linear patterns. During reaching, the finger tip has a bell-shaped velocity. The velocity magnitude is zero at the start of the movement, reaches peak in the middle of the reach and then goes back to zero. The symmetric bell-shaped velocity profile can

be distorted by applying random external perturbations. The bell-shaped velocity profile can be restored through motor adaptation [155]. During drawing, writing or when the arm moves along a curved trajectory, the finger tip velocity is coupled with the curvature of the finger tip trajectory. The power law describes the relationship between the velocity and the curvature of the trajectory [40, 89, 146, 186, 184].

Fitt’s law incorporates the notion that there is a tradeoff between speed and accuracy in arm reaching, that is when speed increases the accuracy will decrease. This has been demonstrated by changing the size of and distance to the target during reaching tasks. The smaller the target and the further away it is, the higher the accuracy demands are and therefore the slower the movements [50]. Movement time has been shown to be dependent on the ratio between movement amplitude and movement precision (target size). Kelso et al. (1979) demonstrated that during a bilateral task when there is a difference in the size of the target for each arm, both arms moved slower in order to accommodate the arm that was moving towards the smaller target [81]. Therefore, in order to ensure that the same conditions are placed on both hands, the distance to the target and target size would have to be the same between hands. Kelso, also demonstrated that these results hold true regardless of the direction during bilateral reaching [80].

Attention may influence the motor behavior of the arms during bilateral tasks. Bilateral movements tend to have longer reaction times than unilateral movements and this may be attributed to increased cognitive demands on the CNS [37, 82, 106, 117, 161, 173, 174]. The more complex the bilateral task is the greater the attentional focus needs to be, as demonstrated in pianists playing a Bach piece versus a scale [125]. Divided attention can cause spatial errors during bilateral tasks. Researchers have found that if a subject is instructed to focus attention on a single limb during a bilateral task, the unattended limb would make greater movement errors [157]. There appears to be an attention bias towards the right arm in right-handed subjects [18]

and that during bilateral reaching there tends to be more saccadic eye movements toward the right arm than the left arm [74]. Furthermore, the right arm tends to lead the left during bilateral cyclical drawing in right arm dominant subjects but not left arm dominant subjects [167]. However, studies have shown that there is no difference in reaction or movement time during bilateral in-phase (symmetrical) and out-of-phase (non-symmetrical) movements [2]. Although in-phase cyclical movement is more stable [25, 167, 168], subjects are still able to learn out-of-phase movements [169]. One of the primary reasons for observed differences between unilateral and bilateral movements may be that a greater amount of attention is required during bilateral movements. What would be interesting to know, is whether attention plays a role in the transfer of learning during a bilateral reaching task. An easy way to test this would be to consider any differences in movement time and reaction time. Longer reaction times and movement times, are often used to indicate that a higher neural activity in the CNS is required to execute complex bilateral movements when compared to simpler unilateral movements.

1.6 Significance

The Center for Disease Control estimates that this year in the United States approximately 600,000 people will suffer from a stroke, which comes to approximately one person per minute [194]. A stroke occurs when a blood clot gets trapped in a blood vessel due to plaque buildup and causes oxygen deprivation to the brain. This often results in movement disability that may be restored through intensive rehabilitation. In stroke rehabilitation there is an ongoing debate as to whether unilateral, bilateral motor learning or a combination thereof may be more beneficial. Studies on unilateral motor learning, such as the Constraint Induced Movement Therapy (CIMT), have demonstrated to be an effective strategy for retraining the affected arm [3, 20, 123, 192]. Other studies have demonstrated that bilateral motor learning also

improves the motor control of the affected arm [29, 92, 63, 109, 134, 165, 187]. The type of therapy that is chosen for a stroke survivor may depend on many factors and may involve a combination of unilateral and bilateral motor learning strategies. What remains unclear for bilateral reaching tasks is whether and how transfer of learning occurs. Understanding the mechanisms of transfer of learning may aid therapists in designing improved rehabilitation therapy for stroke survivors.

Most studies of upper extremity have focused on unilateral motor learning of the right dominant arm [41, 49, 58, 59, 76, 83, 137, 145, 155, 178]. Few have considered the unilateral motor learning of the left dominant arm [46, 172, 191]. In addition, transfer of learning studies have focused on unilateral tasks, where one arm is trained and the opposite arm is tested. From these studies several theories on how transfer of learning may occur have been developed (See Section 1.4 and [28, 91, 124, 137, 175]). However, since these theories are mostly based on unilateral tasks, it remains unclear where and how motor adaptation and transfer of learning occur during simultaneous repeated performance of novel bilateral tasks by both arms.

1.7 Central hypothesis and specific aims

The purpose of the current study is to determine whether transfer of learning occurs during bilateral reaching tasks. This is addressed by comparing the difference in motor adaptation of the arm(s) during bilateral reaching tasks, when the arm(s) are exposed to a novel force environment. For bilateral tasks, there are multiple ways of how the force environment may be applied. The current study examines whether there is a difference in motor adaptation when only one arm or both arms experience the force environment. Furthermore, the current study examines whether the direction in which the forces are applied may affect motor adaptation and transfer of learning.

The central hypothesis of the study is that during bilateral reaching in a novel force environment, either transfer of learning or interference between the arms may

take place depending on the type of sensory feedback (position dependent or external load dependent) from the dominant and non-dominant arm.

1.7.1 Aim 1

Transfer of learning has been shown to occur for unilateral tasks when one arm was trained and then the other arm was tested. Based on results from various experiments three transfer of learning models have been proposed to describe the direction in which transfer of learning occurs: *Callosal Model* [175], *Proficiency Model* [91] and *Cross-Activation Model* [124]. Studies that have examined neural activity during transfer of learning support the *cross-activation model* [185]. The *intermanual cross-talk model* for bilateral motor control is consistent with the cross-activation model which proposes that each arm has its own motor program in the contralateral hemisphere and that motor program related information is transferred from the dominant to the non-dominant hemisphere but not vice versa. It is predicted that during a bilateral task when one arm remains stationary, the stationary arm provides constant movement related position feedback to the opposite moving arm but does not influence the motor adaptation of the opposite arm. When both arms are moving, but only one arm adapts to the force environment, it is predicted that the movement related position feedback from the arm that does not experience the force environment may influence the motor adaptation of the arm that does experience the force environment. Therefore, when incorporating the *cross-activation model* with this rationale, it implies that sensory feedback from the dominant arm may influence the development of the motor program of the non-dominant arm, but not vice versa. The primary question addressed in this study is: Does transfer of learning occur during bilateral tasks? This question will be explored further in Chapter 3, page 42.

Aim 1: Determine the effects of arm dominance on transfer of learning during bilateral reaching.

Hypothesis 1.1: The transfer of learning from the non-dominant to the dominant arm is smaller than the transfer from the dominant to the non-dominant arm, given that one arm learns a force environment and the other simultaneously operates in the natural force environment.

1.7.2 Aim 2

The CNS is thought to use sensory feedback in order to compare the predicted movement against the actual movement. If there is a difference between predicted and actual movement (movement error), the CNS updates the motor program in order to produce improved motor commands. When an unexpected force environment is applied to the arms, large movement errors result. With practice and adaptation to the force environment, these movement errors become smaller. In bilateral tasks, the force environment can be applied in multiple combinations to the arm. However, the current study addressed the question: does motor adaptation depend on whether one or both arms experience the force environment? It is anticipated that during bilateral tasks when both arms experience an intrinsic force environment, the external load feedback available from each arm would be similar. During a bilateral task when only one arm experiences the force environment but the other arm does not, it is anticipated that there would be a difference in the external load feedback between the arms. If it is assumed that transfer of learning occurs during bilateral tasks, then it is predicted that when sensory feedback is similar between the arms, the CNS is able to update the motor programs more efficiently than if there is a difference in sensory feedback between the arms. This will be explored further in Chapter 4 (page 63).

Aim 2: Determine the effects of simultaneous learning of the intrinsic force environment by two arms on transfer of learning during bilateral reaching.

Hypothesis 2.1: When both arms learn the intrinsic force environment during

bilateral reaching, motor adaptation of the dominant arm should be greater than when only the dominant arm learns the force environment during bilateral reaching.

Hypothesis 2.2: When both arms learn the intrinsic force environment during bilateral reaching, motor adaptation of the non-dominant arm should be greater than when only the non-dominant arm learns the force environment during bilateral reaching.

1.7.3 Aim 3

Studies on transfer of learning have demonstrated that the direction in which the force environment is applied does affect the direction in which the information is transferred from one arm to the other. Criscimagna-Hemminger et al. found that transfer of learning occurs from the dominant arm to the non-dominant arm for extrinsic force environments but not for intrinsic force environments [28]. The current study addressed this issue by asking the question: Does the direction of the force environment affect bilateral motor adaptation. It is predicted that during bilateral reaching, transfer of learning should be greater for the extrinsic force environment than the intrinsic force environment. This will be explored further in Chapter 5 (page 73).

Aim 3: Determine the effects of extrinsic and intrinsic force environments on transfer of learning during bilateral reaching.

Hypothesis 3.1: When both arms learn the force environment during bilateral reaching, transfer of learning should be greater for the extrinsic force environment compared to the intrinsic force environment.

1.8 Conclusion

This chapter reviewed studies on motor adaptation and four motor control models (*Generalized Motor Program*, *Intermanual Crosstalk*, *Hierarchical model* and *Optimal Feedback Control*) that may apply to bilateral movements. Motor adaptation is

thought to be an iterative process through which the CNS updates motor commands to the muscles to improve motor behavior. During motor adaptation sensory feedback about the ongoing movement is provided back to the CNS for a comparison with the predicted feedback. The mechanisms of bilateral arm control are still under debate. The four discussed models attempt to address the question of whether there is a single controller for both arms, or whether each arm has its own controller, and how sensory feedback may influence the controllers. One way in which this question has been studied is by considering how learning a motor task by one arm in one condition may transfer to the other arm in a different condition. There are three models that have been proposed to explain transfer of learning, *callosal model*, *proficiency model* and the *cross-activation model*. However, handedness may contribute significantly to the interference or transfer of learning between the arms during bilateral goal-directed reaching tasks, as explained by the *dynamic dominance hypothesis*. Three key questions have been posed with the aims and hypotheses: (1) Does transfer of learning occur during bilateral tasks? (2) Does motor adaptation depend on whether one or both arms experience force environment? and (3) Does the direction of the force affect bilateral motor adaptation? Each of these questions will be addressed in subsequent chapters.

CHAPTER II

METHOD

2.1 Introduction

This chapter covers the methodology used to conduct the studies described in this thesis. Descriptive information about the subjects are provided, along with the experimental equipment and protocol. The task performance measures and how these were analyzed are discussed.

2.2 Subjects

Sixty one (61) subjects were recruited for this study (43 males and 17 females, Table 1, page 32). The selection criteria for the subjects were: (1) 21 years of age or older, (2) had no known neuromuscular disorders, and (3) had to be right hand dominant in that the Edinburgh Inventory [118] had to be between 0.5 and 1. One subject had a small lesion in the right frontal lobe, however upon examining her data this did not seem to alter her performance when compared with other subjects. Data from one subject was lost due to technical difficulties. The only significant difference between gender ($p < 0.05$) was that males tended to be taller than females (Table 2). Subjects were pseudo-randomly assigned to one of six groups to ensure a nearly equal distribution of males and females per group. More details about the groups will be provided later in this chapter (page 37) and in subsequent chapters. Informed consent was obtained prior to the initiation of the experiment. This study was approved by the Georgia Institute of Technology Internal Review Board.

Table 1: Descriptive information across subjects.

	N	Mean \pm Std	Range
Age (years)	60	35 \pm 12	[21,59]
Height (cm)	60	177.82 \pm 8.66	[155,197]
Weight (kg)	60	81.63 \pm 17.06	[49.9,134]
Handedness	60	0.77 \pm 0.14	[0.5,1]

Table 2: Descriptive information by gender.

	Males	Females
N	43	17
Age (years)	33 \pm 11	39 \pm 14
Height (cm)*	181.1 \pm 6.5	169.6 \pm 8.2
Weight (kg)	83 \pm 15.6	78.2 \pm 20.4
Handedness	0.77 \pm 0.14	0.75 \pm 0.17

2.3 *Bilateral exoskeletal robotic equipment*

Kinarm (Kinesiological Instrument for Normal and Altered Reaching Movement; BKIN Technologies, OT, Canada) is a robotic assessment system for quantifying motor function of the upper extremities (Fig. 5, page 34). The Kinarm is a motorized exoskeleton that monitors and manipulates arm motion in the horizontal plane. Elbow and shoulder joints are aligned with the Kinarm robot’s joints. The Kinarm system includes two robots for simultaneous left- and right-arm manipulation. The system integrates a virtual target presentation system and wheel-chair-style seating. The BKIN Dexter-E software allows for creating and controlling behavioral paradigms for recording.

The calibration of the Kinarm involves three steps. The first calibration step is done prior to the subjects arrival and involves locking the robotic arms into a fixed position where all the angles between robotic arm segments are known. Next, the subject is asked to sit in the wheel-chair-style seating while the joints of the robot are aligned with the shoulder and elbow joints of the subjects. The second calibration

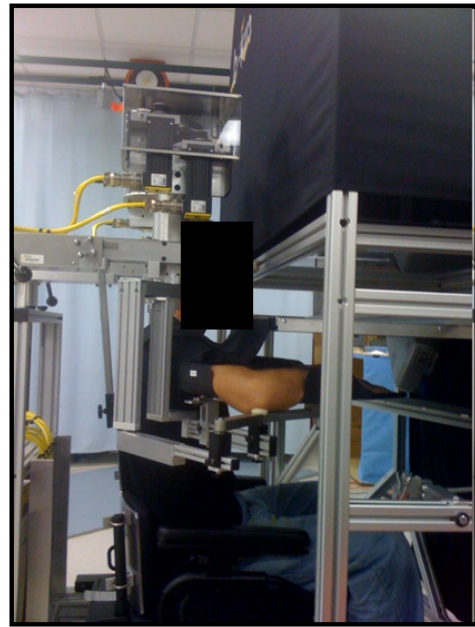
step is called the docking station calibration step and is performed once the subject is wheeled up to the visual display system (Fig. 5.b). The subject moves the robotic arm such that the pin beneath its distal end makes contact with the most lateral docking point of the visual display system, then he/she moves the pin on to the next two docking points located medially. There are three docking points per arm, and this serves to map the visual display system to the subject’s dimensions. The last calibration step involves the finger-tip calibration. At the visual display system, subjects are asked to move his/her index finger tip to each of four projected target points sequentially. This is done separately for each arm and serves to calibrate the projected index finger cursor to the subjects specific anthropometrics. Two white dots are projected onto the screen and serves as cursors that track the movement of the tip of the index fingers of the subject. After the calibration is complete, a non transparent screen is slid forward in the visual display system so that subjects are not able to see their arms. In addition a cloth is draped over their shoulders to further ensure that subjects do not receive visual feedback on their arm position and configuration. Instead the only visual feedback that subjects receive are white dots that coincide with the tip of their index fingers.

2.4 Experimental protocol

In the experimental task subjects were instructed to place the two cursors in two blue targets. These blue targets defined the start positions of the two arms (Fig. 6.a, page 36) with shoulder flexion angles $q_1 = 30^\circ$, elbow flexion angles $q_2 = 60^\circ$, and wrist angles $q_3 = 0^\circ$. The subject was then instructed to reach to eight targets (1 cm diameters) randomly selected and arranged radially 10 cm away from the starting position as quickly and as accurately as possible. In order to start the task, the subject had to remain in the starting position for 3000ms before a green target would appear signaling the subject to initiate the movement. The response time was defined



A.



B.

Figure 5: The Kinarm robotic upper extremity assessment system. (a) Frontal view of the Kinarm shows subjects arms are supported in the horizontal plane. (b) The visual display system on the right uses mirrors and a projector to show targets in the subjects field of view.

as the time between when the green target first turns on and the subject reached the target. If the response time was less than 500ms the green target would turn yellow, indicating that the subject was doing exceptionally well. If the response time took between 500ms and 1000ms to reach the target it turned pink and was an indication that the subject was doing all right. If the response time was longer than 1000ms the target turned red and this was an indication that the subject was performing poorly and had to focus on improving. This immediate feedback served to motivate subjects to reach towards the targets as accurately and as quickly as they could.

There were two types of bilateral goal-directed reaching task conditions: (1) unilateral reaching (Fig. 6.b), and (2) bilateral reaching (Fig. 6.c). During unilateral reaching only one arm would reach to the targets, while the other arm was required to maintain the cursor in the starting position. During bilateral reaching both arms reached towards targets in an out-of-phase pattern. Studies have demonstrated that during out-of-phase reaching, movement time does not vary between the arms if the targets are of the same size and the same distance away from the starting position for each arm [81]. The out-of-phase pattern was used in this study to determine whether discrepancies of the sensory feedback would affect this relationship. Target numbering was based on the out-of-phase pattern observed between the arms. Consecutive reaching towards all eight targets in a random order was defined as a cycle.

