2010

Bimanual skill acquisition : modulation by sex, aging, and auditory feedback

Metzler, Megan J.

Lethbridge, Alta. : University of Lethbridge, Dept. of Neuroscience, c2010

BIMANUAL SKILL ACQUISITION:
MODULATION BY SEX, AGING, AND AUDITORY FEEDBACK

MEGAN J. METZLER
Bachelor of Science in Occupational Therapy, University of Alberta, 2000

A Thesis
Submitted to the School of Graduate Studies
of the University of Lethbridge
in Partial Fulfillment of the
Requirements for the Degree

MASTER OF SCIENCE

Department of Neuroscience
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

Dedication

For Gloria Metzler

My best encourager, my mother,
the sweetest and strongest woman I have ever known.
I miss you.

Thesis Abstract

Bimanual movement is integral to daily function. As such, it is important to understand factors that influence bimanual performance. Playing the piano was employed to examine bimanual movement. Additionally, the weather prediction task was administered as a measure of non-declarative learning.

Sex influenced motor performance. Males tended to perform asymmetrical movements with less skill than females. Age affected motor performance. Older adults were less proficient, but improved similarly with practice as young adults. Further, older adults exhibited differential deterioration of bimanual movement.

Feedback and music training affected motor performance. Females performed bimanual movement less proficiently with auditory feedback. Individuals with music training performed bimanual movements relative to unimanual movements better with feedback. Music training moderated age-related differential deterioration of bimanual movements.

Older adults performed significantly worse than young adults on the weather prediction task. In addition, the weather prediction task correlated with motor measures in a sample including older adults.

Acknowledgements

The assistance offered by several generous individuals was essential to the success of this project. First, thanks to the participants who offered their time to this project. Sincerest gratitude is due to the Lethbridge Senior Citizens Organization, and Marlene Van Eden and Rob Miyashiro especially, for offering space in their building to conduct the study and assisting with recruitment.

Dr. Matthew Tata provided advice and guidance in programming for E-Prime and MATLAB, and offered assurances that what I wanted to do was possible. Jarrod Dowdall and Brian Allen both offered valuable assistance in writing functioning MATLAB code. Thanks to Dr. Robert Sutherland for elucidating some of the intricacies and pitfalls of research.

Peter Visentin generously offered time and support and consented to be a part of my thesis committee. Thanks as well to Ian Burleigh for taking the time to problem-solve a way around extracting huge amounts of MIDI data. Erin Zelinkski's assistance with manuscript editing is appreciated.

Dr. Amanda Price took pity on a graduate student and shared some program components for the weather prediction task. Thanks to Dr. Sergio Pellis for agreeing to be on my thesis committee and offering timely and sage advice. Finally, thanks to my supervisors, Dr. Deborah Saucier and Dr. Gerlinde A. Metz, who made this journey of discovery possible.

I received funding from the Keith and Hope Ferguson Memorial Scholarship. This work was supported by the Canadian Foundation for Innovation (CFI), The Natural Sciences and Engineering Research Council of Canada (NSERC), and Alberta Innovates-Health Solutions.

BIMANUAL SKILL ACQUISITION:
MODULATION BY SEX, AGING, AND AUDITORY FEEDBACK

TABLE OF CONTENTS

CHAPTER 1: GENERAL INTRODUCTION

CHAPTER 2: SEX DIFFERENCES IN BIMANUAL SKILL WITH THE KEYBOARD TASK

CHAPTER 3: AGING DIFFERENTIALLY IMPACTS PERFORMANCE OF BIMANUAL MOVEMENT

CHAPTER 4: MUSIC TRAINING AND SEX INFLUENCE THE EFFECT OF AUDITORY FEEDBACK ON MOTOR LEARNING

CHAPTER 5: WEATHER PREDICTION TASK PERFORMANCE CORRELATES WITH SYMMETRICAL MOVEMENT

CHAPTER 6: FINDINGS, IMPLICATIONS, AND FUTURE DIRECTIONS

List of Tables

List of Figures

List of Abbreviations

ANCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
EEG	electroencephalography
ERP	event-related potential
fMRI	functional magnetic resonance imaging
GG	Greenhouse-Geisser sphericity correction
HF	Huynh-Feldt sphericity correction
M1	primary motor cortex
MIDI	musical instrument digital interface
ms	milliseconds
η^2	eta squared
N/A	not applicable
PET	positron emission tomography
rTMS	repetitive transcranial magnetic stimulation
SA	sphericity assumed
SE	standard error
SMA	supplementary motor area
STG	superior temporal gyrus
TMS	transcranial magnetic stimulation

CHAPTER 1:
GENERAL INTRODUCTION

Rationale for Thesis

Coordination of the upper extremities is necessary for the execution of most activities. For example, opening a jar involves stabilizing the object with the nondominant upper extremity and manipulating the object (i.e. turning the lid) with the dominant upper extremity. This pattern of coordinated movement occurs across a broad range of daily activities such as writing, cutting up an apple, and setting the time on a wristwatch. During a 24-hour period, healthy individuals move their dominant upper extremity on average 8.7 hours with a standard deviation of 1.3 hours and the nondominant upper extremity 8.4 hours with a standard deviation of 1.2 hours, supporting the idea that most functional activities involve bilateral movement (Lang, Wagner, Edwards, & Dromerick, 2007).

Other daily activities involve coordination of the upper extremities in less stereotyped patterns. The act of dressing is one example. During dressing, the upper extremities often move in tandem for some components of the activity, such as when pulling pants on up to the waist. Additionally, the upper extremities are also required to move independently of each other, such as when grasping a button-up shirt by the collar with one hand and simultaneously moving the opposite upper extremity into a sleeve while bringing the hand grasping the shirt towards the shoulder. The complexity of these movement patterns may be even greater for skilled activities such as typing or playing certain types of instruments, such as the clarinet. Understanding the factors that influence bimanual skills is particularly important for effective rehabilitation of neurological injuries and neurodegenerative disorders, many of which preferentially affect older adults.

Aging may result in more variable reaction times (and hence slower reaction times) and decomposition of motor sequences despite normal error rates (Cooke, Brown, &

Cunningham, 1989; Rabbitt, 1989). However, how aging affects the acquisition of skilled movement and if aging differentially impacts bimanual movement is unknown. Further, despite known decrements in non-declarative learning and memory systems as a result of aging (Salthouse, McGuthry, & Hambrick, 1999), the role of these systems in the acquisition of skilled movement is unknown. Certain aspects of keyboard performance, such as initial hand position, likely rely on declarative memory systems. In addition, oversight by conscious systems may be necessary to select the correct motor sequence prior to the onset of movement. However, a significant proportion of keyboard performance likely relies on non-declarative memory systems, particularly for repetition of complex motor sequences (Gazzaniga, Ivry, & Mangun, 2009).

The weather prediction task partially relies on non-declarative systems. The participant predicts an outcome (what the weather will be) based on the presentation of predictors (combinations of four different cards) (Knowlton, Squire, & Gluck, 1994). The task is assumed to employ non-declarative systems because individuals cannot consciously report how they performed the task despite performing better than chance. Further, performance on the weather prediction task may be sensitive to damage in the basal ganglia (Knowlton, Mangels, & Squire, 1996), parts of the brain that are presumably important for motor learning. As such, the weather prediction task may be a means to assess the integrity of neural systems associated with motor learning.

Playing the keyboard is an ideal method of studying bimanual skills for several reasons. The task provides immediate auditory feedback as to the success of the movement (Münte, Altenmüller, & Jäncke, 2002), and allows study of unilateral, symmetrical, and asymmetrical motor performance. Further, task demands may be graded in terms of complexity of self-regulation, speed of movement, excursion of multiple joints, and coordination. Playing a keyboard has been used as a therapeutic medium after stroke (Schneider, Schönle, Altenmüller, & Münte, 2007), and to compare experts and novices on the kinaesthetic and cortical aspects of movement (Furuya & Kinoshita, 2008; Haslinger et al., 2005).

The present studies expand on previous findings and will compare: a) proficiency in learning to play a keyboard between age groups, b) the relationship between non-declarative learning and memory systems and sequenced motor movements, and c) the role of auditory feedback in the production of sequenced movements. The results provide important insight into the influence of these factors on bimanual motor learning and support the view that these factors are relevant to motor performance, and by extension, to the development of motor rehabilitation programs.

Current Research Related to Bimanual Movement

Distinctions among Types of Movements

There is a strong tendency towards symmetrical patterns during bilateral movement (Hughes & Franz, 2008; Swinnen, 2002). During bimanual movement, each hand tends to adopt the spatial characteristics of the other hand, and the hand performing the easier movement accommodates the hand performing the more difficult movement (Hughes & Franz, 2008). The observation of synchronization during bimanual movements has led to the supposition that symmetrical movement is the “default” of neural organization for bimanual movements (Swinnen, 2002).

Ample kinematic evidence supports the notion of varying performance associated with different movements, specifically unimanual, symmetrical bimanual, and asymmetrical bimanual movements. Symmetrical movements are more kinematically stable than asymmetrical movements (Kelso, 1981, 1984; Maki, Wong, Sugiura, Ozaki, & Sadato, 2008). Compared to symmetrical movement, asymmetrical movement, assessed by a bimanual grasp and reach task, exhibits delayed initiation and slower movement (Hughes & Franz, 2008). Concordantly, bimanual grasp and reach tasks incorporating uncomfortable end postures reveal that coupling between upper extremities is strongest during symmetrical movement towards uncomfortable end postures (Janssen, Beuting, Meulenbroek, & Steenbergen, 2009). These studies highlight some of the inherent differences between symmetrical and asymmetrical movements.

While the previous studies examined simple movements, Essers & Adam (2010) used a finger cueing paradigm with four cue conditions: two fingers on the same hand, the same fingers on different hands, different fingers on different hands, and a control condition (no advance information provided). Reaction time for the same hand condition was the fastest (unimanual), followed by the same finger condition (symmetrical), the different finger condition (asymmetrical), and finally the control condition. The authors concluded that there is a dissociation between within- and across-hand finger preparation (Essers & Adam, 2010).

The Impact of Task Parameters

Task complexity, goals, and environmental conditions influence the neural processes underlying bimanual movements, and as a result, the kinematic properties of movements. In some cases, principles and strategies demonstrated with simple tasks hold true as task complexity increases. For example, when visual stimuli are combined with a bimanual task, longer reaction times and reduced accuracy is observed as difficulty of the visual task increases (Matthews, Martin, Garry, & Summers, 2009). Furthermore, this effect is strongest during asymmetrical performance compared to symmetrical performance (Matthews et al., 2009). These results purportedly reflect the increased resources required to stabilize asymmetrical movements and entails top-down processing orchestrated by the frontal attentional network (Matthews et al., 2009).

The hypothesis that symmetrical movement is the preferred mode for bimanual movement was challenged by a study that compared symmetrical and asymmetrical bimanual reaching to comfortable and uncomfortable end postures (Janssen et al., 2009). When given specific end orientations for grasping objects, subjects elected to move asymmetrically and end in a comfortable posture with the dominant hand, but not the nondominant hand. The authors concluded that comfort at end posture supersedes the tendency to move symmetrically (Janssen et al., 2009).