The experimental protocol was as follows (Fig. 7, page 37). Subjects performed 2 cycles during the *warm up* phase to ensure that they understood the instructions and that they were able to see all of the targets and reach all of the targets. If subjects were unable to see or reach any of the targets, adjustments were made to the Kinarm and the system was calibrated during the *warm up* phase. During the *pre-exposure* phase subjects completed 20 cycles in a natural environment, meaning there was no force environment applied to the arm. The *pre-exposure* phase allowed subjects the opportunity to familiarize themselves with the task. After resting for

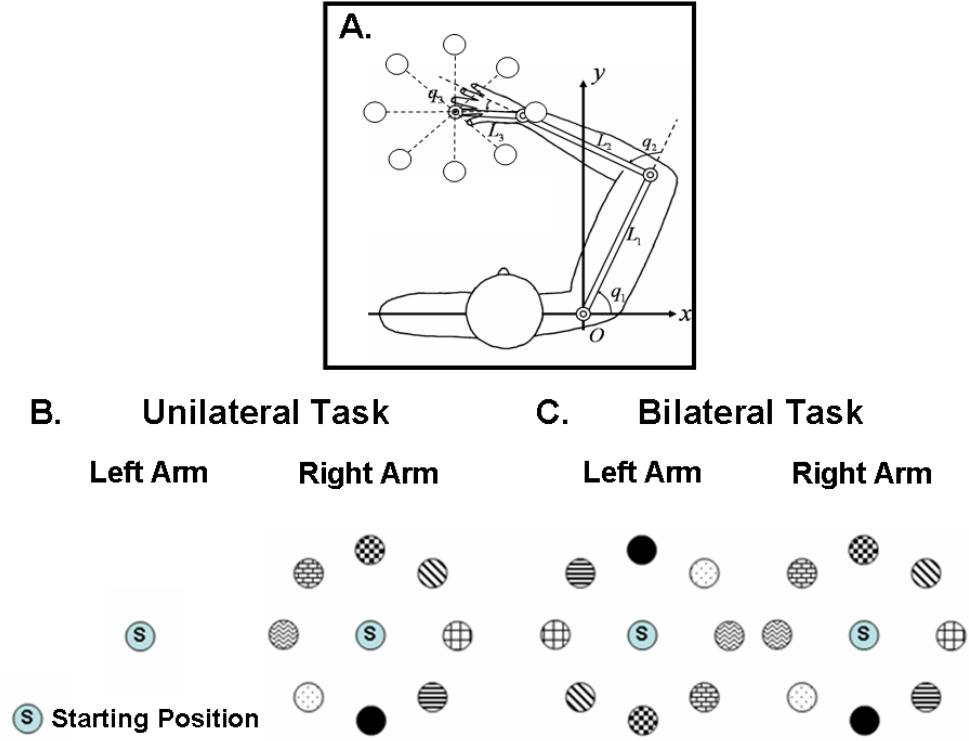


Figure 6: Diagram of the experimental task. (a) Configuration diagram for defining the starting location. (b) Unilateral reaching was defined as one arm reaching to 8 random targets, while the other arm remained stationary in the starting position. (c) Bilateral reaching was defined as reaching with both the arms in an out-of-phase pattern.

Warm Up	Pre-Exposure (No Force)	Rest	Exposure (Force On)	Rest	Exposure (Force On)	Catch Trial
2 cycles	20 cycles	5 min	20 cycles	5 min	20 cycles	10 cycles

Figure 7: Experimental protocol.

5 minutes, subjects proceeded to complete 20 cycles in the *exposure* phase where a velocity dependent force environment was applied to the index finger. The force vector \mathbf{F} , was a function of the index finger velocity vector \mathbf{V}

$$\mathbf{F} = \mathbf{B} * \mathbf{V} \quad (3)$$

where, \mathbf{F} is the force vector $\mathbf{F} = [Fx, Fy]$ applied to the index finger tip (in Newton), \mathbf{V} is the finger tip velocity vector $\mathbf{V} = [Vx, Vy]$ (in meter/second), and \mathbf{B} is the viscosity matrix (in Newton*seconds/meter):

$$\mathbf{B} = \begin{bmatrix} 0 & 10 \\ -10 & 0 \end{bmatrix} \quad (4)$$

As a result the force environment \mathbf{F} was directed clockwise perpendicular to the index finger tip velocity (Fig. 2.c, page 7). Negative viscosity matrix $-\mathbf{B}$ resulted in a counter clockwise force environment. This force environment was applied to either one or both arms, in the same or different directions depending on the experimental conditions (see below). After the initial exposure, subjects rested for 5 minutes before completing 20 more cycles in the *exposure* phase. Between the last *exposure* phase and the *catch trial* phase there was no rest to ensure that subject did not anticipate a change in the reaching conditions. During the *catch trial* phase subjects completed 10 cycles, however during 3 out of the 10 cycles the force environment was pseudo-randomly removed.

Table 3: Experimental groups.

	Exposure		Catch	
	Arm	Field	Arm	Field
Unilateral Right	Right	CW	Right	Null
	Left	Null	Left	Null
Unilateral Left	Right	Null	Right	Null
	Left	CCW	Left	Null
Bilateral Right	Right	CW	Right	Null
	Left	Null	Left	Null
Bilateral Left	Right	Null	Right	Null
	Left	CCW	Left	Null
Bilateral Intrinsic	Right	CW	Right	Null
	Left	CCW	Left	Null
Bilateral Extrinsic	Right	CW	Right	Null
	Left	CW	Left	Null

The specific reaching tasks and the force environments depended on the experimental group assignment. The rationale for these groups will be discussed in subsequent chapters where the specific aims are addressed. There was some overlap in groups between specific aims, therefore Table 3 (page 38) lists all the groups and shows the force environments that each arm experienced. During unilateral reaching, only the arm experiencing the force environment reached to the targets while the other arm remained stationary in the starting position (Unilateral Left and Unilateral Right). During bilateral reaching both arms performed reaches, however the force environment was applied to either one arm, the left non-dominant arm (Bilateral Left) or the right dominant arm (Bilateral Right), or both arms in the intrinsic (Bilateral Intrinsic) or the extrinsic (Bilateral Extrinsic) coordinate frame. Force environments were applied in the clockwise (CW) or counter clockwise (CCW) direction, dependent on the group (Table 3, page 38). Descriptive data broken down by the groups are shown in table 4, page 39.

Table 4: Descriptive information by groups.

Group	N	Age (years)	Height (cm)	Weight (kg)	Handedness
Unilateral Right	10	29±06	178±10	80±14	0.76±0.10
Unilateral Left	10	35±14	176±07	78±13	0.75±0.18
Bilateral Right	10	31±13	177±08	73±11	0.80±0.11
Bilateral Left	10	42±12	178±08	77±11	0.75±0.15
Bilateral Intrinsic	10	33±11	177±12	89±20	0.78±0.15
Bilateral Extrinsic	10	40±12	180±09	93±24	0.77±0.19

2.5 Measures of task performance

Six measures of task performance were calculated from hand trajectory data: (1) perpendicular displacement (PD), (2) final position error (FPE), (3) reaction time (RT), (4) movement time (MT), (5) peak velocity (V_{max}) and (6) peak velocity position (V_{pos}). Perpendicular displacement was defined as the maximum perpendicular displacement of the finger tip trajectory from a straight line connecting the start and end target (Fig. 8.a, page 40). Final position error was taken as the absolute difference in position between the end target and the index finger at movement termination (Fig. 8.b). Reaction time was the difference in time between the moment the target turns on and the onset of movement. The onset and offset of reaching movement was defined using a threshold of 5% of the peak velocity vector. Movement time was the time difference between the index finger movement onset and offset. Peak velocity was the maximum vector velocity magnitude (cm/ms) during a single reach. The position of peak velocity (% movement time) indicates when the peak velocity is reached. The aftereffect was calculated as the difference in the mean perpendicular displacement between the last four cycles of the *exposure* phase and that of the *catch trial* phase (measured in cm).

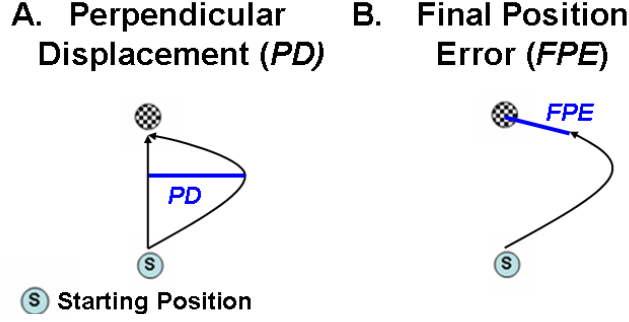


Figure 8: Performance variables. (a) Perpendicular displacement (PD). (b) Final position error (FPE).

2.6 Data analysis and statistics

The index finger tip displacement data recorded by the Kinarm were filtered using a 6th order low pass Butterworth filter with a cut-off frequency of 10 Hz . All kinematic data were normalized to movement time. A successful reach was when: (1) the movement time was less than 1000 ms, and (2) the final position error was less than two standard deviations of the mean of final position errors for each individual subject. Approximately 8.7% of the data was removed because of these criteria.

The perpendicular displacement data were further normalized to the perpendicular displacement of the first reach towards a target. This allowed for comparisons of perpendicular displacement across target directions, subjects and groups. Regression analysis was used to determine the relationship between the normalized perpendicular displacement and cycle number. The rate of adaptation of the normalized perpendicular displacement is the rate constant of the regression line. In order to compare two learning curves against one another for statistical difference, the Rosenbrock and Quasi-Newton method with a custom function and least squares estimation was used. For the other performance variables, typically two-way ANOVA's were conducted with the independent variables being group assignment and arm used. In addition,

correlation coefficients were computed between the performance variables and subjects' characteristics such as age, gender and handedness. Further details regarding exact statistical procedures will be considered in subsequent chapters as each aim is explored in greater depth. Statistica Version 7.0 was used to perform statistical analyses.

2.7 Conclusion

Sixty one subjects were recruited and randomly assigned to one of six groups: (1) Unilateral Right, (2) Unilateral Left, (3) Bilateral Right, (4) Bilateral Left, (5) Bilateral Intrinsic and (6) Bilateral Extrinsic. The Kinarm robotic device was used to capture upper extremity motor behavior of subjects performing unilateral and bilateral reaching while experiencing force perturbations on one or both the arms in the intrinsic or extrinsic coordinate frame. The primary performance variable was the perpendicular displacement, which has been shown to be a good indicator of motor adaptation [155] and has also been used in studies on transfer of learning [28]. Other performance variables were also calculated to gain additional insight into bilateral movement behavior. While this chapter focussed on general methodology, subsequent chapters will contain further details regarding the motivation for the experimental design as it pertains to each specific aim.

CHAPTER III

AIM 1. DOES TRANSFER OF LEARNING OCCUR DURING BILATERAL TASKS?

3.1 Introduction

Transfer of learning has been defined as the process through which learning a motor task in one condition improves performance in another condition. Transfer of learning has been shown to occur between arms when one arm has undergone motor adaptation and the other non-trained arm demonstrated improved performance [11, 38, 76, 99]. Transfer of learning has also been demonstrated to occur when a unilateral motor task was trained, while a bilateral task was tested and demonstrated an improvement in performance [113, 114]. The opposite has also been shown to occur when subjects trained in bilateral motor task demonstrated improved performance in a unilateral task [71, 158]. One key question that has not yet been addressed is: Does transfer of learning occur during bilateral tasks?

There are several models of transfer of learning that predict the direction in which transfer of learning may occur based on previous studies of unilateral reaching. These models have been described in Chapter 2 (page 15) and include: *Callosal model* [175], *Proficiency model* [91] and *Cross-activation model* [124]. In addition to these models, Sainburg and Wang (2002) demonstrated that transfer of learning does occur from one arm to the other during unilateral reaching with a visuomotor perturbation, however only selective information is transferred [142]. Specifically, the final position error information was transferred from the dominant to the non-dominant arm. The information regarding finger tip trajectory (which may be determined by perpendicular displacement) was transferred from the non-dominant to the dominant arm. These

results are consistent with the *dynamic dominance hypothesis*, which states that the dominant arm is an actuator and the non-dominant arm is a stabilizer. Therefore, handedness may affect transfer of learning during bilateral reaching tasks. Motor adaptation has been shown to transfer from one arm to the other during unilateral reaching studies, however in each case the transfer was only tested after completion of training. It is not known whether or how transfer of learning can occur when both arms participate and learn different reaching tasks simultaneously. It is plausible that transfer of learning could be enhanced or worsened depending on continuous sensory feedback from both arms to the Central Nervous System (CNS) that can either compliment or interfere with motor adaptation.

To test if transfer of learning occurs during bilateral tasks, two experimental conditions should be investigated: unilateral reaching and bilateral reaching. During unilateral reaching, only one arm learns to reach in a force environment, while the other arm remains stationary and therefore does not provide movement related position feedback or external load feedback. It is anticipated that the stationary arm will not affect the motor adaptation of the arm that is exposed to the force environment. For the bilateral reaching condition, both arms perform reaching movements but only one arm learns the force environment while the other arm does not. In this condition, the arm moving in the natural environment would provide movement related position feedback but not external load feedback to the arm that is exposed to the force environment. It is further predicted that the effect on motor adaptation of the trained arm (left non-dominant/right dominant) is based on the type of sensory information that it receives from the other arm (right dominant/left non-dominant) as explained by the *dynamic dominance hypothesis*. The following specific aim and hypothesis addresses this issue:

Aim 1. Determine the effects of arm dominance on transfer of learning during bilateral reaching.

Hypothesis 1.1: Transfer of learning from the non-dominant to the dominant arm is smaller than transfer from the dominant to the non-dominant arm, given that one arm learns a force environment and the other simultaneously operates in the natural force environment.

3.2 *Method*

Forty (40) subjects were recruited and randomly assigned to one of four groups (Table 5, page 45):

- Unilateral Right: Right dominant arm learned a clockwise (CW) force environment, while the left non-dominant arm remained stationary and did not experience a force environment.
- Bilateral Right: Both arms were moving, but only the right dominant arm learned a clockwise (CW) force environment while the other arm did not experience a force environment.
- Unilateral Left: Left non-dominant arm learned a counter clockwise (CCW) force environment, while the right dominant arm remained stationary and did not experience a force environment.
- Bilateral Left: Both arms were moving, but only the left non-dominant arm learned a counter clockwise (CCW) force environment, while the other arm did not experience a force environment.

To test whether motor adaptation occurred and to compare rate of adaptation between the conditions, a regression equation was computed between the normalized perpendicular displacement and the cycle number. The regression line equation was of the form

$$y = \exp(-b * x) \tag{5}$$

Table 5: Aim 1: Experimental Groups.

	Exposure		Catch Trial	
	Arm	Field	Arm	Field
Dominant				
Unilateral Right	Right	CW	Right	Null
	Left	Null	Left	Null
Bilateral Right	Right	CW	Right	Null
	Left	Null	Left	Null
Non-Dominant				
Unilateral Left	Right	Null	Right	Null
	Left	CCW	Left	Null
Bilateral Left	Right	Null	Right	Null
	Left	CCW	Left	Null

where, y is the normalized perpendicular displacement, b is a constant and the rate at which motor adaptation occurred, and x is the cycle number. To compare whether the obtained regression lines (or learning curves) differ between experimental groups, the regression lines were compared using the Rosenbrock and Quasi-Newton method with least squares. The effects of experimental groups and arm dominance on the aftereffects were tested using a two-way ANOVA. The aftereffect was calculated as the difference in the mean perpendicular displacement between the last four cycles of the *exposure* phase and that of the *catch trial* phase (measured in cm). Similar effects on all other performance variables measured during the *exposure* and the *catch trial* phases, were also studied using two-way ANOVA's.

3.3 Results

The typical index finger path of a subject in the unilateral right group is shown in figure 9, page 47. When the subject was initially exposed to the clockwise force environment, large movement errors were observed (Fig. 9.a, blue dashed lines). With training the index finger path became straighter (Fig. 9.a, black solid lines). During the *catch trial* phase when the force environment was pseudo-randomly removed,

large movement errors were observed in the opposite direction compared to movement errors during the initial exposure to the force environment (Fig. 9.b). The large movement errors during the *catch trial* is an indication that motor adaptation occurred. The regression analysis of the normalized perpendicular displacement revealed that for all target directions across subjects the rate of adaptation, was statistically significant ($p < 0.05$), except for the target direction 3 (pink line, Fig. 9.c). One possible reason for this is that for target 3, the direction in which the force environment is applied to the finger tip is in line with the upper limb and passes through the shoulder thereby generating small external moments at the elbow. Since the external moments are small, there is not much motor adaptation that needs to occur in order to adequately perform the task.

Similar observations were made for the unilateral left group, where during initial exposure to the force environment, large movement errors were observed however the index finger path straightens out with training (Fig. 10.a, page 48). During the *catch trials* the movement errors were large when the force environment was pseudo-randomly removed (Fig. 10.b). The large movement errors during the *catch trials* were an indication that motor adaptation occurred. The regression analysis of the normalized perpendicular displacement revealed that for all target directions across subjects the rate of adaptation was significant ($p < 0.05$). However, as may be seen in figure 10.c the learning for target direction 7 (purple line) the performance worsened. A potential explanation for this is that the force environment produced for target 7 small external moments on the joints therefore little or no motor adaptation had to occur.

For the bilateral right group, when both arms were moving and only the right dominant arm experienced a force environment, the results demonstrated that motor adaptation occurred (Fig. 11.e-f, page 50). The regression analysis of the normalized perpendicular displacement for the right dominant arm revealed that for all target

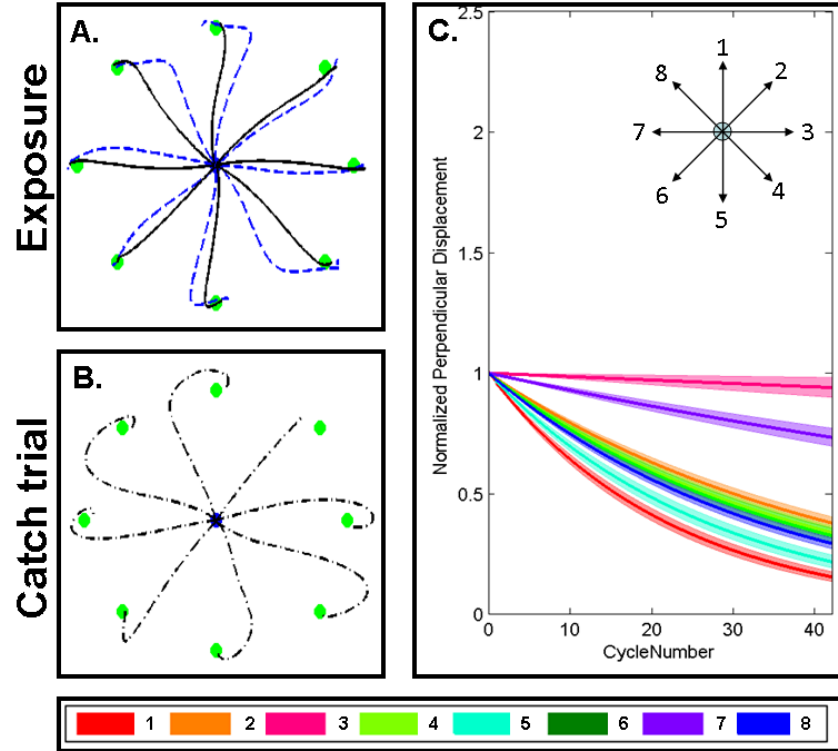


Figure 9: Unilateral Right. (a) Right index finger displacement for a single subject averaged over the first four cycles of the *exposure* phase (dashed blue line) and over the last four cycles of the *exposure* phase (solid black line). (b) Right index finger displacement for a single subject averaged over the *catch trial* phase. (c) Normalized perpendicular displacement (mean \pm standard error) for each target direction averaged across subjects.

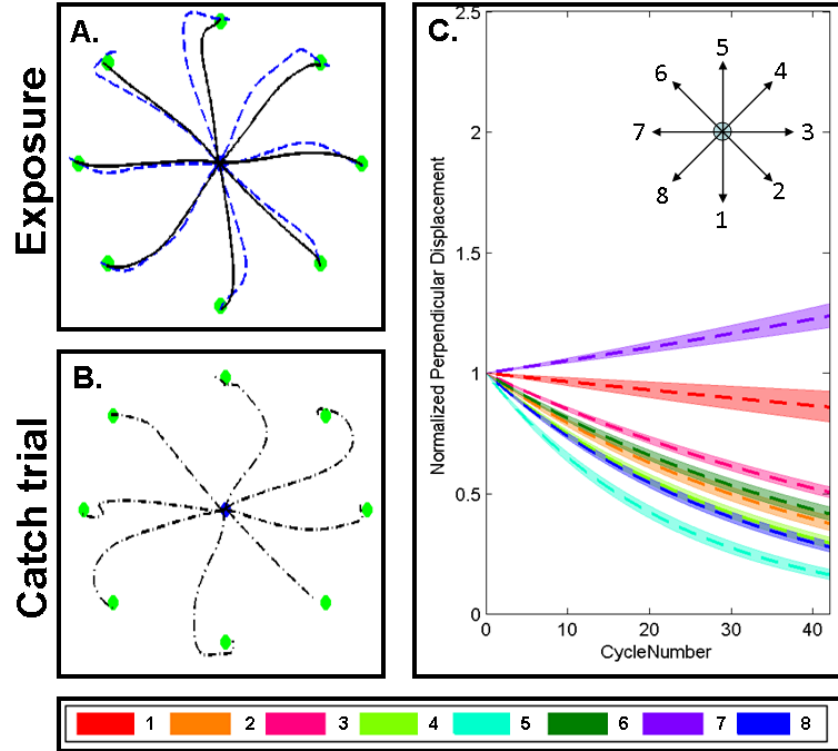


Figure 10: Unilateral Left. (a) Left index finger displacement for a single subject averaged over the first four cycles of the *exposure* phase (dashed blue line) and over the last four cycles of the *exposure* phase (solid black line). (b) Left index finger displacement for a single subject averaged over the *catch trial* phase. (c) Normalized perpendicular displacement (mean \pm standard error) for each target direction averaged across subjects.

directions across subjects the rate of adaptation was significant ($p < 0.05$), even for the target direction 3 (pink line, Fig. 11.d). This result may indicate that transfer of learning of the trajectory information occurred from the left non-dominant arm to the right dominant arm, according to the *dynamic dominance hypothesis*. This would result in improvement of rate of adaptation of the normalized perpendicular displacement for all directions. For the left non-dominant arm no movement errors were observed, and this was expected since this arm was not exposed to a force environment (Fig. 11.b-c). The regression analysis of the normalized perpendicular displacement for the left non-dominant arm revealed that for target directions 1, 2, 3, 6, and 8 the rate of adaptation significantly worsened ($p < 0.05$), but that for target directions 4, 5, and 7 there was no significant difference. Therefore motor adaptation did not occur for the left non-dominant arm.

For the bilateral left group, when both arms were moving and only the left non-dominant arm experienced a force environment, the results demonstrated that motor adaptation occurred for the left non-dominant arm (Fig. 12.b-c, page 51). The regression analysis of the normalized perpendicular displacement for the left non-dominant arm revealed that for all target directions across subjects the rate of adaptation was significant ($p < 0.05$). However, similar to the unilateral left group for the target direction 7 (purple line, Fig. 12.a), performance worsened while for all other target directions the rate of adaptation improved. For the right dominant arm no movement errors were observed, which was expected since this arm was not exposed to a force environment (Fig. 12.e-f). The regression analysis of the normalized perpendicular displacement for the right dominant arm revealed that for all target directions, except target direction 4 (light green line, Fig. 12.d), the rate of adaptation was significant ($p < 0.05$).

Although there was significant difference in the rate of adaptation for some target

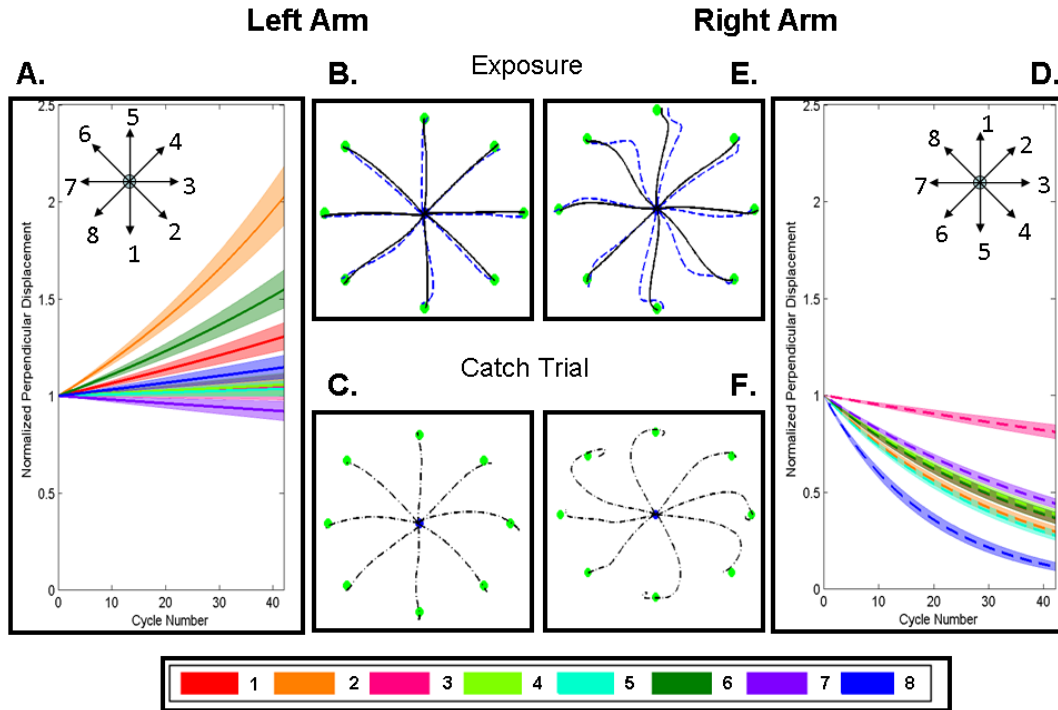


Figure 11: Bilateral Right. (a/d) Left/Right index finger normalized perpendicular displacement (mean \pm standard error) for each target direction averaged across subjects. (b/e) Left/Right index finger displacement for a single subject averaged over the first four cycles of the *exposure* phase (dashed blue line) and over the last four cycles of the *exposure* phase (solid black line). (c/f) Left/Right index finger displacement for a single subject averaged over the *catch trial* phase. Target direction labels are indicated for each arm according to the out-of-phase reaching pattern.

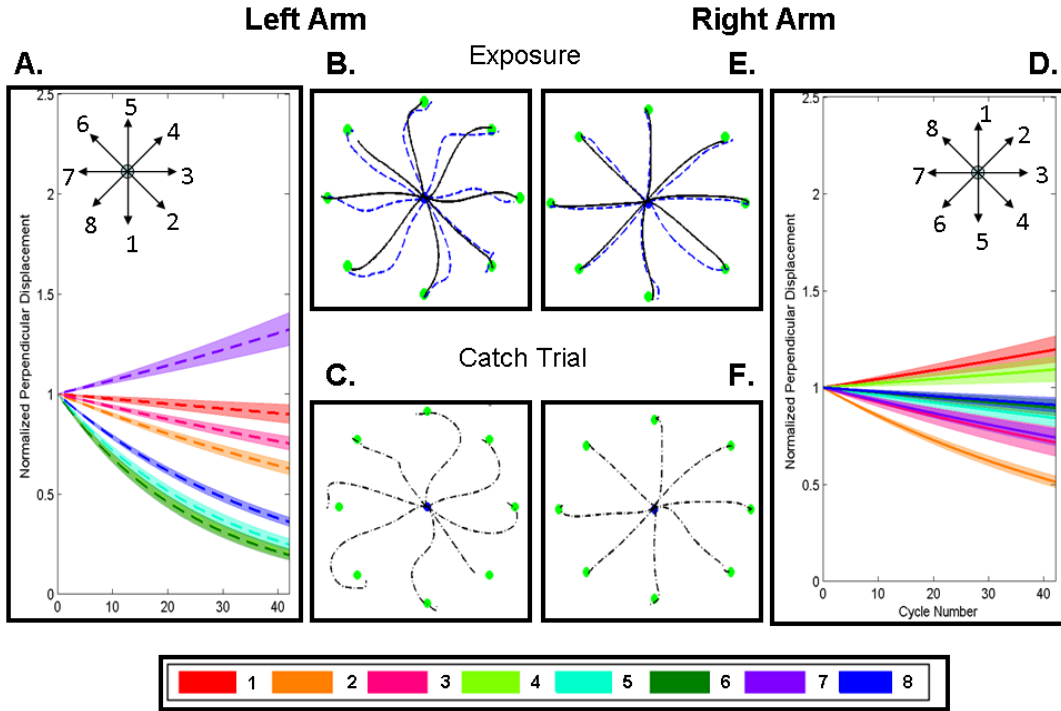


Figure 12: Bilateral Left. (a/d) Left/Right index finger normalized perpendicular displacement (mean \pm standard error) for each target direction averaged across subjects. (b/e) Left/Right index finger displacement for a single subject averaged over the first four cycles of the *exposure* phase (dashed blue line) and over the last four cycles of the *exposure* phase (solid black line). (c/f) Left/Right index finger displacement for a single subject averaged over the *catch trial* phase. Target direction labels are indicated for each arm according to the out-of-phase reaching pattern.

directions, there did not appear to be a consistent pattern with respect to the bilateral reaching tasks, in that in some directions performance worsened while in other directions it improved. Therefore, it may be more beneficial to consider the overall effect by comparing across target directions. Figure 13 (page 53) shows the results for the normalized perpendicular displacement for each group taken across targets and subjects. The results indicate that for the unilateral groups (blue lines, Fig. 13), rate of adaptation was significant for the right dominant arm ($y = \exp^{-0.0212 \pm 0.001 * x}$) and the left non-dominant arm ($y = \exp^{-0.0165 \pm 0.001 * x}$). The rate of adaptation for the right dominant arm was greater than that of the left non-dominant arm during unilateral reaching. For the bilateral right group (red line, Fig. 13), the rate of adaptation was significant for the right dominant arm and the normalized perpendicular displacement decreased with training ($y = \exp^{-0.0234 \pm 0.001 * x}$), while for the left non-dominant arm regression line was also significant, however the normalized perpendicular displacement worsened ($y = \exp^{0.00653 \pm 0.006 * x}$). This may potentially be due to the lack of attention to the non-dominant arm which did not experience the force environment. This suggestion will be addressed when considering movement time and reaction time differences between the arms across groups (page 56). For the bilateral left group (green line, Fig. 13), the rate of adaptation was significant for the left non-dominant arm ($y = \exp^{-0.0138 \pm 0.001 * x}$) but the regression line was not significant for right dominant arm ($y = \exp^{0.0005 \pm 0.001 * x}$). This indicates that the right dominant arm does not experience learning during the bilateral reaching task when only the left non-dominant arm experiences a force environment. The comparison of these learning curves against each other showed that for the right dominant arm there is significant difference between the unilateral right and the bilateral right groups ($p < 0.05$). The only difference between these groups were that in the unilateral right group, the left non-dominant arm was stationary (provides static sensory feedback), and in the bilateral right group, the left non-dominant arm

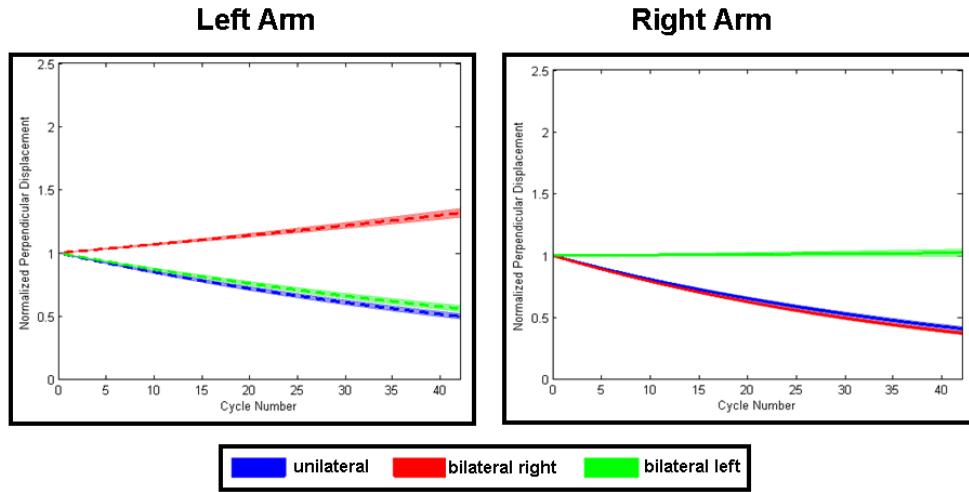


Figure 13: Normalized perpendicular displacement (mean \pm standard error) averaged across all targets for the left non-dominant and right dominant arm for the unilateral (blue line), bilateral right (red line) and the bilateral left (green line) groups.

was moving thereby providing movement related position feedback to the CNS. Since rate of adaptation was significantly slower for the dominant arm during the unilateral right tasks than the bilateral tasks, transfer of learning potentially occurred from the non-dominant to the dominant arm. When considering the left non-dominant arm, there was no significant difference between the unilateral left and bilateral left groups ($p = 0.989$). Therefore, transfer of learning potentially did not occur from the right dominant to the left non-dominant arm. This proposition supports the *dynamic dominance hypothesis*, in that perpendicular displacement information is passed from the left non-dominant arm to the right dominant arm, thereby improving the motor adaptation of the right dominant arm when movement related position feedback was available from the untrained arm.

Since motor adaptation did not occur for the arms that did not experience a force environment during the bilateral reaching tasks, those were not included in the aftereffect evaluation. The two-way (experimental group x arm) ANOVA conducted

on the aftereffect compared the group (unilateral and bilateral single force environment) with the arm (right dominant and left non-dominant) independent variables and revealed that the unilateral group had a significantly larger aftereffect than the bilateral group $F(1, 316) = 11.92, p < 0.01$ (Fig. 14, page 55). Also, the right dominant arm had a significantly larger aftereffect than the left non-dominant arm $F(1, 316) = 14.55, p < 0.01$. In order to determine whether the right dominant arm aftereffect differed between the unilateral and bilateral groups, an independent t-test was conducted and revealed that it was significantly different $t(80) = 2.36, p < 0.05$. For the left non-dominant arm there was also a significant difference in the aftereffect between the unilateral and bilateral groups $t(80) = 2.57, p < 0.05$. These results indicate that the aftereffect for the unilateral reaching conditions were consistently and significantly larger than for the bilateral reaching conditions. This would imply that motor adaptation was more complete during the unilateral reaching tasks than the bilateral reaching tasks. Typically aftereffects have only been used in unilateral studies to quantify the quality of motor adaptation. A key component to this is that during the *catch trial* the response of the arm is solely dependent on the fact that the force environment is suddenly removed. Calculating the aftereffect for a bilateral task may be problematic, because of the influence one arm may have on the other arm when the force environment is suddenly removed. Therefore, aftereffect calculation for bilateral tasks need to be interpreted with caution. Comparisons made between groups may be problematic, seeing that the results of this study indicate that the direction and the type of information shared between the limbs depend largely on the sensory feedback available. However, comparisons within an experimental group could be done.