Neural activation during performance of the same bimanual task varies under different explicit goals (Duque et al., 2009). Increased activation of the superior temporal gyrus (STG), supplementary motor area (SMA), and primary motor cortex (M1) was observed with functional magnetic resonance imaging (fMRI) when the stated goal was coordinated movement, compared to the same movement when the stated goal was independent movement (Duque et al., 2009). Virtual lesions of the SMA, left STG, and left M1 via application of inhibitory transcranial magnetic stimulation (TMS) had no effect on "coordinated" movement. However, inhibitory TMS of M1 of the nondominant motor hemisphere enhanced hand independence, whereas inhibitory TMS of the STG impaired bimanual performance (Duque et al., 2009).

Leading Joint Strategy

The dominant hemisphere for movement drives symmetrical movement (Walsh, Small, Chen, & Solodkin, 2008). The limb contralateral to the dominant hemisphere initiates and moves in advance of the other limb throughout the movement; in addition, stronger input from the dominant to the nondominant hemisphere is typically observed (Walsh et al., 2008). Furthermore, asymmetrical upper extremity movement exhibits enhanced stability when the leading joint strategy is similar to the one used for symmetrical movement (Rodriguez, Buchanan, & Ketcham, 2010).

In contrast, leading limb strategies during bimanual reaching adapt under the influence of external forces (Casadio, Sanguineti, Squeri, Masia, & Morasso, 2010). Application of opposing external forces to the upper extremities resulted in incomplete adaptation for reaches from the central position to more distant targets (Casadio et al., 2010). In addition, the left hand led movements to the left, and the right hand led movements to the right (Casadio et al., 2010). Thus, although there appears to be a tendency for the dominant hand to lead bilateral movements, task constraints and demands may result in the use of other strategies.

Neural Correlates of Bimanual Movement

Investigation of neural correlates associated with bimanual training is sparse. However, after five to six training sessions for asymmetrical sequential finger movements, neural activation during asymmetrical movement more closely resembled symmetrical activation (De Weerd et al., 2003). Further, motor performance approached the same level of proficiency as symmetrical movements. Prior to training, symmetrical movement corresponded to activation of M1 and asymmetrical movement corresponded to activation of M1, SMA, and premotor and parietal cortices (De Weerd et al., 2003). However, following training, M1 was primarily active during asymmetrical movements.

Past research has attempted to pinpoint a specific brain region responsible for bimanual movements. While lesions of the basal ganglia, cerebellum, corpus callosum, parietal lobe, SMA, and cingulate motor area affect aspects of bilateral movement, they do not preclude it (Brown, Jahanshahi, & Marsden, 1993; Cardoso de Oliveira, Gribova, Donchin, Bergman, & Vaadia, 2001; Eliassen, Baynes, & Gazzaniga, 2000; Franz, Ivry, & Helmuth, 1996; Leonard, Milner, & Jones, 1988; Obhi, Haggard, Taylor, & Pascual-Leone; Serrien, Nirkko, Lovblad, & Wiesendanger, 2001; Stephan et al., 1999). Although the SMA was historically hypothesized to be the locus of bimanual movement (Swinnen, 2002), recent research has shifted views. The SMA is active for complex coordinated movements and lesions of the SMA interfere with the initiation of bimanual movements. However, lesions do not prevent bimanual movement and the structure is active in other types of complex movements (Swinnen, 2002). Finally, as suggested above, other brain regions are also active during bimanual movements. The inability to pinpoint a brain region responsible for bimanual movements has led to the supposition that bimanual movement relies on a distributed neural network (Swinnen, 2002; Walsh et al., 2008).

The notion that a distributed network is responsible for bimanual movement has led to investigations into the patterns of neural connectivity associated with bimanual movements. A nonhuman primate study examining activation of bilateral motor cortices with implanted electrodes found that inter-hemispheric correlations of local field potentials were strongest immediately preceding the onset of symmetrical movement and weaker for asymmetrical and unilateral movements (Cardoso de Oliveira et al., 2001). Neural connectivity associated with symmetrical movements (rotating a disc with the second digit in opposite directions) and asymmetrical movements (rotating a disc in the same direction) was modeled from fMRI data (Maki et al., 2008). The model suggests that asymmetric neural input from the dominant M1 to the nondominant M1 occurs during symmetrical movement, but not during asymmetrical movement or rest (Maki et al., 2008).

This technique was employed to examine how areas of the brain interact to produce opposition between the thumb and index finger unilaterally and bilaterally (Walsh et al., 2008). Although patterns of activation were similar between unilateral and bilateral symmetrical conditions, models of connectivity suggested that the dominant hemisphere expressed increased connectivity during right unimanual and symmetrical movements. In addition, electromyography detected muscle activation of the dominant hand prior to the nondominant hand during symmetrical movements, consistent with the idea of a leading joint strategy (Walsh et al., 2008).

In accordance with the theme of inter-hemispheric connectivity associated with bimanual movement, a significant correlation between skilled performance on an asynchronous bimanual coordination task and the degree of “neural traffic” mediated by the corpus callosum (measured with fractional anisotrophy) was reported (Johansen-Berg, Della-Maggiore, Behrens, Smith, & Paus, 2007). Further analysis suggested that neural pathways extend from the corpus callosum to the SMA and the caudal cingulate motor area (Johansen-Berg et al., 2007). Using fMRI and modeling, the probable network for bimanual finger tapping reportedly involves coupling from the dominant to the nondominant M1, connection from the bilateral premotor areas to each M1, inhibition of the connection from the dominant to the nondominant premotor area, and input from the SMA to the nondominant M1 and premotor areas (Zhuang, LaConte, Peltier, Zhang, & Hu, 2005).

In summary, there is an extensive neural network implicated in bimanual movement consisting of the basal ganglia, cerebellum, corpus callosum, parietal lobe, SMA, cingulate motor area, M1, somatosensory and secondary somatosensory areas, premotor cortex, medial prefrontal area, pre-cuneus, and superior temporal area (Walsh et al., 2008). Research suggests that input from the dominant to the nondominant hemisphere is particularly important for the production of symmetrical movements, and that inter-hemispheric connections may be inhibited during asymmetrical movements.

The regions implicated in inter-hemispheric connectivity during bilateral movements vary, and may depend on factors such as task complexity and prior experience. For example, symmetrical movements involving upper extremity movement (Cardoso de Oliveira et al., 2001), index finger rotation (Maki et al., 2008), and index finger tapping (Zhuang et al., 2005) involve increased input from the dominant to the nondominant M1. In contrast, finger opposition is associated with increased input from the dominant to the nondominant SMA (Walsh et al., 2008). Further, simple bilateral wrist movements in temporal asynchrony was associated with increased input from the dominant to the nondominant SMA (Johansen-Berg et al., 2007), which suggests that patterns of connectivity may be different for temporal and spatial deviations. Neural mechanisms associated with bimanual movement have yet to be clearly delineated.

Research Questions, Hypotheses, and Predictions

The importance of bimanual movement to human function and consequent implications to rehabilitation warrant investigation of the factors that influence bimanual learning and indirectly, the neural plasticity necessary for bimanual learning. This thesis targeted four research questions.

Question 1

How does acquisition of different types of skilled movement vary, specifically among a) unimanual movements, b) symmetrical movements, and c) asymmetrical movements?

I hypothesize that nondominant manual movements require relatively more neural resources than dominant manual movements, and symmetrical movements require fewer neural resources relative to asymmetrical manual movements. Males may have a basic motor speed advantage while females may have an advantage for production of complex motor sequences (Nicholson & Kimura, 1996). Considering this hypothesized basic motor speed advantage, males may perform unimanual movements with greater speed and accuracy compared to females. In addition, sex differences in inter-hemispheric structures suggest that females may have more robust inter-hemispheric connections than males (Resnick & Driscoll, 2008). I hypothesize that stronger inter-hemispheric pathways among females confers an advantage for the increased motor programming demands associated with bimanual performance.

Prediction 1. Unimanual movements with the dominant hand will be performed with greater speed and accuracy than with the nondominant hand.

Prediction 2. Symmetrical movements will be performed more quickly and accurately than asymmetrical movements.

Prediction 3. Males will perform unimanual movements more quickly than females.

Prediction 4. Females will perform bimanual movements with greater speed and accuracy than males.

Question 2

How does aging influence the learning of skilled manual movements?

In addition to a global decline of neural structures as a result of the aging process, there is an amplified deterioration of inter-hemispheric structures such as the corpus callosum (Bangert, Reuter-Lorenz, Walsh, Schachter, & Seidler, 2010; Lee et al., 2010). I hypothesize that global neurological decline associated with older age will result in poorer performance of manual movements, but the differential deterioration of inter-hemispheric structures will result in performance deficits of bimanual movements relative to other movements. While symmetrical movements may rely on inter-hemispheric connections relatively more than asymmetrical movements, the increased complexity and neural demands associated with asymmetrical movements relative to other movement types may result in comparable deficits to symmetrical movements.

Prediction 5. Older adults will perform all movements with decreased accuracy and speed compared to young adults.

Prediction 6. Older adults will perform bimanual movements less proficiently than unimanual movements in comparison with young adults.

Question 3

Does auditory feedback from the keyboard affect performance of unimanual and bimanual movements?

Auditory feedback provides immediate information as to the success of the attempted movement (Münte et al., 2002), and co-activation of auditory and sensorimotor cortices occurs rapidly in response to music training (Bangert & Altenmüller, 2003, D'Ausilio, Altenmüller, Belardinelli, & Lotze, 2006). Considering this evidence, I hypothesize that neural networks will rapidly adapt to and exploit auditory feedback as a means to superior motor performance. As music training results in increased size of inter-hemispheric structures (Schlaug, Jäncke, Huagng, Staiger, & Steinmetz, 1995), I hypothesize that music training results in more robust inter-hemispheric connections and consequently corresponds to better performance of bimanual movements relative to unimanual movements.

Prediction 7. Performance of manual movements will be faster and more accurate in the presence of auditory feedback.

Prediction 8. Individuals with past music lessons perform better with feedback.

Prediction 9. Individuals with music training will perform bimanual movements relatively better than unimanual movements.

Question 4

Is learning of skilled manual motor movements related to other learning and memory systems?

Considering that a significant proportion of keyboard performance likely relies on unconscious processes, I hypothesize that non-declarative learning systems underlie components of manual motor performance.

Prediction 10. Performance on a task of non-declarative memory will correlate with performance of skilled manual movements.

Prediction 11. Assuming that older adults demonstrate impaired motor performance, older adults will also show decrements with the weather prediction task.

Experiments

Two experiments were conducted to investigate the aforementioned hypotheses. The first experiment investigated the relationship between sex, aging, non-declarative memory, and learning of skilled manual movements. For this study, young adults and older adults completed two trials of the keyboard task (comprised of unilateral, symmetrical, and asymmetrical movements) interrupted by the weather prediction task. In addition to replicating the findings of the first experiment, the second experiment further investigated the impact of auditory feedback on learning manual movements. For the second study, young adults completed the keyboard task with and without auditory feedback, completed the weather prediction task, and finally repeated the keyboard task in the opposite order. The findings demonstrate that the keyboard task is a sensitive and practical method of studying complex bimanual learning in the general population. Further, the results provide insights into the effects of sex, age, and auditory feedback on motor performance.