A two-way (experimental group x arm) ANOVA was conducted on the final position error as a dependant variable during the *exposure* phase across groups and arms, and no statistical significance was observed ($p > 0.05$). A two-way ANOVA

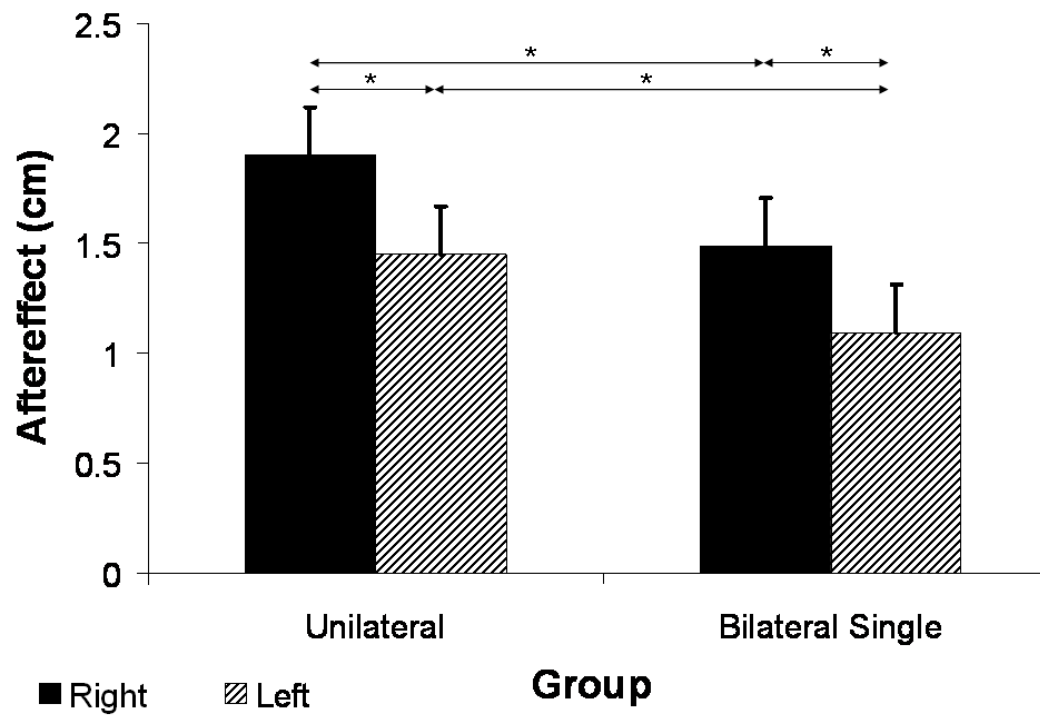


Figure 14: Aftereffects are shown for the right dominant arm (solid) and the left non-dominant arm (hashed) for the unilateral and bilateral single groups when only one arm experiences the force environment. * $p < 0.05$

was also conducted on the final position error during the *catch trial* phase by comparing groups and arms $F(2, 54) = 7.06, p < 0.01$. Upon further investigation it was found that for the right dominant arm there was no significant differences between groups $F(2, 27) = 1.75, p = 0.193$. However, for the left non-dominant arm there was a significant difference in final position error between groups $F(2, 27) = 6.84, p < 0.01$ during the *catch trials*. A Tukey HSD post-hoc test revealed that the final position error of the left non-dominant arm was significantly greater for the bilateral left group when compared to the unilateral left or the bilateral right groups (Fig. 15, page 57). Therefore the movement related position feedback from the dominant arm interfered with the performance of the left non-dominant arm during the *catch trial* phase of the bilateral left group. A one-way ANOVA was conducted for the final position error of the left non-dominant arm during the *pre-exposure* phase. The results showed that there was significant differences between the groups for the left non-dominant arm $F(2, 27) = 10.194, p < 0.01$. A Tukey HSD post-hoc test revealed that the final position error of the left non-dominant arm was significantly smaller for the unilateral left group when compared to the bilateral right and bilateral left groups. Therefore, the movement related position feedback from the dominant arm interfered with the performance of the left non-dominant arm when both were in the natural environment. Therefore, the right dominant arm interferes with the performance of the left non-dominant arm during the *pre-exposure* and *catch trial* phases of the bilateral left group, but not the *exposure* phase. Because of this interference during the *catch trials*, all aftereffect calculations need to be interpreted with caution.

A two-way ANOVA was conducted on the reaction time during the *exposure* phase across groups and arms, and no statistical significance was observed ($p > 0.05$). Since there was no difference in reaction time between the arms regardless of the group, it is plausible that divided attention was not a contributing factor in these experiments. A two-way ANOVA was conducted on the reaction time during the *catch trial* phase

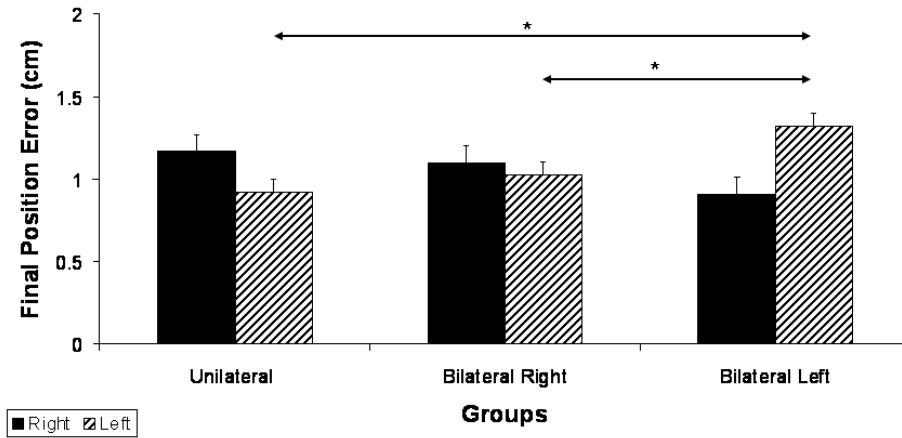


Figure 15: Final position error of the right dominant arm (solid) and the left non-dominant arm (hashed) during catch trials for aim 1. * $p < 0.05$

across groups and arms, and significant difference was observed between the groups $F(2, 54) = 4.56$, $p < 0.05$. A Tukey HSD post-hoc test revealed that the reaction time for the bilateral right group was significantly longer than for the unilateral groups. Upon further examination this difference was due to a difference for the right dominant arm $F(2, 27) = 4.14$, $p < 0.05$, but not for the left non-dominant arm $F(2, 27) = 1.206$, $p = 0.315$. Therefore, during the *catch trial* it takes subjects in the bilateral right group longer to respond with their right dominant arm than the unilateral right group. This may be due to interference from the non-dominant arm on the dominant arm. However, since there is no significant difference in reaction time between the left non-dominant and right dominant arms, divided attention is not a determining factor in these experiments.

A two-way ANOVA was conducted on the movement time during the *exposure* phase across groups and arms, and no statistical significance was observed ($p > 0.05$). A two-way ANOVA was conducted on the movement time during the *catch trial* phase across groups and arms, and a significant interaction affect was observed $F(2, 54) =$

5.804, $p < 0.05$. A Tukey HSD post-hoc revealed that the movement time for the left non-dominant arm was shorter during the bilateral right group when compared to the bilateral left group. Upon following the interaction, results revealed that there was no difference across groups for the right dominant arm $F(2, 27) = 0.334$, $p = 0.719$ during the *catch trial* phase. However, for the left non-dominant arm movement time was significantly shorter during the *catch trial* phase for the bilateral right group than the other groups $F(2, 27) = 10.538$, $p < 0.01$. Upon examining this further, it was found that for the left non-dominant arm for the bilateral group, that there was no significant difference in movement time between the *pre-exposure*, *exposure* and *catch trial* phases $F(2, 27) = 0.393$, $p = 0.678$. Therefore, the reason as to why the left non-dominant arm movement time is shorter for the bilateral right group, when compared to the other groups is because it was never exposed to a force environment. These results are consistent with a previous study by Kelso et al. (1979) [81] where there was no difference in movement time between the arms $p > 0.05$ given that the target sizes and the distance to the targets were the same between the arms. Although, subjects were moving in an out-of-phase pattern this did not influence their performance because there were no differences in movement time between unilateral and bilateral groups during training.

A two-way ANOVA was conducted on the peak velocity during the *exposure* phase and the *catch trial* phase across groups and arms, and no statistical significance was observed ($p > 0.05$). A two-way ANOVA was conducted on the position of the peak velocity during the *exposure* phase and the *catch trial* phase across groups and arms, and no statistical significance was observed ($p > 0.05$).

3.4 Discussion

The question that was posed was whether transfer of learning occurs during bilateral reaching? Four experimental groups were created to examine whether the sensory

feedback of one arm affected the motor adaptation of the other arm. The unilateral reaching groups involved only one arm training in a force environment while the other arm remained stationary in the starting position. The bilateral reaching groups involved reaching with both arms while only one arm experienced a force environment. By comparing the performance of the training arm between the unilateral and bilateral groups, it was possible to determine whether the movement related position feedback of the arm without the force environment affected the motor adaptation of the arm training in the force environment. Results showed that the rate of adaptation was significantly slower for the dominant arm for the unilateral reaching group than for the bilateral reaching group ($p < 0.05$, Fig. 13, page 53). This indicated that the movement related position feedback from the non-dominant arm improved significantly the motor adaptation of the dominant arm during the bilateral reaching task. Therefore, it is plausible that transfer of learning occurred from the non-dominant to the dominant arm. Movement related position feedback from the dominant arm did not affect the rate of adaptation of the non-dominant arm. These results supported the notion that trajectory specific information (in terms of perpendicular displacement) was transferred from the left non-dominant arm to the right dominant arm, but not vice versa during bilateral tasks.

As for the quality of motor adaptation, the aftereffect analysis revealed that motor adaptation was more complete for the unilateral groups than the bilateral groups, and that the aftereffect for the dominant arm was greater than the aftereffect for the non-dominant arm across groups. These results seem to contradict the rate of adaptation results, in that rate of adaptation of the dominant arm was greater for the bilateral right group than the unilateral right group. A plausible explanation for this may be that there was interference from one arm on the other arm during the catch-trial phase that distorted the aftereffect calculations. A key assumption in computing aftereffects are that the movement errors observed during the *catch trial* phase are

solely dependent on the degree to which the force environment had been learned in the *exposure* phase. Results of this study demonstrated that interference occurred from one arm to the other during the *catch trials*, and therefore the movement errors no longer were only due to the removal of the force environment. Therefore the aftereffects results of bilateral tasks needs to be interpreted with caution.

The results showed that for the final position error during the *exposure* phase there was no difference for the left non-dominant arm between the unilateral left and bilateral left groups. This would indicate that the dominant arm did not affect the motor adaptation of the non-dominant arm during the *exposure* phase. When both arms experienced the same natural environment (*pre-exposure* and *catch trial* phases), there was not a discrepancy in the external load feedback between the arms and it was observed that the right dominant arm interfered with the motor behavior of the left non-dominant arm. The final position error was worse during the bilateral task than the unilateral task. The difference between these two tasks are that during the unilateral task the right dominant arm does not move and therefore produces static sensory feedback, whereas for the bilateral task the right dominant arm provides movement dependent movement related position feedback, but not external load feedback. Presumably the CNS uses the sensory feedback from the right dominant arm to update the motor program of the left non-dominant arm, which results in increasing the endpoint final position error. This result suggests that final position information from the right dominant arm interferes with the left non-dominant arm controller and decreases the motor behavior in controlling reaching accuracy of the left non-dominant arm.

Studies on divided attention, have found that reaction times tended to be longer for bilateral tasks than unilateral tasks [174, 37, 82, 117, 161, 173, 106], due to an increased demand on the CNS to control additional degrees of freedom. Researchers have found that if a subject is instructed to focus attention on a single limb during

a bilateral task, the unattended limb would make greater movement errors [157]. In the current study, subjects were not instructed to fixate their eyes towards any specific limb or the center, but were instead left to self-select their preference. A limitation of this study is that, saccadic eye movements were not recorded to verify what subjects fixations points were. This information would have been useful, and should be considered for inclusion in future studies. However, reaction time may be considered as an alternative measure to address divided attention. The results indicated that there was no difference in reaction time ([81]) during the *exposure* phase between the arms or between the groups. Therefore, it is plausible that divided attention did not affect motor adaptation in this study.

The results from the current experiment demonstrated that transfer of learning occurred during bilateral reaching. Trajectory information transferred from the left non-dominant arm to the right dominant arm, but not vice versa. This supported the *callosal model*, which predicted that transfer of learning would occur in that direction. However, this was not the only direction in which information transfer was observed. The right dominant arm interfered with the left non-dominant arm, in that the final position error of the left non-dominant arm was worse for the bilateral task than the unilateral task. These results may be explained by the *dynamic dominance hypothesis*, which incorporates the notion that trajectory information is transferred from the left non-dominant arm to the right dominant arm, while final position information is transferred from the right dominant arm to the left non-dominant arm.

3.5 Conclusion

Transfer of learning does occur during bilateral reaching tasks. The trajectory information transferred from the left non-dominant arm to the right dominant arm during the *exposure* phase, but not vice versa. The dominant arm interfered with the final position performance of the non-dominant arm during the bilateral task when there

was no difference in the load feedback between the arms.

CHAPTER IV

AIM 2. DOES MOTOR LEARNING DEPEND ON WHETHER ONE OR BOTH ARMS EXPERIENCE THE FORCE ENVIRONMENT?

4.1 Introduction

During motor learning the Central Nervous System (CNS) is thought to compare the sensory feedback from the moving limb against the predicted feedback and updates the motor plan as needed in order to reduce movement error. Force environments are often used to perturb the system, in order to determine how movement errors are corrected over the course of practice in the force environment [155, 49]. Studies have shown that motor adaptation occurs in the stationary left non-dominant arm when it resists a force environment that is dependent on the velocity of the moving right dominant arm [10]. Therefore, it is plausible that sensory feedback from one arm may affect the motor adaptation of the other arm during bilateral tasks. When considering force perturbations and bilateral tasks, there are multiple combinations of how the force perturbation may be applied to the arms in order to feature different aspects of sensory feedback to the CNS. In this chapter, this issue is addressed by posing the question: Does motor adaptation depend on whether one or both arms experience the force environment?

In order to answer this question, two experimental conditions were investigated: (1) bilateral reaching single load and (2) bilateral reaching two loads. For the bilateral reaching single load condition, both arms are reaching to targets but only one arm learns the force environment and therefore the other arm provides movement related position feedback but not external load feedback. For the bilateral reaching two loads

condition, both arms are reaching to targets and both learn the force environment (intrinsic coordinate frame), while providing movement related position feedback and external load feedback to the CNS. The distinguishing factor here, is whether external load feedback is available from one or both the arms, depending on the force environment. It is predicted that when there is a difference in the sensory feedback between the arms, that the CNS takes longer to learn the force environments than when the sensory feedback is similar between the arms. The following specific aim and hypotheses addresses this issue:

Aim 2. Determine the effects of simultaneous learning of the intrinsic force environment by two arms on transfer of learning during bilateral reaching.

Hypothesis 2.1: When both arms learn the intrinsic force environment during bilateral reaching, motor adaptation of the dominant arm should be greater than when only the dominant arm learns the force environment during bilateral reaching.

Hypothesis 2.2: When both arms learn the intrinsic force environment during bilateral reaching, motor adaptation of the non-dominant arm should be greater than when only the non-dominant arm learns the force environment during bilateral reaching.

4.2 Method

Thirty (30) subjects were recruited and randomly assigned to one of three groups (Table 6, page 65):

- **Bilateral Right:** Both arms were moving, but only the right dominant arm learned a clockwise (CW) force environment, while the other arm did not experience a force environment.
- **Bilateral Left:** Both arms were moving, but only the left non-dominant arm learned a counter clockwise (CCW) force environment, while the other arm did not experience a force environment.

Table 6: Aim 2: Experimental Groups.

	Exposure		Catch Trial	
	Arm	Field	Arm	Field
Bilateral Reaching Single Load				
Bilateral Right	Right	CW	Right	Null
	Left	Null	Left	Null
Bilateral Left	Right	Null	Right	Null
	Left	CCW	Left	Null
Bilateral Reaching Two Loads				
Bilateral Intrinsic	Right	CW	Right	Null
	Left	CCW	Left	Null

- Bilateral Intrinsic: Both arms were moving, but the right dominant arm learned a clockwise (CW) force environment, while the left non-dominant arm learned a counter clockwise (CCW) force environment.

Both the bilateral right and bilateral left groups, were identical to that described in Chapter 4 (page 42). Therefore, the only new group is the bilateral intrinsic group.

The learning curve was determined by conducting a regression analysis on the normalized perpendicular displacement of the index finger as a function of the cycle number. The rate of adaptation was determined as the rate constant of the regression line. To compare whether the obtained learning curves differed between experimental conditions, the regression lines were compared using the Rosenbrock and Quasi-Newton method with least squares. The effects of the experimental groups and arm dominance on the aftereffects were tested using a two-way ANOVA. The aftereffect was calculated as the difference in the mean perpendicular displacement between the last four cycles of the *exposure* phase and that of the *catch trial* phase (measured in cm). Similar effects on all other performance variables measured during the *exposure* and the *catch trial* phases, were also studied using two-way ANOVA's.

4.3 Results

The typical index finger path of a subject in the bilateral intrinsic group is shown in figure 16, page 67. Large movement errors were observed during the initial exposure to the force environment, when the right dominant arm experienced a clockwise force environment and the left non-dominant arm experienced a counter clockwise force environment. The index finger path for both arms straightened out with training (Fig. 16.b/e). During the *catch trial* phase when the force environment was randomly removed, large movement errors were observed in both arms in the opposite direction compared to the movement errors during the initial exposure to the force environment (Fig. 16.c/f). This was an indication that motor adaptation occurred in both arms. The regression analysis revealed that the rate of adaptation of the normalized perpendicular displacement for all target directions across subjects were statistically significant ($p < 0.05$)(Fig. 16.a/d).

The results of the regression analysis for the other two groups, bilateral right and bilateral left, have been described in the previous chapter (Chapter 4, page 42). Figure 17 (page 69) shows the results for the normalized perpendicular displacement for each group taken across targets and subjects. The results indicated that for the bilateral right group (red line, Fig. 17), the rate of adaptation was significant ($p < 0.05$) for the right dominant arm and the normalized perpendicular displacement decreased with training ($y = \exp^{-0.234 \text{ } pm0.001*x}$), while for the left non-dominant arm the regression line was also significant, however the normalized perpendicular displacement worsened ($y = \exp^{0.00653 \text{ } pm0.006*x}$). Therefore, learning did not occur for the non-dominant arm in the bilateral right group. For the bilateral left group (green line, Fig. 17), the rate of adaptation was significant for the left non-dominant arm ($y = \exp^{-0.0138 \pm 0.001*x}$) but the regression line was not significant for the right dominant arm ($y = \exp^{0.0005 \text{ } pm0.001*x}$). This indicated that the right dominant arm

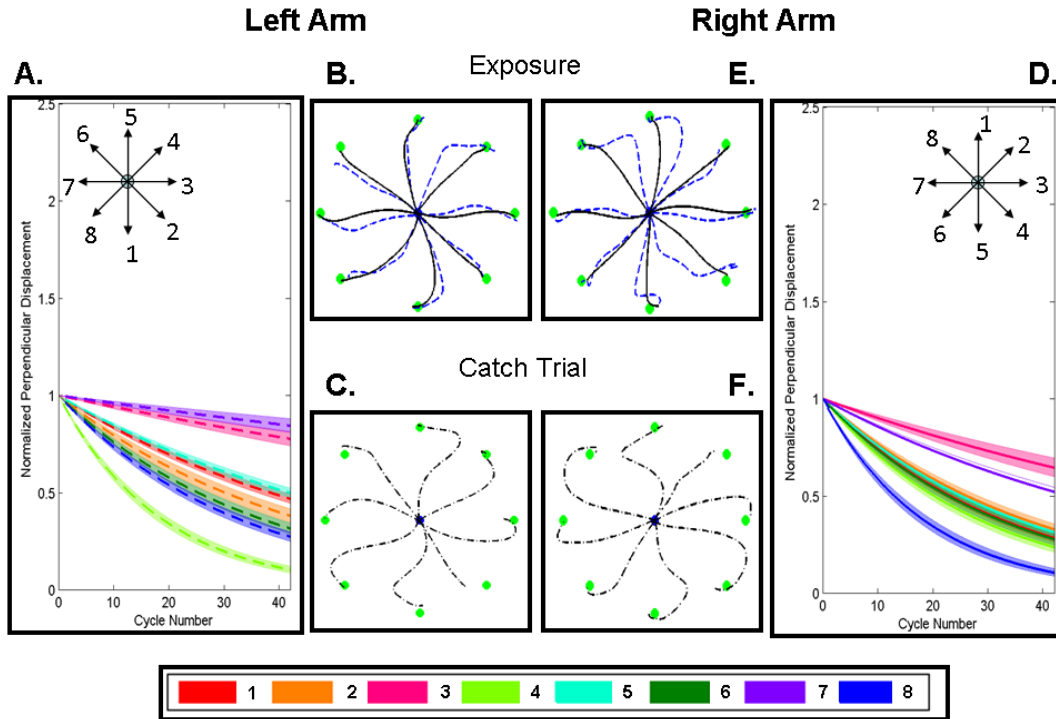


Figure 16: Bilateral Intrinsic. (a/d) Left/Right index finger normalized perpendicular displacement (mean \pm standard error) for each target direction averaged across subjects. (b/e) Left/Right index finger displacement for a single subject averaged over the first four cycles of the *exposure* phase (dashed blue line) and over the last four cycles of the *exposure* phase (solid black line). (c/f) Left/Right index finger displacement for a single subject averaged over the *catch trial* phase. Target direction labels are indicated for each arm according to the out-of-phase reaching pattern.

did not experience learning during the bilateral left group. For the bilateral intrinsic group (purple line, Fig. 17), the rate of adaptation was significant ($p < 0.05$) for the right dominant arm ($y = \exp^{-0.0263 \pm 0.001 * x}$) and the left non-dominant arm ($y = \exp^{-0.0191 \pm 0.001 * x}$). This indicated that both arms were able to learn the force environment at the same time. The comparison of these learning curves against each other showed that for the right dominant arm the rate of adaptation for the bilateral intrinsic group was significantly ($p < 0.05$) faster than for the bilateral right group. In addition, results indicated that for the left non-dominant arm that the rate of adaptation for the bilateral intrinsic group was significantly ($p < 0.05$) faster than for the bilateral left group. These results indicated that transfer of learning occurred in both directions - from the dominant arm to the non-dominant arm and from the non-dominant arm to the dominant arm - when movement related position feedback and external load feedback was available from both arms. The rate of adaptation for the right dominant arm was significantly greater than for the left non-dominant arm during the bilateral intrinsic group ($p < 0.05$). Thus, it seemed that the right dominant arm benefitted more from transfer of learning than the left non-dominant arm.

Since motor adaptation did not occur for the two arms that did not experience a force environment, these conditions were not included in the aftereffect evaluation. The two-way ANOVA conducted on the aftereffect compared the group (bilateral reaching single load and bilateral reaching two loads) with the arm (right dominant and left non-dominant) independent variables. The aftereffect of the right dominant arm was significantly greater than the aftereffect of the left non-dominant arm $F(1, 316) = 17.00$, $p < 0.01$. (Fig. 18). There was no statistically significant differences between the groups ($p = 0.295$), nor did the aftereffect differ within each arm when compared between the groups. This finding contradicts the previous results that there was a difference in rate of adaptation between the groups for each arm.

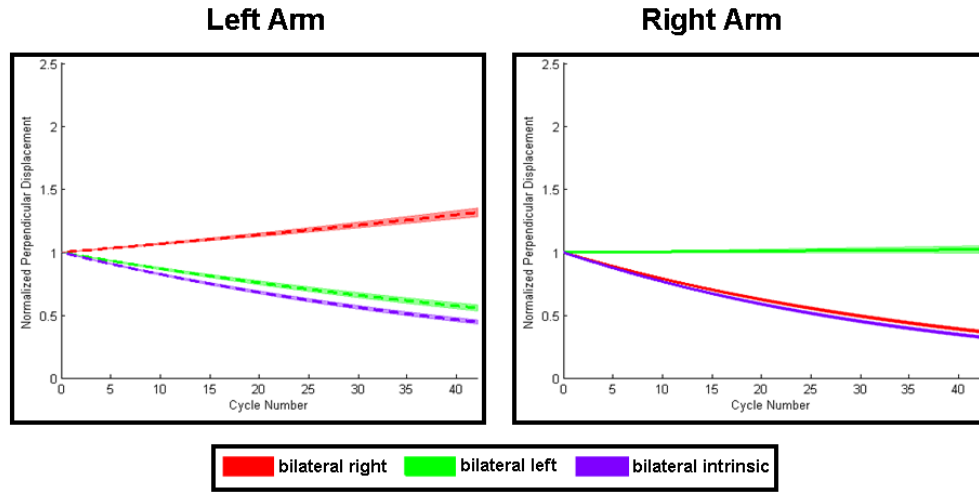


Figure 17: Normalized perpendicular displacement (mean \pm standard error) averaged across all targets for the left non-dominant and the right dominant arm for the bilateral right (red line), bilateral left (green line) and the bilateral intrinsic (purple line) groups.

However, when taking into consideration that transfer of learning occurred during the *catch trial*, it was not unexpected that there should be no difference in the aftereffect between groups. The only conclusion that may be drawn from the aftereffect results with confidence, was that motor adaptation was more complete for the right dominant arm than the left non-dominant arm.

A two-way ANOVA was conducted on the final position error during the *exposure* phase across groups and arms, and no statistical significance was observed ($p > 0.05$) between groups or arms. A two-way ANOVA was conducted on the final position error during the *catch trial*, and a significant interaction effect was observed between groups and arms $F(2, 54) = 4.099$, $p < 0.05$. The Tukey HSD post hoc test revealed, that during the *catch trial* the only significant difference in final position error was between the right dominant arm and the left non-dominant arm during the bilateral left group. Upon further investigation of the interaction effect, it was found that for the right dominant arm there was no significant differences between groups $F(2, 27) = 1.851$,

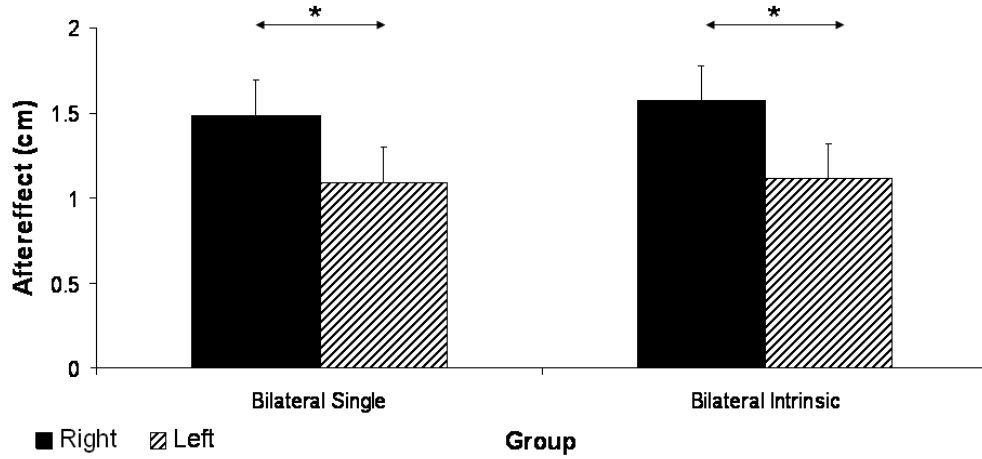


Figure 18: Aftereffects are shown for the right dominant arm (solid) and the left non-dominant arm (hashed) for the bilateral single groups (for the arm experiencing the force environment) and the bilateral intrinsic groups. * $p < 0.05$

$p = 0.176$. For the left non-dominant arm there was a significant effect across groups, $F(2, 27) = 4.04$, $p < 0.05$. A Tukey HSD post-hoc showed the final position error of the left non-dominant arm was significantly lower for the bilateral right group than the bilateral intrinsic group during the *catch trial*. This occurred probably because during the bilateral right group the left non-dominant arm never experienced a force environment. There were no differences in the final position error of the left non-dominant arm between the bilateral left and the bilateral intrinsic group.

A two-way ANOVA was conducted on the reaction time during the *exposure* phase across groups and arms, and no statistical significance was observed ($p > 0.05$). A two-way ANOVA was also conducted on the reaction time during the *catch trial* phase across groups and arms, and no statistical significance was observed ($p > 0.05$). Therefore, since there was no difference in the reaction time between groups or arms, divided attention was not a contributing factor to this set of experiments.

A two-way ANOVA was conducted on the movement time during the *exposure* phase across groups and arms, and no statistical significance was observed ($p > 0.05$). A two-way ANOVA was conducted on the movement time during the *catch trial*

phase, and a significant interaction effect was observed between the groups and arms $F(2, 54) = 7.5, p < 0.01$. There was no difference across groups for the right dominant arm $F(2, 27) = 2.064, p = 0.146$. However, for the left non-dominant arm movement time was significantly shorter during the *catch trial* phase for the bilateral right group than the other groups $F(2, 27) = 10.93, p < 0.01$. This conferred with what was demonstrated in the previous chapter (page 42), that the movement time for the left non-dominant arm for the bilateral right group was much faster, because in this experimental condition the non-dominant arm was never exposed to a force environment.

A two-way ANOVA was conducted on the peak velocity during the *exposure* phase and the *catch trial* phase across groups and arms, and no statistical significance was observed ($p > 0.05$). A two-way ANOVA was conducted on the position of the peak velocity during the *exposure* phase and the *catch trial* phase across groups and arms, and no statistical significance was observed ($p > 0.05$).

4.4 *Discussion*

The question that was posed at the outset of this chapter was: Does motor adaptation depend on whether one or both arms experience the force environment? The hypothesis stated that motor adaptation would be more complete when both arms experienced a force environment than when only one arm experienced the force environment. Three experimental groups were created, in two of which only one arm experienced a force environment while the other arm did not (bilateral right and bilateral left) and for the third group both arms experienced an intrinsic force environment (bilateral intrinsic). The results indicated that the rate of adaptation was significantly ($p < 0.05$) faster for both the non-dominant and the dominant arm during the bilateral intrinsic group than the bilateral left or bilateral right groups. Therefore, the research hypothesis is accepted. This improvement in rate of adaptation during the

bilateral intrinsic group, was likely due to transfer of learning occurring. It appears that trajectory information was transferred in both directions, from the dominant to the non-dominant arm and from the non-dominant arm to the dominant arm when both arms experienced an intrinsic force environment. This would seem to contradict what has been proposed by Sainburg and Wang, who demonstrated that trajectory information is passed from the left non-dominant to the right dominant arm [142] for a unilateral visuomotor perturbation task. Since trajectory information was shared from the right dominant arm to the left non-dominant arm, perhaps this information may be modulated based on the sensory feedback that each arm provides to the CNS. If this is the case, then the CNS would need to be able to compare the sensory feedback against the predicted feedback for each of the arms and then compare the results between the arms.

4.5 Conclusion

Transfer of learning occurred in both direction, from the dominant arm to the non-dominant arm and the non-dominant arm to the dominant arm, when movement related position feedback and external load feedback was available from both arms, when the force environment was applied in the intrinsic environment. The dominant arm had a greater rate of adaptation than the non-dominant arm. Therefore motor adaptation for the right dominant arm was more complete than the left non-dominant arm. Both arms were able to learn the force environments they were placed in at the same time. The next question to be addressed is, does the direction in which the force is applied have an effect?

CHAPTER V

AIM 3. DOES THE DIRECTION OF THE FORCE AFFECT BILATERAL MOTOR LEARNING?

5.1 Introduction

Researchers have found that transfer of learning during reaching tasks in a novel force environment depended on the direction of the force environment. Burgess et al. (2007) demonstrated that transfer of learning occurred from a bilateral to a unilateral reaching task when the same extrinsic forces were applied to the arms [19]. Transfer of learning has also been shown to occur from the dominant to the non-dominant arm in a unilateral reaching study, but only in the extrinsic coordinate frame but not in an intrinsic coordinate frame [28]. Fine and Thoroughman, demonstrated that the direction but not the magnitude of the force environment affected motor behavior during a unilateral reaching study [49]. Therefore, the direction in which the force environment was applied to the arms seemed to affect unilateral motor adaptation. The question becomes, does the direction of the force environment (extrinsic versus intrinsic) affect bilateral motor adaptation?

In order to answer this question, two experimental conditions were investigated: (1) bilateral intrinsic and (2) bilateral extrinsic. For the bilateral intrinsic experimental condition, both arms moved and both arms experienced a force environment in the intrinsic coordinate frame (i.e. the force environment was applied in the joint space). For the bilateral extrinsic experimental condition, both arms moved and both arms experienced a force environment in the extrinsic coordinate frame (i.e. the force environment had the same direction, clockwise, on both the arms). Based on the literature discussed above [19, 28, 49] it was predicted that transfer of learning would

Table 7: Aim 3: Experimental Groups.

	Exposure		Catch Trial	
	Arm	Field	Arm	Field
Bilateral Intrinsic	Right	CW	Right	Null
	Left	CCW	Left	Null
Bilateral Extrinsic	Right	CW	Right	Null
	Left	CW	Left	Null

occur from the dominant to the non-dominant arm if both arms learned the task in the extrinsic coordinate frame. The following specific aim and hypothesis addresses this issue:

Aim 3. Determine the effects of extrinsic and intrinsic force environments on transfer of learning during bilateral reaching.

Hypothesis 3.1: When both arms learn the force environment during bilateral reaching, transfer of learning should be greater for the extrinsic force environment compared to the intrinsic force environment.

5.2 *Method*

Twenty (20) subjects were recruited and randomly assigned to one of two groups (Table 7, 74):

- **Bilateral Intrinsic:** Both arms were moving, but the right dominant arm learned a clockwise (CW) force environment, while the left non-dominant arm learned a counter clockwise (CCW) force environment.
- **Bilateral Extrinsic:** Both arms were moving and both arms experienced a clockwise (CW) force environment.

The bilateral intrinsic group, was identical to that described in chapter 5 (page 63). Therefore, the only new group was the bilateral extrinsic group.

The learning curve was determined by conducting a regression analysis on the normalized perpendicular displacement of the index finger as a function of the cycle number. The rate of adaptation was determined as the rate constant of the regression line. To compare whether the obtained learning curves differed between experimental conditions, the regression lines were compared using the Rosenbrock and Quasi-Newton method with least squares. The effects of the experimental groups and arm dominance on the aftereffects were tested using a two-way ANOVA. The aftereffect was calculated as the difference in the mean perpendicular displacement between the last four cycles of the *exposure* phase and that of the *catch trial* phase (measured in cm). Similar effects on all other performance variables measured during the *exposure* and the *catch trial* phases, were also studied using two-way ANOVA's.

5.3 Results

The typical index finger path of a subject in the bilateral extrinsic group is shown in figure 19, page 76. During initial exposure to the force environment, when both arms experienced a clockwise force environment, large movement errors were observed. The index finger path for both arms straightened out with training (Fig. 19.b/e). During the *catch trial* phase when the force environment was randomly removed, large movement errors were observed in both arms in the opposite direction compared to the movement errors during the initial exposure to the force environment (Fig. 19.c/f). This was an indication that motor adaptation occurred in both arms. The regression analysis revealed that the rate of adaptation of the normalized perpendicular displacement for all target directions across subjects were statistically significant ($p < 0.05$) (Fig. 19.a/d). Similar results for the bilateral intrinsic group have been discussed in the previous chapter (page 63).