CHAPTER 2:
SEX DIFFERENCES IN BIMANUAL SKILL WITH THE KEYBOARD TASK

Introduction

Bilateral movement is functionally important to humans, and tools for assessing bimanual skills are essential precursors to understanding factors that influence learning and performance. The piano keyboard is an ideal means of studying complex bimanual motor learning. It is feasible to grade the task for level of difficulty, degree of self-regulation of attention, speed of movement, joint excursion, and coordination. Practice time may be monitored because an instrument is required for the activity. Moreover, playing the piano is arguably ecologically valid, socially valued, and relevant to most of the developed world (Altenmüller, n.d.).

Of particular relevance to this study, keyboard performance can be structured to study different types of bimanual movements. During piano performance, the upper extremities may move symmetrically, in which hand and finger movements are mirror images, or the upper extremities may move asymmetrically, in which hand and finger movements contrast each other. In bimanual studies, these types of movements are kinematically different and have similar, but distinctly unique, neural correlates (Kelso, 1981, 1984; Maki et al., 2008). In addition, comparison may be made with unimanual movements.

Playing a musical instrument results in macro-anatomical changes over the long term, specifically of the primary motor and somatosensory areas, inferior temporal gyri, anterior corpus callosum, and left cerebellum (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Gaser & Schlaug, 2003; Schlaug et al., 1995). However, changes in neural function are apparent in the short term (Münte et al., 2002). After practicing a piano piece for 30 minutes, increased intracortical excitability while listening to the left-hand portion of the piece was evident; cortico-spinal facilitation was observed after five days of rehearsal (D'Ausilio et al., 2006).

Playing a musical instrument provides immediate auditory feedback about the success of the movement (Münte et al., 2002). In fact, practice with a musical instrument results in co-activation of auditory and sensorimotor cortices, triggered by either the motor movements or auditory stimuli in isolation (Bangert et al., 2006; Haslinger et al., 2005). This co-activation with auditory stimuli occurred after just 20 minutes of practice with naïve pianists, and consolidation was identified after five weeks of training (Bangert & Altenmüller, 2003). Playing the piano has been used as a therapeutic medium after stroke (Schneider et al., 2007) and as a method to compare experts and novices on the kinaesthetic and cortical aspects of motor performance (Furuya & Kinoshita, 2008; Haslinger et al., 2005).

Scale analysis was employed to examine focal dystonia in professional pianists (Jabusch et al., 2004). Subjects played two-octave C major scales unilaterally with standard fingering. Data were analyzed for velocity, tone duration, inter-onset interval, and tone overlap, as well as the standard deviation of each parameter. Tone durations and inter-onset intervals were higher for professional pianists with dystonia than matched controls. Further, pianists with dystonia showed higher duration and inter-onset interval values for the affected hand compared to the unaffected hand. Although the study demonstrated the usefulness of scale analysis with professional pianists with focal dystonia, the utility of playing scales on a keyboard to study bimanual skills within the general population is unknown.

The purpose of this study is twofold. First, the study will characterize the keyboard task and demonstrate its utility for examining manual motor skills with the general population. Secondly, unimanual and bimanual performance with naïve individuals will be examined with the keyboard task. Central to these purposes is the question: How does acquisition of different types of skilled movement vary, specifically among unimanual, symmetrical, and asymmetrical movements?

I hypothesize that nondominant unimanual movements require relatively more neural resources than dominant unimanual movements, and consequently nondominant motor performance will be poorer in comparison to dominant motor performance. Similarly, I expect that symmetrical manual movements require fewer neural resources relative to asymmetrical manual movements, and consequently bimanual symmetrical performance will be superior to asymmetrical performance.

Males may have a basic motor speed advantage while females may have an advantage for production of complex motor sequences once baseline speed is taken into account, particularly with task repetition (Nicholson & Kimura, 1996; Lissek et al., 2007). I expect males to perform simple unimanual movements with greater proficiency than females as baseline speed will not be entered as a covariate for these analyses.

Sex differences in inter-hemispheric structures, namely of the anterior commissure and splenium (Resnick & Driscoll, 2008), likely correspond to functional differences. Increased inter-hemispheric connectivity among females bears potential implications for symmetrical performance in particular, as increased inter-hemispheric connectivity characterizes symmetrical movements (Cardoso de

Oliveira et al., 2001; Maki et al., 2008; Walsh et al., 2008). I hypothesize that stronger inter-hemispheric connections among females confers an advantage for bimanual performance in comparison to males.

Materials and Methods

Subjects

University-age students (*n*=31, aged 18-28 years, mean age= 21.2 ± 2.5 years, 14 males) participated in the study for credit in undergraduate courses through the Department of Psychology's Human Subject Pool. Older adults (*n*=34, aged 55-95 years, mean age= 73.0 ± 9.6 years, 14 males) were recruited through a local senior centre and word of mouth. Exclusion criteria included history of neurological or motor impairment and prior experience playing the piano. However, the latter criteria needed to be relaxed as several potential participants had played at some time in the remote past. Participants were seen at a laboratory at the university or a local senior centre organization. Four cases were excluded due to movement disorders resulting from neurological or orthopaedic conditions; one subject withdrew from the study. Ethics approval for the study was obtained from the University of Lethbridge Human Subject Committee. The study procedures were explained, after which the participant signed a consent form.

Experimental Apparatus and Task

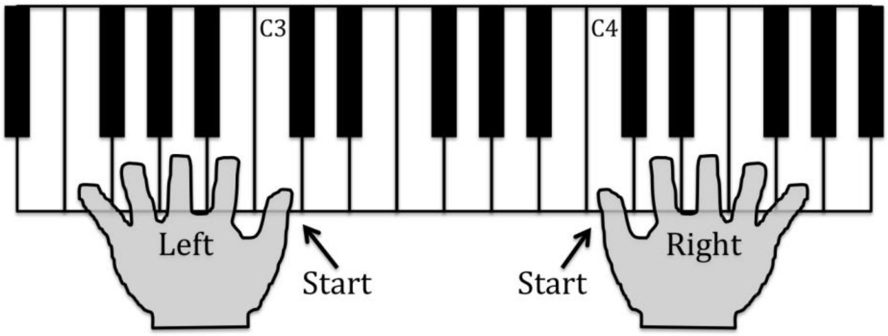
Hand dominance determination. Determination of hand dominance was ascertained via questionnaire (Elias, Bryden, & Bulman-Fleming, 1998). The questionnaire consisted of questions related to which hand is used for particular activities, as well as frequency of use. Responses were assigned values and the values were summed to yield a score that indicated hand dominance. Each participant completed the questionnaire at the beginning of the session and the questionnaire was scored prior to beginning the keyboard task. To confirm hand dominance, participants were asked to press a single key on a computer keyboard as many times as possible with the second digit (index finger) of the right hand for 30 seconds followed by the left hand. Participants performed two, 30-second trials with each hand. The total number of key presses for each hand was recorded. The hand with the greater number of key presses was considered to be the dominant hand. In seven out of 60 cases, the hand score and speed of tapping with the dominant hand disagreed; in cases of disagreement, the hand score was used to assign dominance for analysis.

Demographic questionnaire and vocabulary test. Participants were asked to report current medications, education level, and familial handedness via a written questionnaire. Due to the likelihood of educational differences between the younger university-enrolled sample and the older community sample, a vocabulary task was used to assess intelligence indirectly (Ekstrom, French, & Harman, 1976). The tool is considered to be a valid measure of intelligence even in individuals who have had brain damage (Lezak, Howieson, & Loring, 2004).

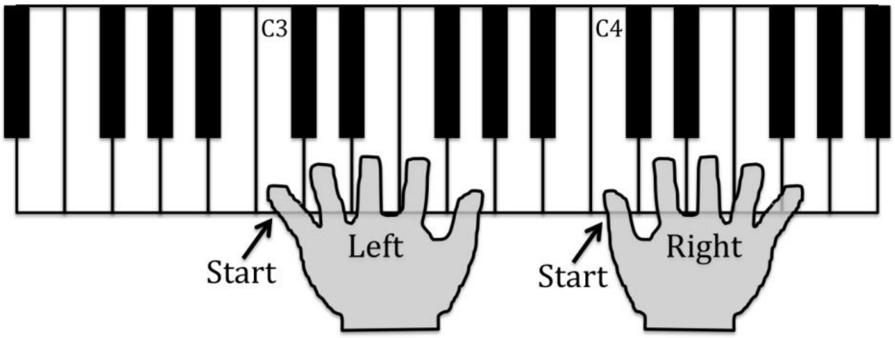
Keyboard task. Motor skill was assessed via performance on four tasks: 1) unilateral performance with the dominant hand, 2) unilateral performance with the nondominant hand, 3) bilateral symmetrical performance, and 4) bilateral asymmetrical performance. The order of the unimanual conditions was counterbalanced among participants; approximately half of the participants started with the dominant condition, while the remainder started with the nondominant condition.

Unimanual dominant movement involved performing a C major scale using only the first five notes with the dominant hand (ascending from C to G and then descending back to C for the right hand or descending from C to F and then ascending back to C with the left hand). Unimanual nondominant movement involved performing a C major scale using only the first five notes with the nondominant hand (as described above). For symmetrical movement, participants performed both unimanual movements concurrently. Participants placed the thumbs on the keys in tandem and ascended with the right and descended with the left hand through the scale with each digit in turn. For the asymmetrical condition, participants made keystrokes simultaneously with the right and left hands, but initiated the movement with the fifth digit (i.e. pinkie) of the left hand and first digit (i.e. thumb) of the right hand. Both hands ascended in a C major scale in unison and then descended to the starting note in unison.

For all movement conditions, the right hand started on middle C and the left hand started an octave below middle C (Figure 2.1). A demonstration was provided before asking the participant to perform the movement. Participants were instructed to complete the task as quickly and as accurately as possible. For bimanual movements, participants were instructed to “not let one hand get ahead of the other.” The examiner obtained eight clean trials of each condition (where possible) and recorded the participant’s performance as a MIDI file in Cubase Essential 4. Following a period of 15 to 20 minutes during which other tasks were done, including the weather prediction task (addressed in Chapter 5), the participant then repeated the keyboard task.



Hand positions for the unimanual and symmetrical movement conditions.



Hand positions for the asymmetrical movement condition.

Figure 2.1. Hand positions for the keyboard task.

Data Analysis

In order to extract data from the MIDI files, the MIDI Toolbox was used within MATLAB to write the MIDI data to a matrix. The matrix included the time stamp for each keystroke, the note played, the velocity of the keystroke (an indirect measure of force), and the duration for which the key was pressed. An additional MATLAB code was written to search the matrix for clean trials and export clean trials to Excel. MATLAB was also used to identify failed attempts for each movement within the matrix.