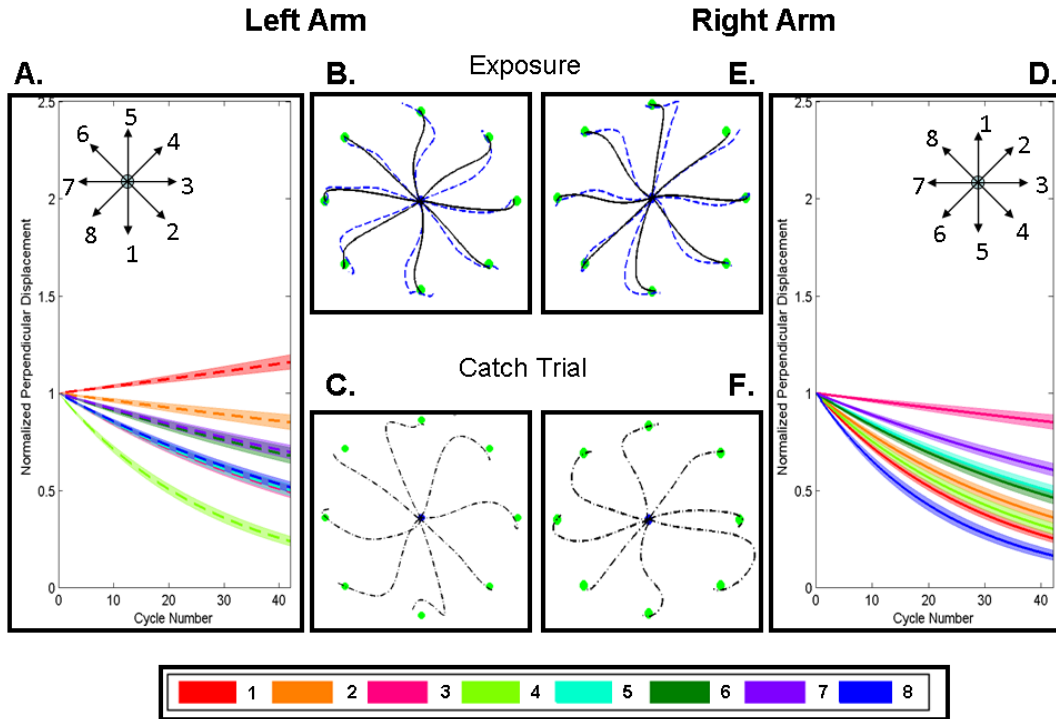


Figure 19: Bilateral Extrinsic. (a/d) Left/Right index finger normalized perpendicular displacement (mean \pm standard error) for each target direction averaged across subjects. (b/e) Left/Right index finger displacement for a single subject averaged over the first four cycles of the *exposure* phase (dashed blue line) and over the last four cycles of the *exposure* phase (solid black line). (c/f) Left/Right index finger displacement for a single subject averaged over the *catch trial* phase. Target direction labels are indicated for each arm according to the out-of-phase reaching pattern.

Figure 20 (page 78) shows the results for the normalized perpendicular displacement for each group taken across targets and subjects. For the bilateral intrinsic group (purple line, Fig. 20), the rate of adaptation was significant ($p < 0.05$) for the right dominant arm ($y = \exp^{-0.0263 \pm 0.001 * x}$) and the left non-dominant arm ($y = \exp^{-0.0191 \pm 0.001 * x}$). This indicated that both arms were able to learn the force environment at the same time. For the bilateral extrinsic group (orange line, Fig. 20), the rate of adaptation was significant ($p < 0.05$) for the right dominant arm ($y = \exp^{-0.0202 \pm 0.001 * x}$) and the left non-dominant arm ($y = \exp^{-0.0108 \pm 0.001 * x}$). This indicated that both arms were able to learn the force environment at the same time. The comparison of these learning curves against each other showed that for the right dominant arm there was no significant difference between the bilateral intrinsic and the bilateral extrinsic groups ($p = 0.802$). For the left non-dominant arm, rate of adaptation of the bilateral extrinsic group was significantly slower than for the bilateral intrinsic group ($p < 0.05$). Therefore, the dominant arm interfered with the motor adaptation of the non-dominant arm during the bilateral extrinsic experimental condition. The rate of adaptation of the right dominant arm was greater than the rate of adaptation of the left non-dominant arm for both the bilateral intrinsic and extrinsic groups ($p < 0.05$).

The aftereffect was compared between the experimental groups (bilateral intrinsic and bilateral extrinsic) and the arms (right dominant and left non-dominant). The aftereffect of the right dominant arm was significantly greater than that of the left non-dominant arm $F(1, 316) = 14.52$, $p < 0.01$ (Fig. 21, page 78). There was no statistical significance observed between the groups ($p = 0.3384$). The aftereffect was not sensitive enough to measure differences in quality of motor adaptation between different bilateral tasks, because of the transfer of learning or interference that occurred during the *catch trials*.

There was no significant differences in the final position error between the groups

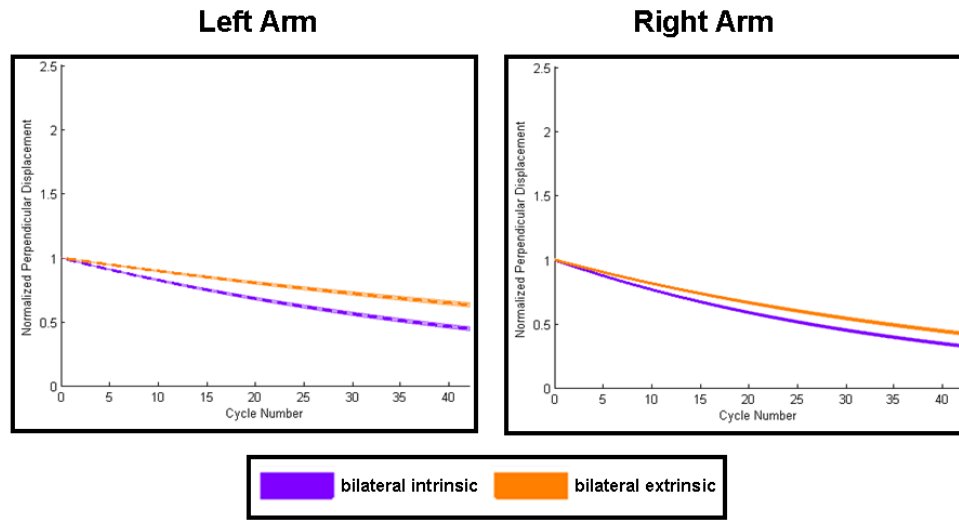


Figure 20: Normalized perpendicular displacement (mean \pm standard error) averaged across all targets for the left non-dominant and the right dominant arm for the bilateral intrinsic (purple line) and the bilateral extrinsic (orange line) groups.

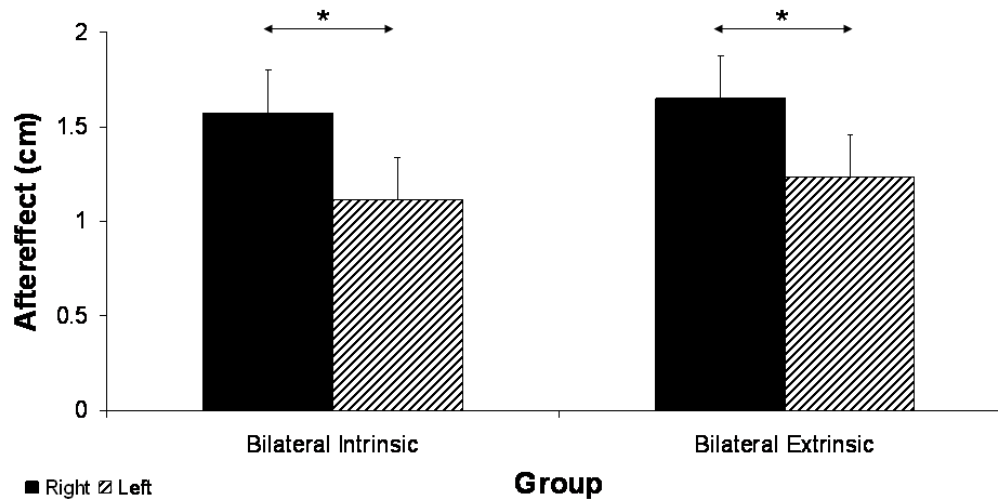


Figure 21: Aftereffects are shown for the right dominant arm (solid) and the left non-dominant arm (hashed) for the bilateral intrinsic and bilateral extrinsic groups.
* $p < 0.05$

and arms for the *exposure* or *catch trial* phases ($p > 0.05$). There was no significant differences in the reaction time between groups and arms for the *exposure* and *catch trial* phases ($p > 0.05$). Therefore, divided attention is not likely to be a contributing factor. Also, no significant difference was observed for the movement time between groups and arms for the *exposure* and *catch trial* phases ($p > 0.05$).

A two-way ANOVA was conducted on the peak velocity during the *exposure* phase and a statistically significant interaction effect between the experimental groups and arms was observed ($F(1, 36) = 4.676$, $p < 0.05$). However, upon further examination there was no difference in peak velocity of the left non-dominant arm between groups ($p = 0.208$), nor of the right dominant arm ($p = 0.074$). A post-hoc Tukey HSD test did not reveal any significant interactions either. Therefore, it was concluded that during the *exposure* phase, there was no difference in the peak velocity between the arms and groups. A two-way ANOVA was conducted on the peak velocity for the *catch trial* phase across groups and arms, and no significant difference was observed ($p > 0.05$). There was no significant difference in the peak velocity position between experimental groups and arms for the *exposure* and the *catch trial* phases ($p > 0.05$).

5.4 Discussion

Previous studies have indicated that transfer of learning during a unilateral task occurred from the right dominant arm to the left non-dominant arm in the extrinsic coordinate frame but not the intrinsic coordinate frame [19, 95, 28]. This chapter considered whether similar results would hold true for bilateral reaching tasks, and addressed the question: Does the direction of a novel force environment (extrinsic vs intrinsic) affect bilateral motor adaptation? In order to answer this question, two experimental groups were studied, where one group experienced force environments in the intrinsic coordinate frame (bilateral intrinsic) and the other group experienced the force environments in the extrinsic coordinate frame (bilateral extrinsic). When

both arms learn the force environment during bilateral reaching, transfer of learning should be greater for the extrinsic force environment compared to the intrinsic force environment. Results demonstrated that the rate of adaptation of the bilateral intrinsic task by the left non-dominant arm was significantly faster than that of the bilateral extrinsic task. This result suggested that the dominant arm interfered with the motor adaptation of the non-dominant arm when the extrinsic forces were applied to both arms. Thus, the research hypothesis must be rejected. For the dominant arm, there was no difference in the rate of adaptation between the two experimental groups, therefore, the non-dominant arm neither interfered nor helped the motor adaptation of the dominant arm. These results demonstrated that the direction in which the force environments were applied to the arms, did affect the motor adaptation of the non-dominant arm but not the dominant arm.

The aftereffect results showed that there was no difference in the quality of motor adaptation between the groups. However, the right dominant arm did have larger aftereffects than the left non-dominant arm. This corresponds to the rate of adaptation results, in that the rate of adaptation for the right dominant arm was faster than the rate of adaptation for left non-dominant arm. Therefore, the right dominant arm learned and performed bilateral tasks better than the left non-dominant arm.

5.5 Conclusion

The rate of adaptation by the non-dominant arm was faster for the bilateral intrinsic group than for the bilateral extrinsic group. The rate of adaptation for the dominant arm did not differ between the experimental groups. It appears therefore that the sensory movement related position feedback and force feedback from the dominant arm interfered with the motor adaptation of the non-dominant arm during the bilateral extrinsic task. Thus the direction of the force environment affects the motor behavior of the non-dominant arm but not the dominant arm.

CHAPTER VI

GENERAL TRENDS

6.1 *Introduction*

Studies on motor learning have shown that there may be other contributing factors such as age [152], gender [107] and handedness [118] that can affect motor behavior. These factors were examined to see whether they may have biased the results of this study.

6.2 *Method*

All of the groups, as outlined in Chapter 3 (Table 3, page 38), were considered in these analyses. The correlation analyses were conducted between age and handedness (determined by the Edinburgh Inventory) and the following performance variables: (1) rate of adaptation, (2) final position error, (3) movement time, (4) reaction time, (5) peak velocity and (6) peak velocity position. T-tests were conducted to see whether the performance variables differed between gender.

6.3 *Results*

The rate of adaptation data were only considered for those experimental groups where the right dominant arm demonstrated motor adaptation. The following groups were included in the analysis: unilateral right, bilateral right, bilateral intrinsic and bilateral extrinsic. There was no statistically significant correlation between the rate of adaptation and age ($r = 0.08$, $p = 0.543$), handedness ($r = -0.0697$, $p = 0.597$) nor was there a statistical difference in rate of adaptation for gender ($t(58) = -0.086$, $p = 0.932$). The rest of the performance variables were correlated with age, handedness and gender using data from all groups. The final position error did not

correlate with age ($r = 0.17$, $p = 0.1$), handedness ($r = 0.05$, $p = 0.61$) nor was there a statistical difference in final position error for gender ($t(98) = 0.708$, $p = 0.48$). Reaction times did not correlate with age ($r = 0.03$, $p = 0.799$), handedness ($r = -0.02$, $p = 0.806$) nor was there a statistical difference in reaction time for gender ($t(98) = -1.245$, $p = 0.216$). Movement time did not correlate with age ($r = 0.19$, $p = 0.064$) or handedness ($r = -0.17$, $p = 0.096$). Males tended to have shorter movement times (599.93 ± 90.1 milliseconds) than females (659.63 ± 57.28 milliseconds) ($t(98) = -3.25$, $p < 0.05$). There was no significant difference in movement time between the experimental groups ($p = 0.308$), since there was an almost equal distribution of males and females in each group. Therefore, gender did not bias the results of movement time in this study. The peak velocity did correlate with age, in that older individuals tended to have lower peak velocities, however the correlation coefficient was low ($r = -0.25$, $p = 0.012$). To investigate further the effects of age and experimental group on peak velocity, a two-way ANOVA was conducted on peak velocity. The results indicated that age did not affect peak velocity between groups ($p > 0.05$). The peak velocity did not correlate with handedness ($r = 0.02$, $p = 0.855$). Males tended to have greater peak velocities (0.001663 ± 0.0025 cm/msec) than females (0.000646 ± 0.0017 cm/msec) ($t(98) = 1.99$, $p < 0.05$). Upon conducting a two-way ANOVA on peak velocity between groups and gender, no significant effects were found. Therefore, age, handedness and gender did not affect the peak velocity results. The peak velocity position did correlate with age ($r = -0.32$, $p < 0.01$) but not with handedness ($r = -0.09$, $p = 0.356$). There was no statistical difference in the peak velocity position for gender ($t(98) = 0.141$, $p = 0.88$). A two-way ANOVA was conducted on the peak velocity position to test the effects of age and groups. The results indicated that age did not affect the peak velocity positions between groups ($p > 0.05$). Therefore, the general conclusion was that age, handedness and gender did not affect the results of this study.

Handedness, as measured by the Edinburgh Inventory [118] was used to determine subjects' hand preference. On average across all groups handedness did not affect the results, as shown above. However, handedness could affect the results within the groups. The following variables were found to significantly correlate with handedness within the following experimental groups:

- Unilateral Right: rate of adaptation for the right dominant arm ($r = 0.66$).
- Unilateral Left: none.
- Bilateral Right: reaction time for both arms ($r = -0.80$).
- Bilateral Left: final position error ($r = 0.46$) and movement time (-0.49).
- Bilateral Intrinsic: movement time ($r = -0.53$) and reaction time ($r = -0.45$).
- Bilateral Extrinsic: none.

For the unilateral right condition, where only the right dominant arm learned a force environment, rate of adaptation decreased with increasing the degree of right hand dominance. The more right handed someone was the shorter their reaction times were for the bilateral right and bilateral intrinsic experimental groups. For the bilateral left and bilateral intrinsic experimental groups, movement time was shorter the more right handed the individual was. The results were not consistent across all groups which may have been due to interference or transfer of learning from one arm to the other arm during the bilateral tasks. In addition when rate of adaptation, final position error, reaction time, and movement time were compared across all groups with respect to handedness, no statistical significance was observed ($p > 0.05$).

Movement time was analyzed between experimental phases across all of the experimental groups for each arm. The results indicated that the movement time for the right dominant arm was longer for the *catch trial* phase (739.433 ± 50.43 msec) compared to the *pre-exposure* (597.63 ± 27.52 msec) and *exposure* phases ($606.75 \pm$

30.02 msec) across all groups $F(2, 135) = 22.533, p < 0.05$ (Fig. 22, page 85). The results of the two-way ANOVA on movement time of the left non-dominant arm revealed that there was a significant interaction effect between the experimental groups and the phases $F(8, 135) = 2.123, p < 0.05$ (Fig. 23, page 86). When this interaction was followed, it was found that the movement time for the left non-dominant arm during the *pre-exposure* phase and the *exposure* phase did not depend on the group ($p > 0.05$). However, the movement time of the left non-dominant arm did differ between groups for the *catch trial* phase $F(4, 45) = 6.287, p < 0.05$. A Tukey HSD post hoc test showed that the movement time of the left non-dominant arm was different for the bilateral right group when compared to the unilateral left and bilateral left groups. As has been discussed in chapter 4 (page 42), the left non-dominant arm's movement time did not change between the phases for the bilateral right group because it was not exposed to a force environment. For all other experimental groups, the left non-dominant arm experienced a force environment.

A one-way ANOVA was conducted on the peak velocity position of the left non-dominant arm across groups. Results indicated that there was a significant difference $F(4, 145) = 5.32, p < 0.05$ (Fig. 25, page 88). A bonferroni post-hoc test revealed that the peak velocity position of the left non-dominant arm was significantly greater for the unilateral left task than the bilateral intrinsic and bilateral extrinsic tasks. Therefore peak velocity of the left non-dominant arm occurred much sooner for the bilateral reaching groups when both arms were experiencing force environments than for the unilateral left group. This may be an indication that for the left non-dominant arm the bilateral tasks were more complicated to perform than the unilateral task. A one-way ANOVA was conducted on the peak velocity position of the right dominant arm, and revealed that there was no significant difference between groups $F(4, 145) = 2.09, p = 0.08$ (Fig. 24, page 87).

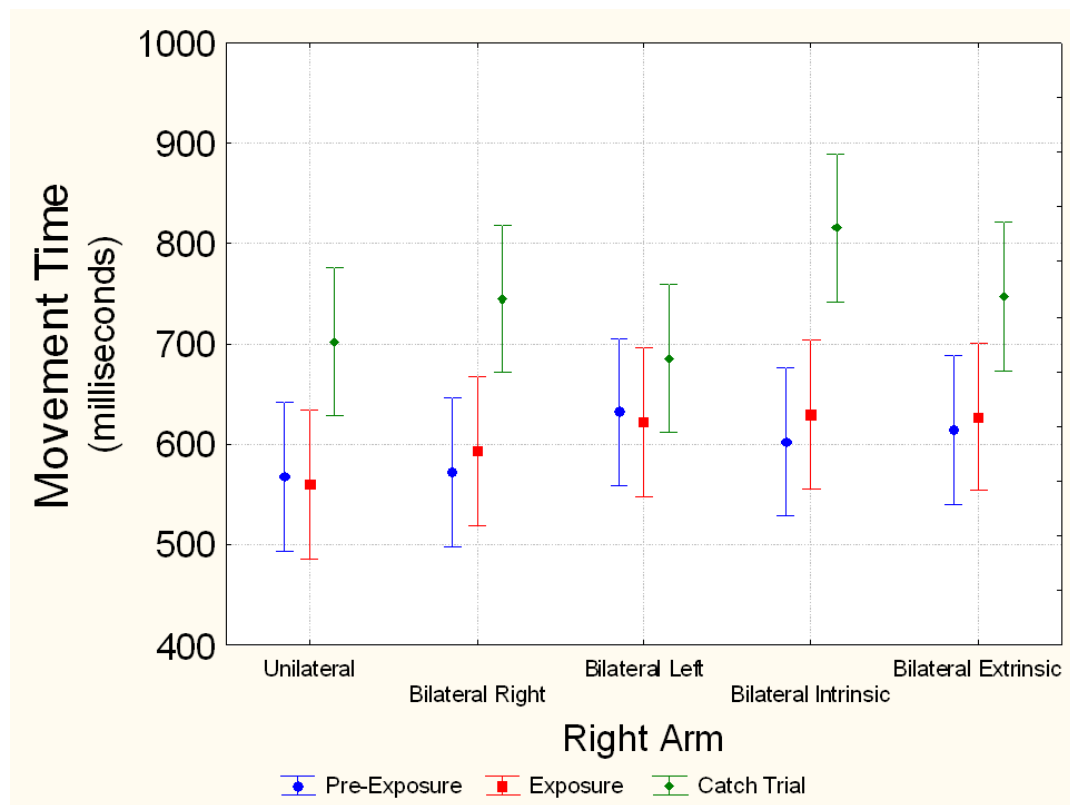


Figure 22: Movement time (mean \pm standard deviation) of the right dominant arm during the pre-exposure (blue), exposure (red) and catch-trial (green) phases for all the groups.

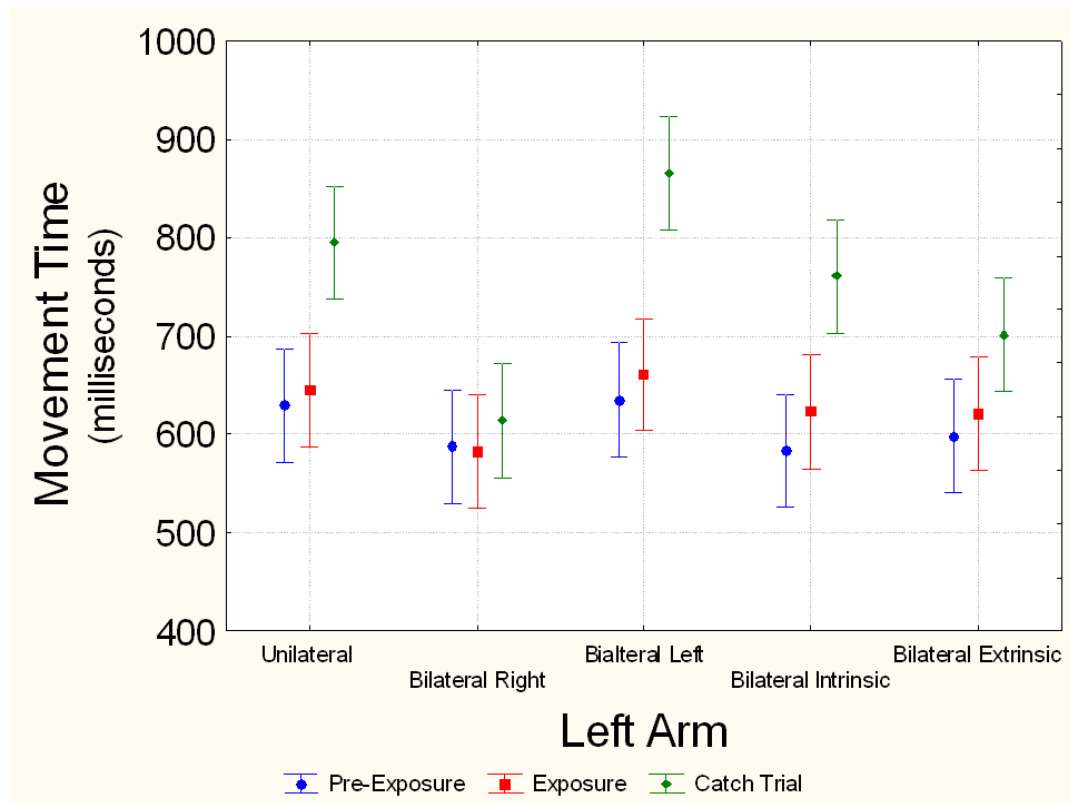


Figure 23: Movement time (mean \pm standard deviation) of the left non-dominant arm during the pre-exposure (blue), exposure (red) and catch-trial (green) phases for all the groups.

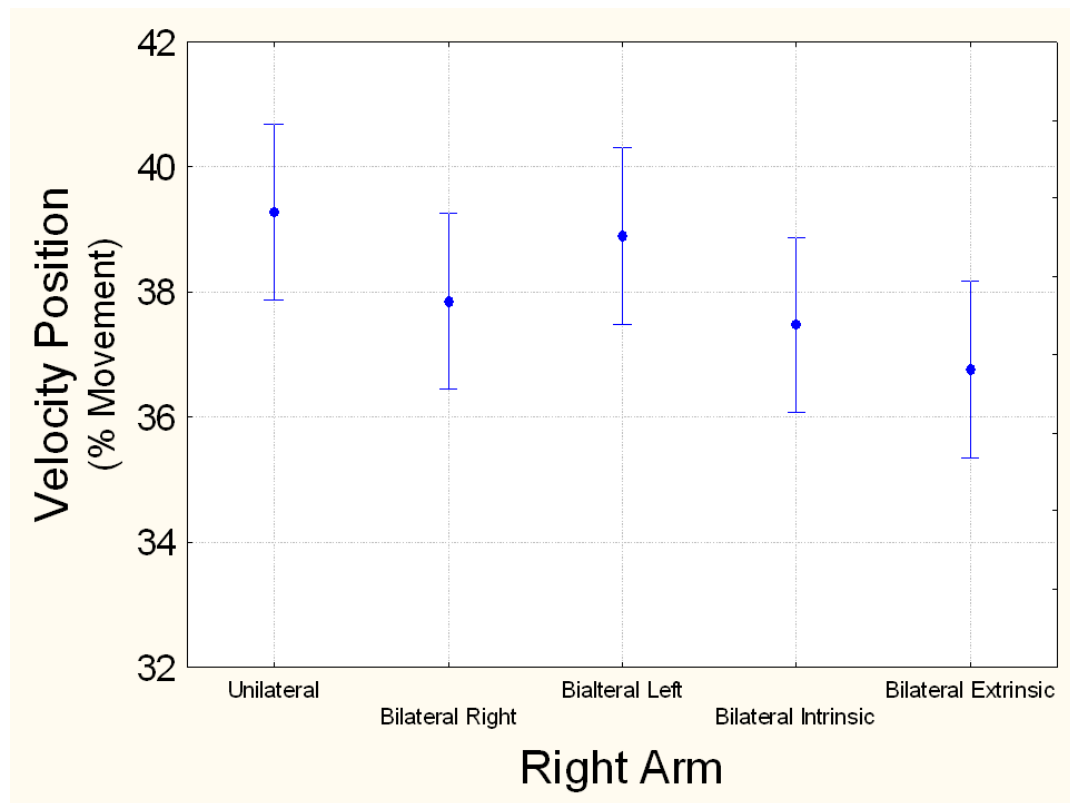


Figure 24: Peak velocity position (mean \pm standard deviation) for the right dominant arm for all groups.

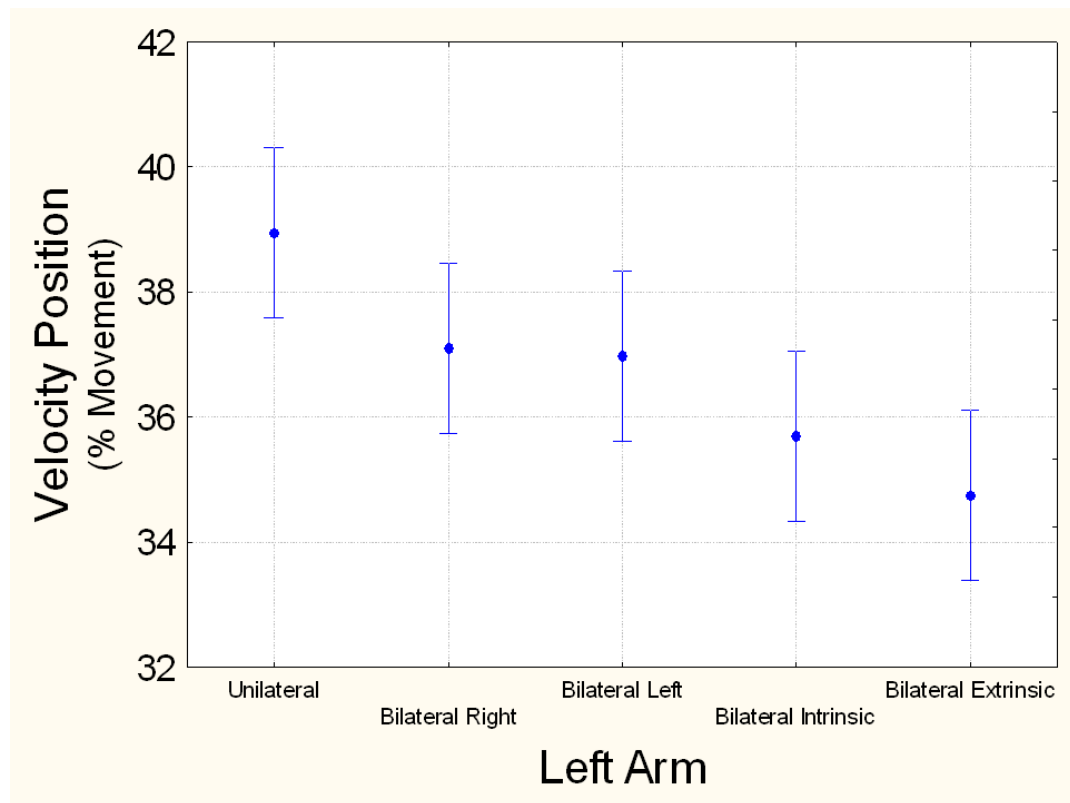


Figure 25: Peak velocity position (mean \pm standard deviation) for the left non-dominant arm for all groups.

6.4 *Discussion*

Age [152] and gender [107] have been shown to have potential influence on motor control and motor adaptation. In order to account for these possible confounding factors, all of the performance variables were correlated with age and gender. Results indicated that age and gender did not bias the results of this study.

One of the most common methods to determine handedness is by taking the Edinburgh Inventory [118]. Performance variables were correlated to the handedness score in order to determine if there were any significant relationships. Results indicated that there was no correlation between the handedness score and the performance variables when looking across all groups. However, when considering the correlation between the handedness score and the performance variables within each group, some variables significantly correlated with handedness. For the unilateral right group, when only the right arm moved, the rate of adaptation became slower the more right hand dominant the subjects were. For the bilateral groups, movement time and reaction time appeared to decrease with increasing levels of handedness. Therefore, the handedness score may have been an indication of how the subject responded to these tasks and the specific performance variables. However, further studies need to be conducted to determine how the Edinburgh Inventory correlates with performance variables. The results here are only valid for subjects that had handedness scores greater than 0.5 to 1, meaning they were strongly right hand dominant. It is unclear whether these performance variables would still correlate if subjects were strongly left hand dominant.

The design of the experimental task was so that the target size and the distance to the targets were similar between arms. This ensured that the speed and accuracy trade off would be the same between the arms [50] even though they were moving in an out-of-phase pattern [81]. Previous chapters have demonstrated that there was no difference in movement time between the arms and groups, except for the left

non-dominant arm of the bilateral right group. When considering movement time across groups and experimental phase, results indicated that for the right dominant arm and the left non-dominant arm the movement time was consistently longer for the *catch trial* phase than the *pre-exposure* and *exposure* phases across all groups. However, movement time did not differ between the arms across all groups. Therefore, movement time did not depend on the differences in force environments between the arms.

6.5 Conclusion

In conclusion, age, gender and handedness did not influence the results of this study, when comparing between arms and across groups.

CHAPTER VII

DISCUSSION

7.1 *Introduction*

The purpose of this study was to determine whether transfer of learning occurs during bilateral reaching tasks. It was hypothesized that transfer of learning would occur from the non-dominant to the dominant arm during bilateral tasks and that movement related position feedback and external load feedback from the arms would affect rate of adaptation and transfer of learning. Three groups of bilateral tasks were examined: (1) *unilateral reaching*, where one arm learned to reach in a novel force environment, while the other arm remained in a stationary position and therefore did not provide movement related position feedback or external load feedback; (2) *bilateral reaching single load*, where both arms performed reaching movements but only one arm learned a novel force environment and therefore the other arm provided movement related position feedback but not external load feedback; (3) *bilateral reaching two loads*, where both arms performed reaching movements and both arms learned a novel force environment, while providing movement related position feedback and external load feedback to the CNS.

7.2 *Transfer of learning*

The first part of the study has considered whether transfer of learning occurs during bilateral goal-directed reaching. The results of the study have demonstrated that transfer of learning occurs during bilateral goal-directed reaching tasks. The rate of adaptation, quantified by changes in the normalized perpendicular displacement of the right dominant arm, is greater for the *bilateral reaching single load* task than

for the *unilateral reaching* task (Fig. 13, page 53). This suggests that arm endpoint trajectory information of the left non-dominant arm enhances the adaptation of the right dominant arm to the force environment. This result supports the *callosal model* [58, 67, 175], which predicts that transfer of learning occurs from the left non-dominant arm to the right dominant arm. The arm endpoint final position error analysis suggests that there is interference from the right dominant arm to the left non-dominant arm. Specifically, the endpoint final position error of the left non-dominant arm was worse during *bilateral reaching single load* task when compared to the *unilateral reaching* task, for the pre-exposure and the catch-trial phases (Fig. 15, page 57, Table 5, page 45). For the exposure phase there was no difference in the endpoint final position error of the left non-dominant arm between the experimental tasks, when the left non-dominant arm experienced the force environment. The difference between these two tasks are that during the *unilateral reaching* task the right dominant arm does not move and therefore produces static sensory feedback, whereas for the *bilateral reaching single load task* the right dominant arm provides movement related position feedback, but not external load feedback to the CNS. Presumably the CNS uses the sensory feedback from the right dominant arm to update the motor program of the left non-dominant arm, which might inadvertently result in increasing the endpoint final position error (Fig. 15, page 57). This result suggests that final position information from the right dominant arm interferes with the left non-dominant arm controller and decreases the performance in controlling reaching accuracy of the left non-dominant arm. These findings supports the study by Sainburg and Wang (2002) that demonstrated that trajectory information (e.g., trajectory shape) is transferred from the left non-dominant arm to the right dominant arm, whereas final endpoint position information is transferred from the right dominant arm to the left non-dominant arm [142]. According to Sainburg’s *dynamic dominance hypothesis*, the right dominant arm is better at controlling endpoint trajectory, while

the left non-dominant arm is better in controlling for final endpoint position [137]. Therefore, the type of information transferred between the arms would be specific and consistent with functional specialization of each arm [138]. Sainburg and Wang (2002) proposed a modified access model, in which they state that the information that is stored during motor adaptation of either arm controller, may be accessed by the contralateral controller.

The second part of the study considered whether there would be a difference in motor adaptation and transfer of learning when one or both the arms experience a force environment during bilateral reaching task. The results have indicated that there is a difference in motor adaptation between these conditions. Specifically, the rate of adaptation, quantified by the normalized perpendicular displacement, is faster for the *bilateral reaching two loads* task with the same intrinsic force environment than for the *bilateral reaching single load* tasks (Fig. 17, page 69). This result suggests that transfer of learning occurs between the arms in both directions at the same time. The trajectory information is likely transferred from the left non-dominant to the right dominant arm, as well as from the right dominant arm to the left non-dominant arm. This result does not support the *dynamic dominance hypothesis* [138], in that this study demonstrated that transfer of trajectory information occurs from the right dominant arm to the left non-dominant arm during a bilateral task. When both arms experience an intrinsic force environment, *bilateral reaching two loads*, both arms produce movement related position feedback and external load feedback. This bilateral reaching task differed from the motor task studied by Sainburg and Wang [142]; in the latter only one arm at a time practiced a visuomotor perturbation. It is therefore possible that the CNS is using the movement related position feedback and external load feedback from both arms to improve the motor adaptation of each arm. During the *bilateral reaching single load* task, one arm produces both movement related position feedback and external load feedback, while the other arm produces

only movement related position feedback. For this task transfer of learning only occurred from the left non-dominant arm to the right dominant arm (Fig. 13, page 53). Therefore, it is plausible that the CNS, based on sensory feedback received from both arms, selectively modulates the transfer of information between the arms, which may either improve, decrease or keep constant the speed and quality of adaptation for each arm.