A failed attempt was defined as the completion of the first three keystrokes of each hand in the correct sequence for a given movement without interjecting keystrokes, but an error in the sequence thereafter. Therefore, for bimanual movements, the first three keystrokes of both hands in sequence denoted a trial attempt. Errors for each movement were recorded by scanning the matrix for failed attempts in relation to the time of the eighth successful trial. Where eight clean trials of a movement were not available because of task difficulty for the participant, data was averaged over the available trials to avoid skewing results in favour of the more skilled participants. If eight accurate trials were not available, errors were calculated by multiplying counted errors by the desired number of trials (eight) divided by the actual number of clean trials obtained.

For participants unable to complete symmetrical or asymmetrical movements, values were assigned for inter-onset interval mean and inter-onsets standard deviation by adding .001 to the highest value obtained by a participant who was able to complete the task. Errors were assigned by adding one to the highest error rate obtained by a participant able to complete that movement during that particular trial. In cases where only one trial was available, the data were coded as missing; this occurred for three instances for symmetrical movement and 13 instances for asymmetrical movement. In terms of missing data, between two and seven clean trials were available for analysis in one instance for dominant movement, for two instances for nondominant movement, for 11 instances for symmetrical movement, and for 14 instances for asymmetrical movement. For each movement, there were 130 instances as each participant completed two trials of the keyboard task. As almost half of the older males were unable to complete the asymmetrical movements, this method minimized skewing the results further by testing additional older men to find participants in this group that were able to complete the movements.

Extracted MIDI data were entered into an Excel template to compute several measures related to motor performance, averaged over eight trials for each movement condition. Inter-onset interval describes the speed at which the participant moves from one key to the next and inter-onset interval standard deviation indicates the variability associated with speed of movement. The duration for which notes were held, velocity of key presses, and overlap between adjacent notes was also calculated. To determine how rhythmically the participant played the movement, downbeat-offbeat ratios for each movement were calculated. As movements were demonstrated in 4/4 time, the velocity of notes falling on a downbeat were averaged and divided by the average velocity of notes that fell on an offbeat.

Dominant-nondominant onset was calculated by subtracting the time of onset of the dominant hand from the nondominant hand and averaging paired strikes for each movement. This resulted in a positive score when averaged paired keystrokes were led by the dominant hand and a negative score when averaged paired keystrokes were led by the nondominant hand. The standard deviation for dominant-nondominant onset is the standard deviation of this measure. While a study of professional pianists with focal dystonia showed significant effects related to tone duration (Jabusch et al., 2004), this measure was not analyzed with this population as tone duration preferences (i.e. legato vs. staccato sounds) may vary among participants who have not received formal music training. Further, although sequences were demonstrated with legato note durations, many participants clearly experimented with tone length during the task.

Statistical Analysis

The differences between unimanual and bimanual movements in terms of kinematic and neural parameters, such as the tendency for the dominant limb to slow in order to move synchronously with the nondominant limb during bilateral movement, warranted separate analyses of these movements (Nicholson & Kimura, 1996; Swinnen, 2002; Walsh et al., 2008). Data were analyzed using PASWStatistics18.0 software for analysis. A mixed factorial ANCOVA (2x2x2x2) was employed to analyze unimanual motor performance for within-subject factors of trial and hand (dominant and nondominant), and between-subject factors of age (young and older adults) and sex (males and females) for error rates, inter-onset interval (a measure of speed), and inter-onset interval standard deviation. Bivariate correlations showed a relationship between prior music lessons and motor measures. To take into account this confounding factor, years of lessons were entered into the model as a covariate (note that this impacts reported degrees of freedom).

A second mixed factorial ANCOVA (2x2x2x2) with years of music lessons as a covariate was employed to analyze bimanual motor performance for within-subject factors of trial and movement condition (symmetrical and asymmetrical), and between-subject factors of age (young and older adults) and sex (males and females). Performance parameters assessed included error rates, speed, speed standard deviation, dominant-nondominant onset, and dominant-nondominant onset standard deviation. Tone length, tone overlap, and velocity as well as their respective standard deviations were not included the analyses.

As outlined in the introduction, movements of the dominant and nondominant hands as well as unimanual and bimanual movements both show differences in terms of kinematics and neural correlates. To address this and compare across these factors, downbeat-offbeat ratio was assessed in a factorial ANCOVA (2x6x2x2) with years of music lessons as a covariate for trial, movement (dominant unilateral, nondominant unilateral, dominant symmetrical, nondominant symmetrical, dominant asymmetrical, and nondominant asymmetrical), age, and sex. Significant interactions for unimanual and bimanual movements and downbeat-offbeat ratio were further examined with pairwise comparisons and Bonferroni corrections using syntax in PASWStatistics18.0.

Results related to trial, movement condition, hand, and sex are reported and discussed in this chapter. Effects related to age are discussed in Chapter 3.

Results

Unimanual Movements

For unimanual errors, the ANCOVA with years of music lessons as a covariate revealed a main effect of trial, with errors significantly decreasing from trial 1 to trial 2, $F(1,15)=19.540$, $p<.001$ (Table 2.1). There was a significant interaction of trial, hand, and sex, $F(1,51)=6.540$, $p=.014$ (Table 2.1). Pairwise comparisons (with a Bonferroni correction) showed that while performance of both the dominant and nondominant hands improved for males from trial 1 to trial 2, only performance of the dominant hand improved significantly for females (Table 2.2, Figure 2.2). Males showed a small effect of practice for unimanual movements, and females showed a large effect of practice, but only for the dominant hand (Cohen, 1988). Comparisons between males and females and dominant and nondominant hands failed to reach significance, although there was a trend for females to make fewer errors than males for nondominant performance at trial 1 (mean difference= 2.826, standard error= 1.541, $p=.072$).

For unimanual speed, the ANCOVA with years of music lessons as a covariate revealed a main effect of trial, with increasing speed from trial 1 to trial 2, $F(1,51)=61.925$, $p<.001$ (Table 2.1). The analysis also revealed a main effect of hand on unimanual speed, with the dominant hand performing movements more quickly than the nondominant hand, $F(1,51)=30.378$, $p<.001$ (Table 2.1).

Measure	Main Effect / Interaction			Mean [Standard Error (SE)]	Partial η^2	Observed Power
Error Rate	Trial	Trial 1		3.695 (.463)	.277	.991
		Trial 2		1.902 (.316)		
	Sex x Trial x Hand	Male	T1, Dominant	3.323 (.513)	.114	.709
			T1, Nondominant	5.325 (1.066)		
			T2, Dominant	2.090 (.369)		
			T2, Nondominant	2.583 (.652)		
		Female	T1, Dominant	3.634 (.514)		
			T1, Nondominant	2.499 (1.068)		
			T2, Dominant	1.302 (.370)		
			T2, Nondominant	1.632 (.654)		
Speed	Trial	Trial 1		.304 (.011)	.548	1.000
		Trial 2		.269 (.010)		
	Hand	Dominant		.273 (.010)	.373	1.000
		Nondominant		.299 (.011)		
Speed Standard Deviation	Trial	Trial 1		.105 (.009)	.314	.999
		Trial 2		.081 (.007)		

Table 2.1. Means, effect sizes, and power of significant effects for unimanual movements. Mauchly’s Test of Sphericity did not indicate violations, so sphericity corrections were not applied.

Comparisons for unimanual error rates	Mean Difference	SE	Signi- ficance	Cohen’s *d*
Males, dominant, trial 1 – trial 2	1.233*	.501	.017	.455
Males, nondominant, trial 1 – trial 2	2.742*	.752	.001	.440
Females, dominant, trial 1 – trial 2	2.332*	.502	<.001	1.171
Females, nondominant, trial 1 – trial 2	.866	.753	.255	N/A

Table 2.2. Pairwise comparisons of the interaction of sex, hand, and trial for unimanual error rates (* denotes significance).

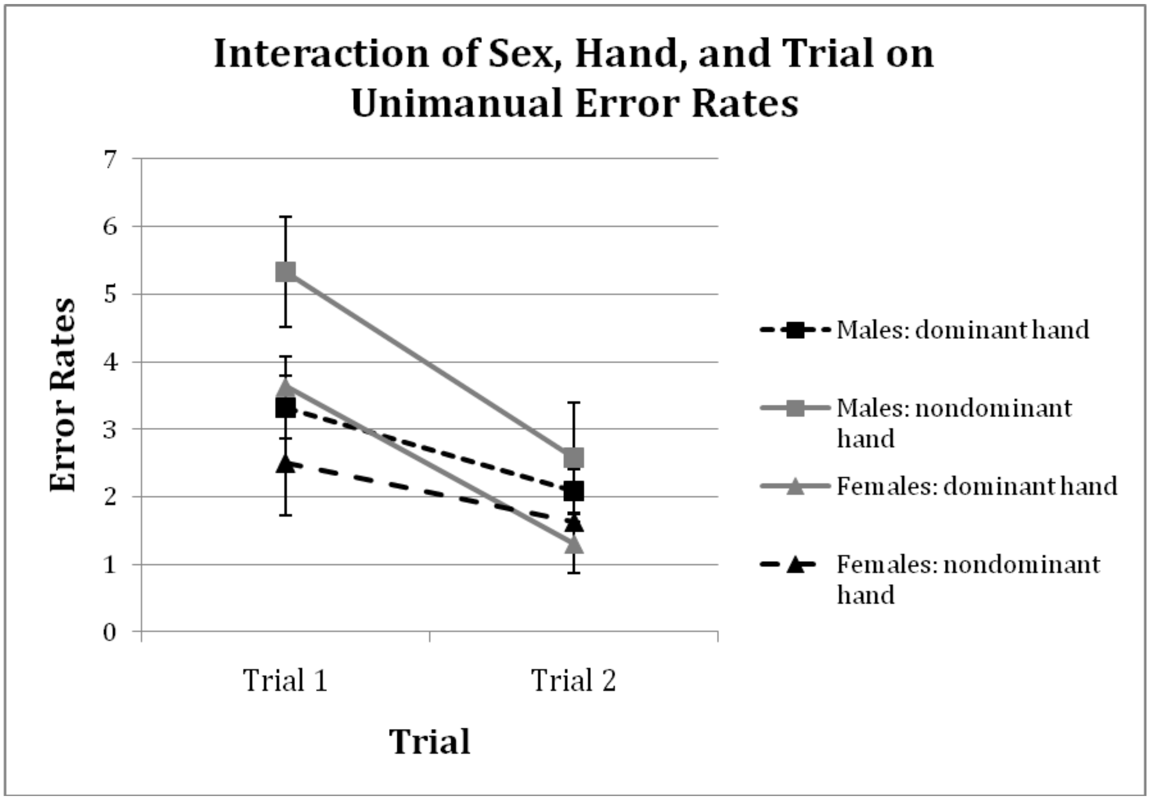


Figure 2.2. Interaction of sex, hand, and trial on unimanual error rates. Symbols represent the means and error bars represent the standard error of the mean.

For the standard deviation of unimanual speed, the ANCOVA with years of music lessons as a covariate revealed a main effect of trial, with standard deviation of speed decreasing from trial 1 to trial 2, $F(1,51)= 25.670$, $p<.001$ (Table 2.1).

The ANCOVA showed significant main effects of the covariate, years of music lessons, for errors, $F(1,51)= 4.163$, $p=.047$, speed, $F(1,51)=23.238$, $p<.001$, and speed standard deviation, $F(1,51)=10.938$, $p=.002$. The interaction between years of lessons and trial for unimanual movement speed approached significance, $F(1,51)=3.777$, $p=.058$.

Bimanual Movements

For bimanual errors, the ANCOVA with years of music lessons as a covariate revealed main effects of trial and movement. For trial, errors decreased significantly from trial 1 to trial 2, $F(1,44)= 10.133$, $p=.003$ (Table 2.3). For movement, significantly more errors were made with asymmetrical movements compared to symmetrical movements, $F(1,44)=17.135$, $p<.001$ (Table 2.3). In addition, the analysis showed an interaction between trial and movement on bimanual errors, $F(1,44)=5.480$, $p=.024$ (Table 2.3). Pairwise comparisons (with a Bonferroni correction) revealed a significant difference between asymmetrical and symmetrical movements at trial 1, but failed to find a significant difference between the movements at trial 2 (Table 2.4, Figure 2.3). Although the comparisons failed to find a significant difference between trials for symmetrical movements, the error rate for asymmetrical movements improved significantly over trial, corresponding to a medium effect size (Cohen, 1988).

Measure	Main Effect / Interaction		Mean (SE)		Partial η^2	Observed Power
Error Rate	Trial	Trial 1	7.511 (1.109)		.187	.876
		Trial 2	4.129 (.547)			
	Movement	Symmetrical	4.297 (.592)		.280	.982
		Asymmetrical	7.344 (.954)			
	Trial x Movement		Trial 1	Trial 2	.111	.629
		Symmetrical	5.158 (.863)	3.436 (.657)		
		Asymmetrical	9.865 (1.636)	4.822 (.666)		
Speed	Trial	Trial 1	.482 (.029)		.570	1.000
		Trial 2	.389 (.022)			
	Movement	Symmetrical	.341 (.014)		.570	1.000
		Asymmetrical	.530 (.037)			
	Trial x Movement		Trial 1	Trial 2	.183	.867
		Symmetrical	.368 (.017)	.313 (.014)		
		Asymmetrical	.595 (.044)	.464 (.031)		
	Sex x Movement x Trial		Male	Female	.119	.665
		Symmetrical T1	.375 (.025)	.361 (.023)		
		Symmetrical T2	.324 (.020)	.303 (.019)		
		Asymmetrical T1	.679 (.065)	.512 (.060)		
		Asymmetrical T2	.495 (.047)	.433 (.043)		
Speed Standard Deviation	Trial	Trial 1	.199 (.026)		.212	.920
		Trial 2	.133 (.015)			
	Movement	Symmetrical	.118 (.016)		.421	1.000
		Asymmetrical	.214 (.026)			
Dominant-Nondominant Onset Standard Deviation	Movement	Symmetrical	.035 (.003)		.286	.984
		Asymmetrical	.054 (.006)			
	Sex	Male	.034 (.005)		.169	.832
		Female	.055 (.005)			
	Sex x Movement		Male	Female	.138	.738
		Symmetrical	.031 (.004)	.039 (.003)		
		Asymmetrical	.036 (.008)	.072 (.008)		

Table 2.3. Means, effect sizes, and power of significant effects for bimanual movements. Mauchly's Test of Sphericity did not indicate violations, so sphericity corrections were not applied.

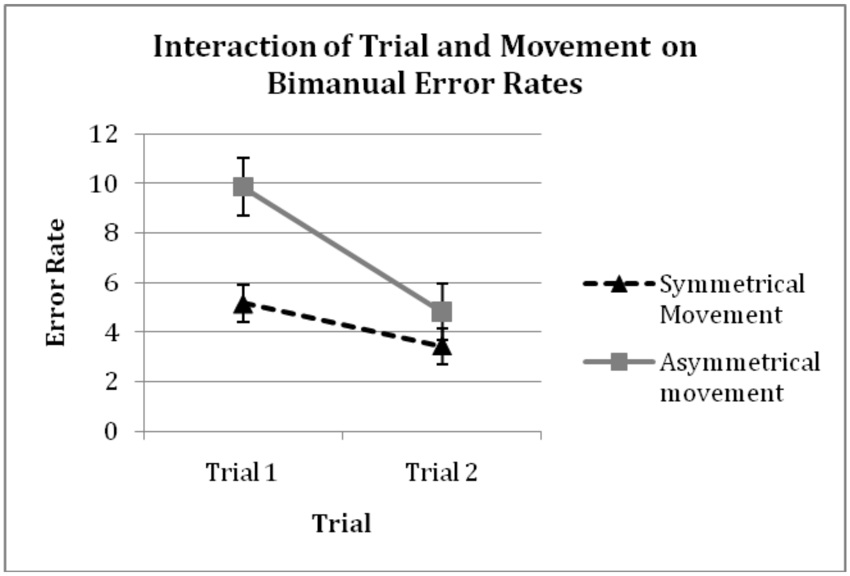


Figure 2.3. Interaction of trial and movement on bimanual error rates. Symbols represent the means and error bars represent the standard error of the mean.

Comparisons for bimanual error rates	Mean Difference	SE	*p* value	Cohen's *d*
Symmetrical, trial 1 – trial 2	1.722	.975	.084	N/A
Asymmetrical, trial 1 – trial 2	5.043*	1.612	.003	.596
Trial 1, symmetrical - asymmetrical	-4.707*	1.387	.001	-.532
Trial 2, symmetrical - asymmetrical	-1.387	.741	.068	N/A

Table 2.4. Pairwise comparisons of the interaction of movement and trial for bimanual error rates (* denotes significance).

For bimanual speed, the ANCOVA with years of music lessons as a covariate revealed main effects of trial and movement. For trial, speed increased significantly from trial 1 to trial 2, $F(1,44) = 58.305$, $p<.001$ (Table 2.3). For movement, speed was significantly slower for asymmetrical movements compared to symmetrical movements, $F(1,44)=58.305$, $p<.001$ (Table 2.3). In addition, the analysis showed an interaction between trial, movement, and sex on bimanual speed, $F(1,44)=5.964$, $p=.019$ (Table 2.3, Figure 2.4). Pairwise comparisons (with a Bonferroni correction) showed significant improvement over trial and greater speed for symmetrical movements compared to asymmetrical movements (Table 2.5). There was a near-significant comparison between males and females at trial 1 for asymmetrical movement, with a trend for women to perform asymmetrical movements more quickly (mean difference= .167, standard error= .090, $p=.072$).

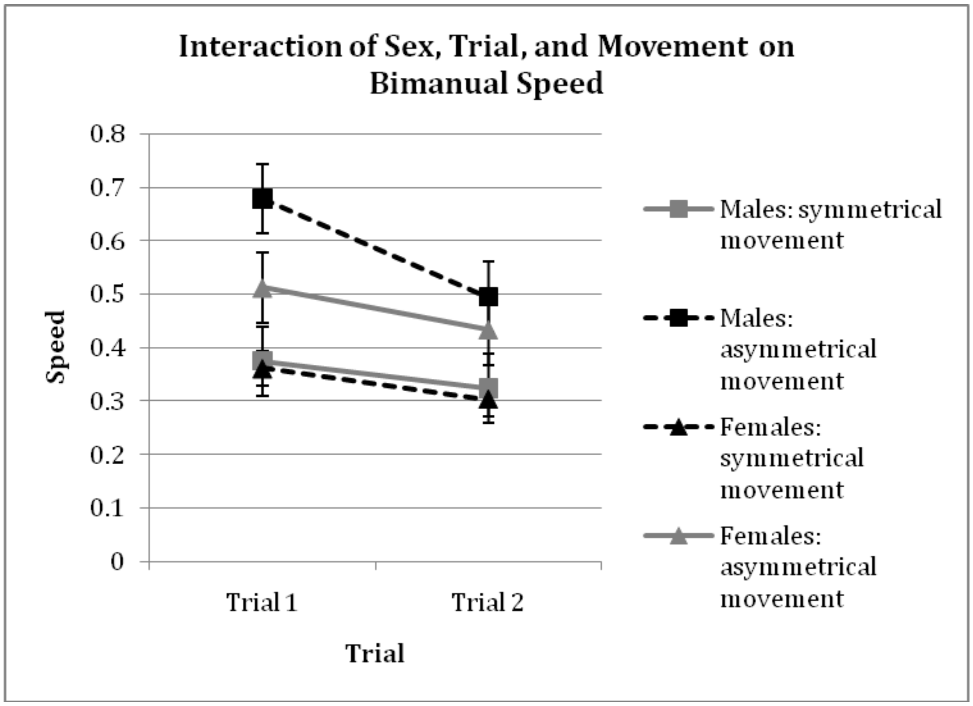


Figure 2.4. Interaction of sex, trial, and movement on bimanual speed. Symbols represent the means and error bars represent the standard error of the mean.

Comparisons for bimanual speed	Mean Difference	SE	*p* value	Cohen's *d*
Males, trial 1, asymmetrical - symmetrical	.303*	.048	<.001	1.113
Males, trial 2, asymmetrical - symmetrical	.171*	.033	<.001	.898
Females, trial 1, asymmetrical - symmetrical	.151*	.045	.001	.647
Females, trial 2, asymmetrical - symmetrical	.130*	.031	<.001	.659
Symmetrical, males, trial 1 – trial 2	.051*	.014	.001	.369
Asymmetrical, males, trial 1 – trial 2	.184*	.032	<.001	.569
Symmetrical, females, trial 1 – trial 2	.058*	.013	<.001	.396
Asymmetrical, females, trial 1 – trial 2	.079*	.030	.011	.271

Table 2.5. Pairwise comparisons of the interaction of trial, movement, and sex for bimanual speed (* denotes significance). Comparisons between males and females failed to reach significance and are not included in the table

For standard deviation of speed, the ANCOVA with years of music lessons as a covariate revealed main effects of trial and movement. For trial, speed standard deviation decreased significantly from trial 1 to trial 2, *F*(1,44)= 11.818, *p*=.001 (Table 2.3). For movement, speed standard deviation was significantly higher for asymmetrical movements compared to symmetrical movements, *F*(1,44)=32.934, *p*<.001 (Table 2.3).

The ANCOVA with years of music lessons as a covariate failed to reveal significant effects for dominant-nondominant onset. Dominant-nondominant onset reflects the time between paired dominant and nondominant keystrokes; negative values result from the nondominant digit striking the key first while positive values result from the dominant digit striking the key first.

For dominant-nondominant onset standard deviation, the ANCOVA with years of music lessons as a covariate revealed main effects of movement and sex. For the main effect of movement, dominant-nondominant onset standard deviation was higher for asymmetrical movements in comparison to symmetrical movements, *F*(1,44)= 17.614, *p*<.001 (Table 2.3). For the main effect of sex, dominant-nondominant onset standard deviation was higher for females compared to males, *F*(1,44)= 8.919, *p*=.005 (Table 2.3).

The analysis showed an interaction of movement and sex on dominant-nondominant onset standard deviation, *F*(1,44)= 7.047, *p*=.011 (Table 2.3, Figure 2.5). Pairwise comparisons (with a Bonferroni correction) revealed that the standard deviation of dominant-nondominant onset was significantly higher for females compared to males for asymmetrical movements (Table 2.6). In addition, women demonstrated significantly greater standard deviation for asymmetrical movements compared to symmetrical movements; this comparison failed to reach significance for males.