The final part of the study has considered whether the direction in which the forces are applied to both arms during bilateral reaching would affect motor adaptation and transfer of learning. The results have indicated that the rate of adaptation by the left non-dominant arm was lower in the extrinsic force environment compared to the intrinsic force environment (Fig. 20, page 78). This finding suggests that the CNS is sensitive to the direction in which the force environment is applied to the left non-dominant arm during bilateral reaching tasks. One limitation of this part of the study should be mentioned. During the *bilateral reaching two loads* tasks, the direction of the force environment on the left non-dominant arm was changed (extrinsic versus intrinsic), but the direction of external forces for the right dominant arm were unchanged (Table 7, page 74). Therefore, it may be that the results for the right dominant arm would be different if the direction of the force environment changes. However, some studies have shown that transfer of learning for unilateral reaching occurs from the dominant to the non-dominant arm only in extrinsic coordinate frame but not vice versa [28].

The transfer of learning models have been proposed based on unilateral reaching studies, and have only considered discrete transfer of learning, that is, transfer of learning was tested at the end of training (see Chapter 1, page 15). The current study explored whether transfer of learning is ongoing during a bilateral reaching task. The transfer of learning models predict unidirectional transfer of learning (*callosal model* [58, 67, 175], and *cross-activation model*, [62, 91, 124, 150, 182, 189]) or an

equal degree of transfer of learning between the arms (*proficiency model*, [177]). The results of this study have demonstrated that transfer of learning may occur in both directions simultaneously during bilateral tasks, and that the type of information that is transferred between the arms may depend on the sensory feedback available from both the arms. Therefore, the obtained results cannot be directly compared with any of the transfer of learning models for bilateral goal-directed reaching tasks. However, it is plausible that the Parietal Cortex is able to compare the sensory feedback from both the arms simultaneously against the predicted feedback. This comparison may be mediated by the fronto-parietal-cerebellar pathway [45] and intrahemispheric connections between the Parietal Cortices [22, 151].

The key findings of this study are: (1) Transfer of learning or/and interference occurs between the arms during goal-directed bilateral reaching tasks, (2) The extent to which transfer of learning or interference occurs depends on movement related position feedback and external load dependent feedback from each arm and on arm dominance. The following section discusses the possible motor control mechanisms and potential neural pathways that could explain the observations of this study.

7.3 *Bilateral motor control*

The results of Aim 1 of this study have demonstrated that movement related information is transferred between the arms during bilateral reaching. In accordance with the *intermanual crosstalk* model, each arm is controlled by an independent motor program during bilateral tasks [7, 96, 31]. Each arm controller has access to the contralateral motor program via the corpus callosum [21, 9, 43, 54, 110, 43, 153, 163]. However, the *intermanual crosstalk* model does not specify the nature of the information or the direction in which the information is transferred. The results of Aim 1 support the *dynamic dominance hypothesis* in that transfer of trajectory information occurs from the non-dominant to the dominant arm, while final position information

is transferred from the dominant to the non-dominant arm. However the results from Aim 2 are inconsistent with the *dynamic dominance hypothesis*. Specifically, during the *bilateral reaching two loads* task, transfer of trajectory information (evaluated by straightness of trajectory) was observed in both directions (Fig. 17, page 69), not just from the non-dominant to the dominant arm as predicted by the *dynamic dominance hypothesis*. The transfer of learning in both directions could be explained within the framework of the *optimal feedback control (OFC)* model.

The *OFC* model suggests that in order for movement to occur three problems need to be solved: system identification, state estimation and optimal control. Neurophysiological studies have suggested that the cerebellum is involved with system identification [112, 193, 154], the parietal cortex allows for state estimation [135, 60, 33], and the basal ganglia is involved with optimal control [122, 100]. During system identification, the cerebellum is thought to receive an efference copy of the motor command and to build an internal model that generates the predicted feedback of the intended movement [112, 193, 154]. For state estimation, the parietal cortex has been suggested to compare the predicted feedback against the actual feedback from the ongoing movement and to perform the movement evaluation, that is, determining where in space the arm is actually located and how it is moving [135, 60, 33]. The basal ganglia is thought to be involved with the optimal control and selection of the motor commands, by weighing the cost versus the reward for a specific movement [122, 100].

A diagram in figure 26 (page 100) is consistent with several models of bilateral motor control described previously (page 10) and can explain the results of the present study. The bilateral motor control schematic incorporates the *OFC* model and the *intermanual crosstalk* model. This schematic suggests that each arm has its own controller in the contralateral hemisphere. Interhemispheric communication occurs between the dominant and non-dominant hemispheres via the corpus callosum [21].

The intention to generate a movement starts in the motor association area where the motor program is formed [143]. The motor association area uses information from the somatosensory areas, cerebellum, parietal cortex and basal ganglia to update the motor program [56, 86, 185, 143, 154]. The primary motor cortex integrates the available information and generates descending motor commands [143]. These motor commands descend via the corticospinal tract to the spinal interneurons and motor neurons and activate the contralateral muscles. The activated muscles contract and cause the arm to move. As a result, the arm's mechanical state changes which is reflected in changes in proprioceptive feedback from the muscle spindles, Golgi tendon organs, and joint receptors. In addition, visual information about arm position is also received by the CNS although with a longer feedback delay. The sensory feedback information from the spindles, Golgi tendon organs, joint receptors and the retina on the inner surface of the eye (y_D and y_{ND} , Fig. 26, page 100) is transmitted via the thalamus to somatosensory and visual cortexes (see Section 1.2.2, page 7 for details). The cerebellum also receives movement related information and based on an efference copy of the motor command from the primary motor cortex builds the internal model of the environment (system identification) which in turn is used to predict sensory consequences of the intended movement (\hat{x}_D and \hat{x}_{ND}). The predicted feedback is then transmitted from the cerebellum to the parietal cortex.

The posterior parietal cortex compares the actual feedback against the predicted feedback in order to update the current state of the arms and the external environment (state estimation). Studies have demonstrated that there are intrahemispheric and interhemispheric pathways between the posterior parietal cortex and the primary motor cortex [22, 151]. Therefore, it is plausible that the posterior parietal cortex not only updates the state of the contralateral arm, but is also capable of comparing the states between the two arms. This could explain why the differential sensory feedback from the dominant and non-dominant arms could affect transfer of learning

and/or interference between the arms depending on the nature of the feedback and arm dominance, as has been demonstrated by the results of this study. Based on the predicted and actual sensory feedback from each arm, the posterior parietal cortex updates the state estimations of the arms relative to one another in the world and contributes to updating the motor program in the motor association and primary motor areas [143].

The basal ganglia are thought to be involved with the optimal control and selection of the motor commands, by weighing the cost versus the reward for a specific movement [122, 100]. The cost of moving the arm is greater than keeping the arm stationary, because energy is required to move the arm. (i.e. *unilateral reaching* from Aim 1). The cost of moving the arm in a force environment is greater than moving it in the neutral environment (null force field), since greater energy expenditure is needed to overcome the imposed force (i.e. *bilateral reaching single load* from Aim 1 and 2). In the same manner the cost of moving both the arms through a force environment (i.e. *bilateral reaching two loads* from Aim 2) is different from the cost of moving just one arm in a force environment and the other arm in a neutral environment (i.e. *bilateral reaching single load* from Aim 1 and 2). This different cost could explain differences in the rate of adaptation between the groups that were observed in Aim 1 and 2. Also, the direction in which the force environment is applied (intrinsic vs. extrinsic) may affect the cost (Aim 3). When the same intrinsic force environment is applied to both arms, the muscle force feedback is consistent between the arms (e.g., flexors of both arms counteract external forces that tend to extend the arm). However, for the same extrinsic force environment the muscle force feedback is inconsistent between the arms. Inconsistent muscle force feedback may cause a less coordinated movement resulting in higher muscle coactivation [93]. Therefore, the cost associated with moving the arms in the same intrinsic or extrinsic force environments could be different. The results of Aim 3 suggest that muscle force feedback

contributes to motor adaptation. Inconsistent muscle force feedback from the two arms in the same extrinsic force environment apparently contributes to interference between the arms.

One way to examine the importance of sensory feedback for the update of the cost function and subsequent update of the controller commands, would be to repeat the Aim 1 experiment, however this time manipulate sensory feedback (y_D and y_{ND} , 26, via tendon vibration causing activation of Ia spindle afferents, cooling the arm or with a blood pressure cuff, as well as removing visual feedback) from the arm that is moving in the neutral environment during the *bilateral reaching single load task*. It is predicted that there should be no differences in the rate of adaptation to a novel force environment when comparing between the *bilateral reaching single load task* and the *unilateral reaching* task.

7.4 *Implications for rehabilitation*

It has been suggested that for unilateral reaching each arm has its own specialization in that the dominant arm tends to be more proficient in specifying trajectory information, whereas the non-dominant arm is better in controlling the final arm position [137]. These natural tendencies of the arms movement organization have been demonstrated to influence the contents and direction of shared information between the hemispheres/arms during unilateral reaching tasks [138, 5]. The current study has demonstrated that information is shared between the arms during a goal-directed bilateral reaching task. The direction and the type of information that is shared between the arms depend on the sensory feedback that is available from each arm. This study suggests that the rehabilitation strategy for the arms may depend on: (1) whether or not the affected arm is dominant or non-dominant, (2) the goals of the rehabilitation and (3) the amount and kind of sensory feedback available depending

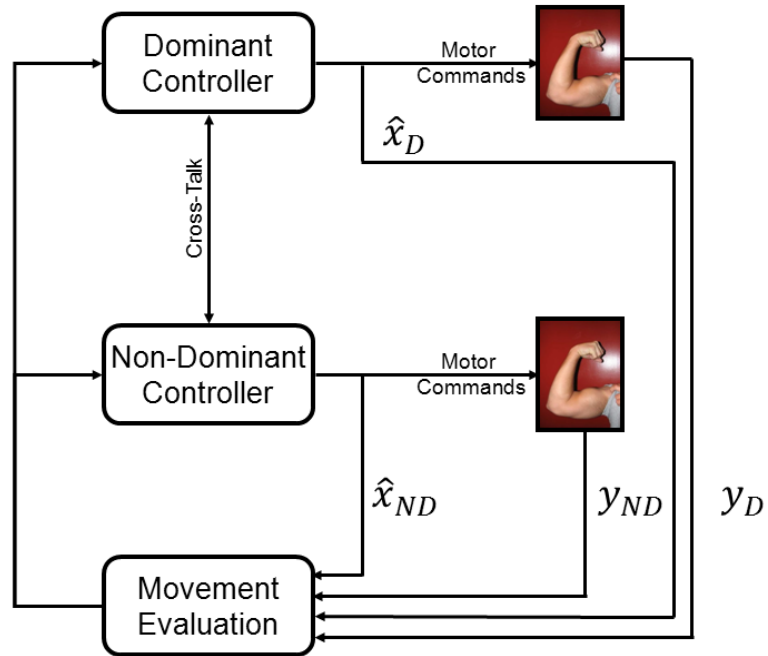


Figure 26: A schematic illustrating a possible bilateral motor control. \hat{x}_D and \hat{x}_{ND} represents the predicted feedback from the dominant controller and non-dominant controller, respectively. y_D and y_{ND} represents the actual sensory feedback from the dominant arm and the non-dominant arm, respectively.

on the pathology of the individual. The goals may relate to the accuracy of the movement, final position error of the arm or the smoothness of the arm trajectory. The results of the current study indicate that in healthy young subjects, both the dominant and the non-dominant arms learn the trajectory information fastest when both arms are moving in the same intrinsic force environment. If the goal is to train for accuracy in a healthy young subject, then the results of this study suggest that the left non-dominant arm should practice unilateral tasks, whereas for the right dominant arm there is no difference between training in unilateral and bilateral tasks. Future work should investigate whether these findings are applicable to individuals with a pathology, like stroke.

Robotic-assisted rehabilitation is a new promising direction in rehabilitation. Robotic devices have been used in studying motor adaptation and learning because they can provide repeated and precise movement perturbations while assessing and cataloging sensory-motor performance [131]. Examples of robotic devices whose effectiveness in rehabilitation of neurological patients has been studied in clinical trials include the MIT-Manus, which is a manipulandum [87] and an exoskeleton robotic arm, for example the T-Wrex [119, 144, 75]. The studies cited above have shown that stroke survivors with moderate neurologic arm impairment improved function (measured by clinical tests) due to robotic-assisted motor learning. Several studies have shown that robotic-assisted practice resulted in motor learning and neural plasticity [131, 47, 73, 78, 126, 133, 162]. The Kinarm can be used for motor learning and rehabilitation research. It has been recently shown that the Kinarm robot may provide accurate quantitative assessment of arm sensory function and the ability to perform visually guided arm reaching movements in stroke survivors [42, 23, 24]. The major advantage of the Kinarm is its ability to study movements of both arms simultaneously and control the task for each arm independently (applying external force environments, presenting targets to both arms, etc.). Therefore, the Kinarm

may be useful to address fundamental questions about motor adaptation and transfer of learning between the arms that may provide useful information for designing quantitative diagnostic methods and novel rehabilitation therapy.

7.5 Limitations and future work

The task protocol involved a limited number of trials, 160 for the pre-exposure phase and 320 reaches for the exposure phase, which took 3 hours to be completed. Since 60 subjects were recruited for the study, it was decided not to increase the experimental time in order to accommodate that many subjects. More trials could have resulted in more complete motor adaptation. Another constraint was that the Kinarm equipment was only able to safely apply a force environment with a viscosity matrix of 10 Ns/m. This is somewhat small when compared to other studies [28, 147]. A greater force environment may have resulted in greater differences in the performance variables between the arms and the groups. Furthermore, this study only considered right arm dominant subjects. It is unclear whether the findings of this study would apply to left non-dominant individuals.

The current study considered whether transfer of learning would occur during bilateral reaching tasks where the arms performed non-homologous arm movements. Studies have shown that there is no difference in reaction or movement time between bilateral in-phase (homologous) and out-of-phase (non-homologous) movements [2]. Although in-phase cyclical movement is more stable [25, 167, 168], subjects are still able to learn out-of-phase movements [169]. However, as has been demonstrated by Kelso et al. (1979), there is an entrainment effect between the arms during cyclical movements [81]. The arms will switch from an out-of-phase to an in-phase pattern at higher frequencies. The results of the current study only apply to out-of-phase movements. A comparative study should be conducted to determine if there are any differences in transfer of learning during a bilateral task between in-phase and

out-of-phase movements.

Subjects' arms were continually supported throughout the entire arms length in the Kinarm. This eliminated the involvement of anti-gravity muscles during the task. Most of the tasks that people perform everyday do not happen in this type of environment. Therefore, the results of this study need to be interpreted with caution. The Kinarm and similar robotic devices used in motor adaptation studies [131, 47, 73] are designed to reduce or completely eliminate the effect of gravity on the arms. This design feature of the Kinarm is advantageous for simplifying complexities of arm motor control and allows the study of specific questions related to motor learning in isolation from other factors. This reduction in complexity of movement in the current study allowed the focus on specific questions of motor learning transfer and interference between the arms. At the current stage of the limited understanding of bilateral reaching movements, this approach may be partly justified by the studies demonstrating that robotic-assisted practice in gravity eliminated environment result in motor learning and neural plasticity [131, 47, 73, 78, 126, 133, 162]. Whether or not the results obtained in this study hold in more natural conditions should be the subject of further research.

Divided attention may be another contributing factor to bilateral reaching movements and should be considered in greater detail in the future. It has been found that if a subject is instructed to focus attention on a single limb during a bilateral task, the unattended limb would make greater movement errors [157]. In the current study subjects were allowed to self select their strategy as to which arm they would pay attention. However, it would have been beneficial to track their eye movements to evaluate which arm they spent more time focusing on and whether this would correlate with any of the results presented in this study.

The current study addressed the issue as to whether transfer of learning occurs during a bilateral task. This is not the traditional method for testing transfer of

learning where one arm is trained in a force environment and then the other arm is tested. However, the traditional paradigm could be employed in a bilateral reaching task in the way of the bilateral single load experimental condition. During the training phase both arms would move, however only one arm would train the force environment. During the testing phase, both arms would move, but the force environment would be placed on the other arm. This would allow for measuring whether discrete transfer of learning occurs between the arms at the end of bilateral training.

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VITA

Linda Harley was born in Durban, South Africa and at the age of 7 developed a love for music. Her love for playing the piano has been a great motivational factor in pursuing her research in trying to understand how humans are able to learn to perform complex tasks with both arms at the same time. She received a BS and MS in Civil Engineering from the Georgia Institute of Technology, USA in 2002 and 2004, respectively. In 2005, she set out on her journey towards obtaining a PhD from the Georgia Institute of Technology, in the School of Applied Physiology. For the first three years she worked as a Teaching Assistant, and in 2007 was nominated for the “CETL/BP Outstanding Teach Assistant Award”. In 2008, she joined the Student Government Association at the Georgia Institute of Technology, and received an award for “Senator of the year”. She quickly rose through the ranks and in 2009 was elected by the Georgia Tech graduate student body, to serve as the Graduate Student President. She was only the second female to have ever held the position, since the inception of the Georgia Tech Student Government Association in the 1970’s. During this same period of time, she also worked as a Research Assistant at the Georgia Tech Research Institute (GTRI), where she was part of the “Ergonomic Worker Safety Assessment” project that evaluated the ergonomics of workers in poultry plants. In 2010, she received the GTRI division award “ATAS 2010 Award for Outstanding Student” for putting together and executing a grant proposal to the Health Systems Institute regarding the development of a prototype Rehab System. Her work has been presented at the Society of Neuroscience annual conference in 2009, the Society for the Neural Control of Movement in 2010, and the HCI International Conference in 2011. Her research interests are in understanding the mechanisms of learning to perform

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