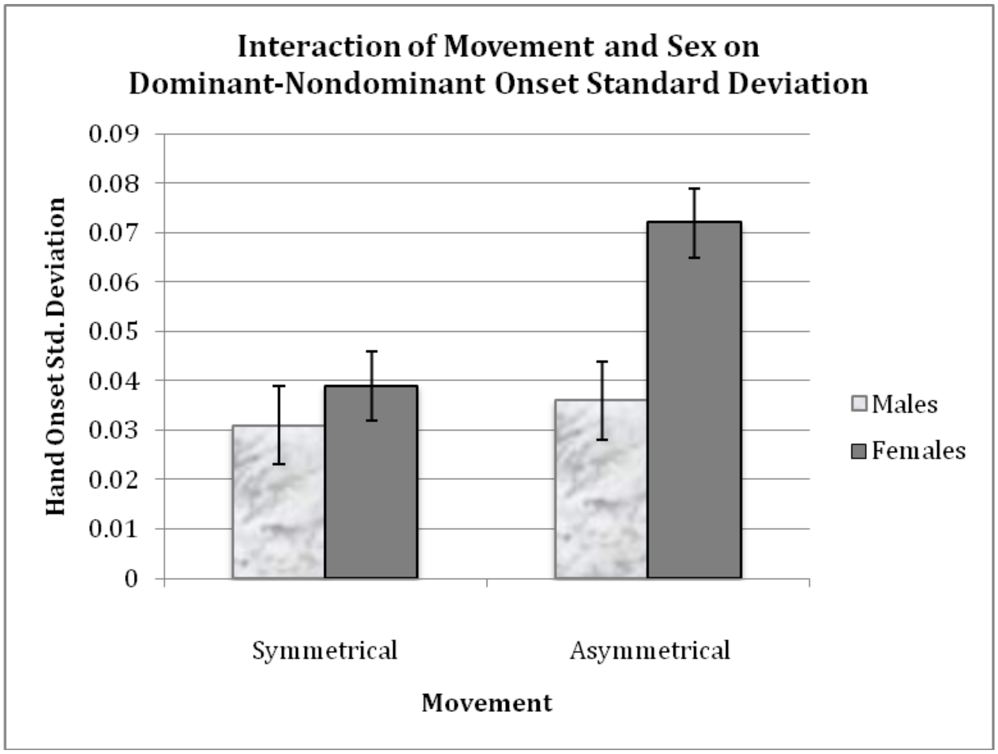


Figure 2.5. Interaction of movement and sex on dominant-nondominant onset standard deviation. Bars represent the means and error bars represent the standard error of the mean.

Comparisons for dominant-nondominant onset standard deviation	Mean Difference	SE	*p* value	Cohen's *d*
Symmetrical, male – female	-.008	.005	.148	N/A
Asymmetrical, male – female	-.036*	.012	.004	-.437
Males, symmetrical – asymmetrical	-.005	.008	.530	N/A
Females, symmetrical – asymmetrical	-.033*	.007	<.001	-.406

Table 2.6. Pairwise comparisons of the interaction of movement and sex for dominant-nondominant onset standard deviation (* denotes significance).

Downbeat-Offbeat Ratios

For downbeat-offbeat ratios, the ANCOVA with years of music lessons as a covariate revealed a main effect of trial, with stronger downbeat-offbeat ratios at trial 2 compared to trial 1, $F(1,220)=9.895$, $p=.003$ (Table 2.7). The main effect of movement approached significance, $F(5,220)=2.209$, $p=.054$ (Table 2.7). However, pairwise comparisons (with a Bonferroni correction) revealed significant effects of downbeat-offbeat ratios in relation to the nondominant hand (Table 2.8).

The ANCOVA showed significant main effects of the covariate, years of music lessons, for errors, $F(1,44)= 10.713$, $p=.002$, speed, $F(1,44)=18.540$, $p<.001$, speed standard deviation, $F(1,44)=9.668$, $p=.003$, and dominant-nondominant onset, $F(1,44)=6.438$, $p=.015$. There was an interaction between years of lessons and trial for speed, $F(1,44)=8.358$, $p=.006$. There was a significant interaction of years of lessons and movement for bimanual errors, $F(1,44)=4.450$, $p=.041$, speed, $F(1,44)=8.234$, $p=.006$, speed standard deviation, $F(1,44)=6.104$, $p=.017$, and dominant-nondominant onset standard deviation, $F(1,44)=4.401$, $p=.042$. In addition, the analysis showed a significant effect of the covariate on downbeat-offbeat ratio, $F(1,44)=8.093$, $p=.007$, but no interactions with the covariate reached significance on this measure.

Main Effect / Interaction		Mean (SE)	Partial η^2	Observed Power
Trial	Trial 1	.997 (.004)	.184	.868
	Trial 2	1.008 (.004)		
Movement	Dominant unilateral	.992 (.006)	.048	.715
	Nondominant unilateral	1.014 (.005)		
	Dominant symmetrical	1.001 (.005)		
	Nondominant symmetrical	1.018 (.006)		
	Dominant asymmetrical	.993 (.006)		
	Nondominant asymmetrical	.998 (.005)		

Table 2.7. Means, effect sizes, and power of significant effects in relation to downbeat-offbeat ratios. Mauchly's Test of Sphericity did not reach significance, so no sphericity corrections were applied.

Movement Comparisons for Downbeat-Offbeat Ratios	Mean Difference	SE	*p* value	Cohen's *d*
Nondominant unilateral - Dominant asymmetrical	.022	.006	.025	.617
Nondominant unilateral - Nondominant asymmetrical	.017	.006	.016	.480
Nondominant symmetrical - Dominant unilateral	.025	.007	.020	.715
Nondominant symmetrical - Dominant asymmetrical	.025	.007	.019	.619
Nondominant symmetrical - Nondominant asymmetrical	.020	.005	.005	.496

Table 2.8. Statistically significant results of pairwise comparisons of movement for downbeat-offbeat ratios.

Discussion

The present findings confirm the usefulness of the piano keyboard task as a means to study motor learning. Importantly, the keyboard task assesses a socially valued and functional activity. Performance may be altered as a function of salience attributed to the movement (Kurniawan et al., 2010). Therefore, this task most likely reflects genuine functional ability. In addition, the keyboard task allows for fine-tuning of degree of difficulty, study of in-phase and out-of-phase bimanual movements, and examination of independent and combined finger movement in any imaginable combination.

Consistent with the hypothesis that nondominant movements require relatively more neural resources than dominant manual movements, dominant unimanual movement was performed with greater speed compared to nondominant unimanual movement, although effects related to error rates failed to reach significance. This replicates prior research findings of faster movement with the dominant hand (Lissek et al., 2007).

The prediction that males would perform unimanual movements more quickly than females was not supported by the study; effects for sex related to unimanual speed failed to reach significance. However, this study included a diverse population of older and young adults, which may have obscured sex effects in relation to unimanual speed. An interaction of sex, trial, and movement in relation to unimanual error rates was identified, but post-hoc comparisons between males and females failed to reach significance.

In keeping with the hypothesis that symmetrical movement requires decreased neural resources relative to asymmetrical movement, prior studies have reported decreased errors, faster movement, and decreased movement variability for symmetrical movements in comparison to asymmetrical movements (Essers & Adam, 2010; Hughes &

Franz, 2008; Matthews et al., 2009). These findings were replicated; symmetrical movements were performed with fewer errors, greater speed, and decreased variance of speed compared to asymmetrical movements (partial η^2 of .28, .57, and .42 respectively). However, practice reduced the differences in error rate between symmetrical and asymmetrical movements.

Bimanual asymmetrical patterns may be the most challenging of the tested movements. The study failed to find main effects of sex in relation to speed and error rates as hypothesized. However, the study found an interaction of trial, movement, and sex in relation to movement speed. While comparisons between males and females failed to reach significance, there is an apparent gender trend of sex when effect sizes for the significant comparisons are considered. Males exhibited a large effect size difference between bimanual movements for both trials, while the effect sizes for females were moderate (Cohen, 1988). This suggests that males experience more difficulty with asymmetrical movements relative to symmetrical movements compared to females. Further, the practice effect for asymmetrical movement was moderate for males, while symmetrical movement for males and both movements for females demonstrated small effect sizes in relation to trial (Cohen, 1988).

In support of the hypothesis that stronger inter-hemispheric connections among females confers an advantage for bimanual performance, the results of this study suggest that asymmetrical movements are relatively more difficult for males than females, in that differences in speed between the two types of movements were smaller for females. To the writer's knowledge, this is the first study to identify sex differences in relation to bimanual movement. Asymmetrical movements requires the use of additional neural resources (De

Weerd et al., 2008; Maki et al., 2008; Walsh et al., 2008). It appears, then, that females may be better able to coordinate the complex motor programming associated with bimanual movements.

Surprisingly, effects related to nondominant-dominant onset failed to reach significance. Given prior research related to the dominant hand leading symmetrical movements (Walsh et al., 2008), one would expect positive values for dominant-nondominant onset for symmetrical movements and high, positive values in relation to better performance. There are a few possible reasons why this measure failed to reach significance. First, the measure reflects which digit strikes the bottom of the key first, and as a result does not reflect movement initiation. Second, movements may be "chunked" by neural systems (Loehr & Palmer, 2007), and therefore only keystrokes at the start of a "chunk" may be relevant to assessment of a leading joint strategy. This issue requires further research to identify definitive answers.

The finding that females exhibited significantly higher dominant-nondominant onset standard deviation may provide insight into sex differences related to movement strategies. Importantly, the decreased coupling between limbs shown by females during asymmetrical movements (as evidenced by increased dominant-nondominant onset standard deviation) corresponds with the trend for females to perform asymmetrical movements faster than males at trial 1. Females may be better able to inhibit inter-limb coupling to improve execution of independent limb movements.

The findings of more rhythmic movement with the nondominant compared to the dominant hand and for symmetrical compared to asymmetrical movements initially appears contradictory. Intuitively, nondominant performance is more difficult than dominant performance while symmetrical performance is easier than asymmetrical performance. As such, the findings do not fit with the notion that playing rhythmically is a strategy to cope with increased neural demands.

Considering the increased input of the dominant primary motor cortex to the contralateral hemisphere during symmetrical movements, the significant finding of a small increase in downbeat emphasis may correspond with a limb-locking strategy and increased input from the dominant hemisphere. By extension, the increased downbeat emphasis exhibited by the nondominant hand across movements may result from increased reliance on the dominant primary cortex for the temporal aspects of movement in particular. This idea is further supported by the decreased variance related to bilateral keystrokes for symmetrical movements.

In summary, the keyboard task appears to be a sensitive measure of change associated with practice and is capable of differentiating between different types of bimanual movements. The method is an effective means of studying bimanual learning in the general population. The study findings suggest that there are sex differences with regard to performance of bimanual movements, and point to possible strategies that facilitate proficiency of symmetrical movements. These results must be replicated and shown to generalize to other types of tasks prior to application in the clinical setting.

CHAPTER 3:
AGING DIFFERENTIALLY IMPACTS PERFORMANCE OF BIMANUAL MOVEMENT

Introduction

Movement and the ability to acquire new motor skills are crucial to normal function. The essential role movement plays in everyday life becomes exquisitely clear when motor function is compromised by disease, injury, or the aging process. While disease or injury may impair motor abilities for part of the population, aging is a gradual and biologically inevitable process. Further, aging may compound the effects of injury or disease.

Motor Performance and Aging

Aging is implicated in slower motor reaction times (Poston, Van Gemmert, Barduson, & Stelmach, 2009; Riecker et al., 2006; Rossit & Harvey, 2008) and slower execution of movements during standardized motor tests (Ruiz, Bernardos, Bartolomé, & Torres, 2007), drawing tasks (Lee, Fradet, Ketcham, & Dounskaia, 2007), and reaching movements (Poston et al., 2009; Rossit & Harvey, 2008). In addition, older adults exhibit shorter reach lengths for both the dominant and nondominant upper extremities (Poston et al., 2009) and extended deceleration phases at the end of the reach (Cooke et al., 1989). Older adults also demonstrate shortened primary submovements with increased frequency of secondary submovements (Fradet, Lee, & Dounskaia, 2008).

Older adults process complex, novel and cognitive motor responses more slowly than young adults (Gorus, De Raedt, & Mets, 2006). In addition, older adults adjust and inhibit motor movements more slowly than their younger counterparts (Rossit & Harvey, 2008; Sarlegna, 2006). In one study, most adults over 60 years of age failed to inhibit a previously learned movement in favour of a novel one, and approximately 40% of adults between 50 and 80 years failed to inhibit on the second attempt (Potter & Grealy, 2006). Even among 50 year olds, 60% inhibited on the first trial, but only 10% did so in the same time as the youngest adults (Potter & Grealy, 2006). These findings point to a decreased capacity to program complex motor responses as a result of aging.

MIDI sound from a piano keyboard and a motion capture system were used to investigate inhibition of learned finger sequences (Trewartha, Endo, Li, & Penhune, 2009). Older adults inhibited previously learned motor responses more slowly in comparison to young adults despite similar performance of prepotent responses (i.e. the initial sequences). The finding extends to bimanual movements. During a bimanual coordination task with altered feedback, older adults were less adept at inhibiting prepotent responses in comparison to young adults (Swinnen et al., 1998).

Increased variability of movement is often reported as a consequence of aging. Despite similar rates of unilateral tapping, older adults exhibit increased variability with unilateral tapping compared to young adults (Bangert et al., 2010). Further, the variability of asynchronous tapping increases with age (Bangert et al., 2010). During reaching movements, older adults exhibit increased variability of movement in general, but particularly during deceleration (Cooke et al., 1989). During object manipulation, both younger and older adults adapt to external forces, but older adults exhibit higher non-functional variation of grip force in interacting with a finger-object interface (Danion, Descoins, & Bootsma, 2007).

Young and older adults exhibit divergent strategies for a range of movements. During arm movements with a velocity-dependent force field, older adults compensated by more involvement of the shoulder and increased variability of strategies (Cesqui, Macrì, Dario, & Micera, 2008). Similarly, during a tracing task requiring multi-joint shoulder and elbow movement, younger and older adults used different strategies (Ketcham, Dounskaia, & Stelmach, 2004). Specifically, young adults increased elbow amplitude in response to distortions while older adults failed to increase elbow muscle torque as frequency increased (Ketcham et al., 2004).

In examining past research related to aging and movement, several themes emerge. Older adults exhibit increased reaction times, increased movement time, and segmentation of movements in relation to varying performance demands (Cooke et al., 1989; Fradet et al., 2008; Lee et al., 2007; Poston et al., 2009; Riecker et al., 2006; Rossit & Harvey, 2008; Ruiz et al., 2007). In addition, adaptation to external forces and inhibition of previously learned patterns may be compromised (Danion et al., 2007; Rossit & Harvey, 2008; Potter & Grealy, 2006; Swinnen et al., 1998; Trewartha et al., 2009). Older adults also demonstrate increased movement variability and use different motor strategies to execute tasks (Cesqui et al., 2008; Cooke et al., 1989; Ketcham et al., 2004).

Neural Function and Aging

Studies of neural function point to a neural basis for motor changes and strategy differences in particular as a function of aging. Event-related potentials

(ERP) were examined during a motor priming paradigm consisting of a dual-choice button press in response to three possible visual stimuli (Sterr & Dean, 2008). Older adults (aged 68 to 83 years) failed to demonstrate the pattern of activation characteristic of valid trials—namely decreased reaction time, increased fore-period amplitudes, and lateralized activation over motor regions. Rather, older adults showed greater positive frontocentrally distributed potentials in the P300 range (Sterr & Dean, 2008).

In contrast, a relatively younger sample (mean age of 58.3 ±2.1 years) was assessed with electroencephalography (EEG) during a motor choice reaction task consisting of four possible finger flexion responses corresponding to four visual stimuli (Falkenstein, Yordanova, & Kolev, 2006). Older adults were found to respond more slowly due to alteration of movement components rather than differences in centrally mediated stimulus processing or response selection (Falkenstein et al., 2006).

Older adults exhibit temporal declines of bimanual circle drawing and simultaneous tapping (Bangert et al., 2010). Interestingly, lower executive function correlated with asynchronous inter-manual timing deficits, and better performance of the most difficult bimanual circling task was associated with better working memory for older adults (Bangert et al., 2010). The authors postulate that for the older adults, executive and working memory functions are engaged for difficult tasks (Bangert et al., 2010).

Age differences in neural connectivity were evaluated with diffusion tensor fMRI (Bennett, Madden, Vaidya, Howard, & Howard, 2010). Three patterns of diffusivity were identified: increased radial diffusivity indicates axonal shrinkage and demyelination and was found in regions corresponding to frontal, posterior pericallosal, superior longitudinal fasciculus, and sagittal striatal white matter (Bennett et al., 2010). Increased radial and axial diffusivity indicates more severe axonal demyelination, shrinkage, and loss, and was found in the genu of the corpus callosum, the external capsule, and the fornix. Finally, increased radial diffusivity and decreased axial diffusivity is proposed to indicate disrupted macrostruture (such as axonal loss) in areas of small, densely packed and crossing fibres, and was observed in the anterior pericallosum and anterior-superior corona radiata (Bennett et al., 2010).

Attempts have been made to attribute motor changes observed with aging to either increased or decreased lateralization. Motor overflow, recorded via surface electromyography during unilateral finger tapping, is associated with faster tapping rates, cognitive distraction, and fatigue (Bodwell, Mahurin, Waddle, Price, & Cramer, 2003). Further, among older adults, maximal tapping rates and fatigue resulted in differentially more overflow, and better performance with the nondominant hand correlated with increased overflow to the dominant hand (Bodwell et al., 2003). Conversely, a relatively younger sample of older adults demonstrated amplitude enhancement and longer cortex motor-related potentials contralateral to the moving hand with EEG, suggesting increased lateralization (Falkenstein et al., 2006).

Neural activation during externally paced dominant index finger tapping among individuals from 18 to 79 years old was examined with fMRI; a significant negative correlation between age and the weighted Laterality Index in relation to

M1 activation was found (Naccarato et al., 2006). The authors postulate that increased bilateral M1 recruitment is a compensatory strategy used by older adults to engage more resources in order to produce similar motor responses as young adults. Similarly, although tapping frequency, tapping interval, and error rates failed to differ significantly between age groups, reaction time was significantly slower for older adults (Riecker et al., 2006). Imaging with fMRI revealed significant overactivation at higher movement rates of the ipsilateral sensorimotor and premotor cortex among older adults (Riecker et al., 2006).

Brain activation and connectivity of older and younger adults during voluntary movement was studied with repetitive transcranial magnetic stimulation (rTMS) and positron emission tomography (PET) (Rowe et al., 2006). Older adults exhibited increased bilateral activation of the premotor cortex, more inhibition by rTMS, more local connectivity, and reduced connectivity between distant motor-related areas (Rowe et al., 2006). Similarly, older adults showed decreased lateralization and additional areas of activation during bimanual movement, including the SMA, inferior parietal cortex, and dorsolateral prefrontal cortex, despite slower movement speed (Goble et al., 2010).

Reports of neural activation changes associated with aging conflict, which may in part depend on the type of movement studied, task difficulty, and the inconsistent definition of “older age.” However, current research suggests that older adults have distinctly different patterns of neural activation during movement than young adults, possibly including increased use of networks commonly associated with executive function (Bangert et al., 2010; Sterr & Dean, 2008). Further, decreased lateralization of neural function in older adults may point to increased recruitment of neural resources as compensation for deterioration of frontal and key intra-hemispheric networks, especially callosal structures (Bangert et al., 2010; Bennett et al., 2010; Naccarato et al., 2006; Riecker et al., 2006; Rowe et al., 2006). The deterioration of inter-hemispheric connections as a result of aging may be particularly responsible for degradation of bimanual movement.

Causative Factors Associated With the Aging Brain

Causative factors associated with brain aging and motor changes are difficult to identify because of the systemic and interactive nature of the motor system. However, there are some promising lines of research. Caloric restriction modifies age-related brain changes in nonhuman primates, slowing the rate of iron accumulation in the basal ganglia and parietal, temporal, and peri-rhinal cortices (Kastman et al., 2010). Importantly, the deterioration of fine motor movement speed associated with aging was reduced (Kastman et al., 2010). The findings suggest that accumulation of iron in the aging brain contributes to the decline in motor function observed with aging. Somatosensory changes associated with aging and alterations in cortical plasticity among older adults may also contribute to motor decline (Fathi et al., 2010).

Considerable attention has been directed toward the relationship between cognition and vascular compromise, evidenced by white matter hyperintensities. While the relationship between vascular integrity and motor function has received less attention, it appears that white matter hyperintensities are associated with decreased gait speed (Soumare et al., 2009), impaired balance (Starr et al., 2003), and step length variability (Rosano, Brach, Studenski, Longstreth, & Newman, 2007). Of importance to this study, white matter hyperintensities were associated with reduced fine motor coordination among a sample of 478 adults, aged 60 to 64 years (Sachdev, Wen, Christensen, & Jorm, 2005). By extension, white matter hyperintensities may correspond to impaired performance of other types of movements, specifically bimanual movements.

Vascular compromise may also occur in conjunction with decreased cerebral blood flow. A comparison of cerebral blood flow between a small sample of healthy young adults (median age 29 years) and older adults (median age 87 years) revealed that older subjects had significantly lower cerebral flow by 246mL/min (Spilt et al., 2005). Vascular factors have also been implicated in deterioration of specific brain regions. Using diffusion tensor imaging, a recent study found a relationship between vascular risk factors and reduced corpus callosum integrity across participants with Alzheimer disease, mild cognitive impairment, and normal cognition (Lee et al., 2010).

Prior research highlights age-specific effects in relation to movement and points to shifts in strategy and patterns of neural activation as clues to potential sources of age-related motor decline. Vascular factors may account for both the general and specific neural alterations that have been implicated in motor changes associated with aging (Potter & Grealy, 2006; Bangert et al., 2010), but further investigation is required. Further, how aging impacts bimanual skill acquisition and if aging differentially impacts learning of certain movement patterns more than others is unknown.

The aforementioned questions are extremely important to address, given the range of bimanual tasks encountered in everyday situations. Furthermore, the necessity of relearning tasks in the context of neurological conditions, many of which preferentially affect aged adults, is of ever-increasing importance. The purpose of this study is to examine how aging influences the acquisition of different types of skilled movement via the keyboard task. It is hypothesized that global neurological decline associated with aging will result in older adults performing movements with higher error rates and more slowly than younger adults. In addition, it is hypothesized that differential deterioration of inter-hemispheric connections associated with aging will result in poorer performance of bimanual movements relative to unimanual movements.

Materials and Methods

The materials and methods for this study have previously been described in Chapter 2 (pp. 18-22).

Additional Statistical Analysis

Inter-hemispheric connectivity may be compromised as a consequence of aging (Bennett et al., 2010; Lee et al., 2010). Thus, bimanual movement may be more sensitive to age-related decline compared to unimanual movement. To examine if aging resulted in differentially poorer performance in relation to bimanual movement, a ratio score was calculated for the measures of errors, speed, and speed standard deviation for each trial. For the ratio score, averaged unimanual scores were subtracted from averaged bimanual scores and then the resulting number was divided by the sum of the averaged unimanual and averaged bimanual scores. A mixed factorial ANOVA (2x2x2) was employed to compare ratios for the between-subject factors of age groups (young and older), sex (male and female), and prior music lessons (less than a year and equal to or greater than a year).

Results

Unimanual Movements

A Pearson correlation was used to determine if younger adults performed better because of past music lessons (self-report) or greater intelligence as measured by performance on the Vocabulary Test. Age did correlate significantly with years of music lessons (P=.294, p=.025) and the Vocabulary Test (P=.596, p<.001), but in favour of the older adults. That is, older adults tended to score higher on the Vocabulary Test and had taken greater number of years of music lessons. As mentioned in Chapter 2, years of music lessons were entered into the models as a covariate because prior music lessons and motor measures correlated significantly.

For errors, the ANCOVA with years of music lessons as a covariate revealed a main effect of age, with older adults making significantly more errors than younger adults, $F(1,51)=6.211$, p=.016 (Table 3.1).

Measure	Main Effect / Interaction		Older Adults	Young Adults	Partial η^2	Observed Power
			Mean (SE)	Mean (SE)		
Error Rate	Age Group		3.690 (.496)	1.907 (.514)	.109	.686
Speed	Age Group		.344 (.014)	.229 (.015)	.382	1.000
	Trial x Age Group	Trial 1	.367 (.015)	.241 (.016)	.108	.683
		Trial 2	.321 (.014)	.216 (.014)		
	Hand x Age Group	Dominant	.325 (.014)	.221 (.014)	.115	.714
		Nondominant	.363 (.015)	.236 (.016		
Speed Standard Deviation	Age Group		.120 (.011)	.066 (.012)	.182	.911
	Trial x Age Group	Trial 1	.140 (.013)	.070 (.014)	.149	.835
		Trial 2	.099 (.010)	.062 (.010)		

Table 3.1. Means, effect sizes, and power of significant effects for unimanual movements. Mauchly's Test of Sphericity did not indicate a violation of sphericity, so no corrections were applied.

Comparisons for unimanual speed	Mean Difference	SE	*p* value	Cohen's *d*
Interaction of trial and age				
Trial 1, young – older adults	-.126*	.022	<.001	-1.243
Trial 2, young – older adults	-.105*	.020	<.001	-1.207
Young adults, trial 1 – trial 2	.025*	.006	<.001	0.454
Older adults, trial 1 – trial 2	.046*	.006	<.001	0.375
Interaction of hand and age				
Dominant hand, young – older adults	-.104*	.020	<.001	-1.174
Nondominant hand, young – older adults	-.127*	.022	<.001	-1.292
Young adults, dominant – nondominant hand	-.015*	.006	.026	-0.271
Older adults, dominant – nondominant hand	-.038*	.006	<.001	-0.308

Table 3.2. Pairwise comparisons of interactions for unimanual speed (* denotes significance).

For speed, the ANCOVA with years of music lessons as a covariate revealed a main effect of age, with older adults performing significantly slower than younger adults, $F(1,51)=31.526$, $p<.001$ (Table 3.1). Two significant interactions with age as a factor were observed. There was a significant interaction between trial and age group, $F(1,51)=6.165$, $p=.016$. Pairwise comparisons (with a Bonferroni correction) revealed large effect sizes of age for both trials, and small effect sizes related to practice for both young and older adults (Table 3.2, Figure 3.1). There was also a significant interaction between hand and age group, $F(1,51)=6.630$, $p=.013$. Pairwise comparisons (with a Bonferroni correction) showed that both young and older adults performed the movements more quickly with the dominant hand, but younger adults performed unimanual movements much more quickly than older adults for both the dominant and nondominant hands (Table 3.3, Figure 3.2). The analysis showed large effect sizes of age for both trials, and small effect sizes related to practice for both young and older adults (Cohen, 1988). The four-way interaction between trial, hand, sex, and age group approached significance, $F(1,51)=3.093$, $p=.054$.

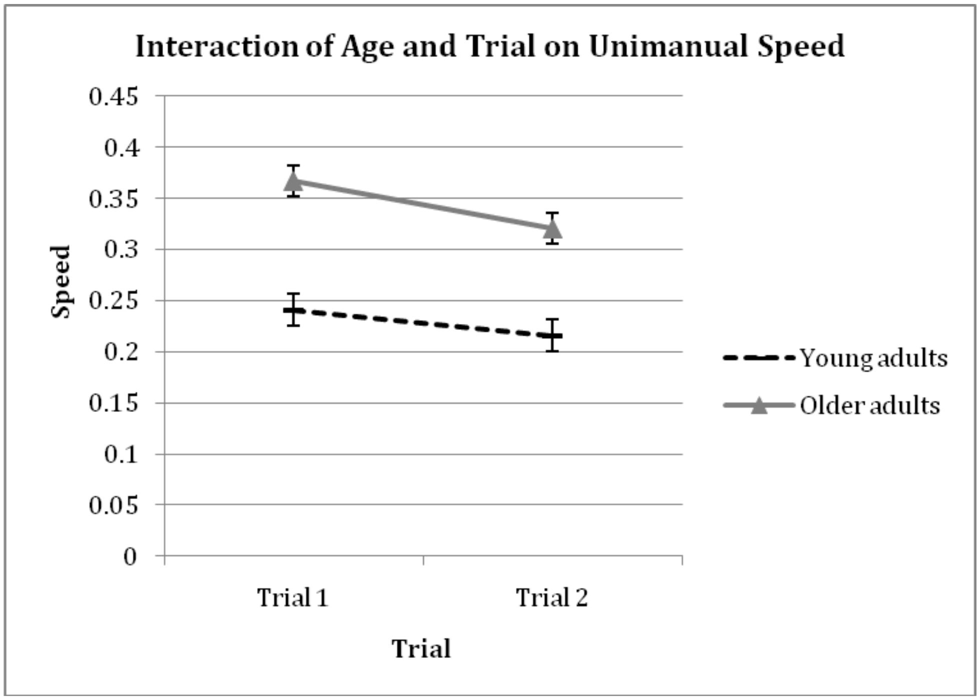


Figure 3.1. Interaction of age and trial on unimanual speed. Symbols represent the means and error bars represent the standard error of the mean.

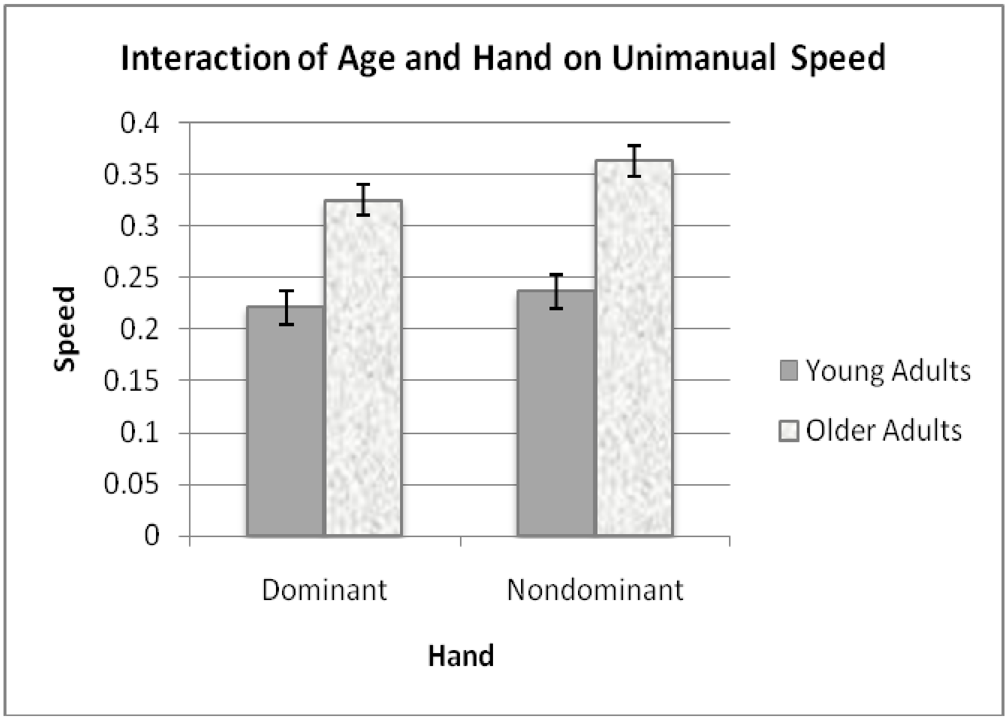


Figure 3.2. Interaction of age and hand on unimanual speed. Bars represent the means and error bars represent the standard error of the mean.

For standard deviation of speed, the ANCOVA with years of music lessons as a covariate revealed a main effect of age, with older adults performing with significantly higher standard deviation of speed than younger adults, $F(1,51)= 11.363$, $p=.001$ (Table 3.1). There was a significant interaction between trial and age group, $F(1,51)= 8.951$, $p=.004$ (see Table 3.1). Pairwise comparisons (with a Bonferroni correction) failed to reveal a difference between trials for young adults in relation to speed standard deviation, but did find a significant difference between trials for older adults (Table 3.3, Figure 3.3). Speed standard deviation decreased significantly from trial 1 to trial 2, and corresponded to a small effect size (Cohen, 1988). In addition, older adults demonstrated significantly higher speed standard deviation than young adults at both trial 1 and trial 2, although the difference decreased from a medium effect at trial 1, to a small effect at trial 2 (Cohen, 1988).

Comparisons for speed standard deviation	Mean Difference	SE	*p* value	Cohen's *d*
Young adults, trial 1 – trial 2	.009	.008	.274	N/A
Older adults, trial 1 – trial 2	.041*	.007	<.001	0.378
Trial 1, young – older adults	-.070*	.019	.001	-0.775
Trial 2, young – older adults	-.038*	.015	.012	-0.494

Table 3.3. Pairwise comparisons of the interaction of trial and age for unimanual speed standard deviation (* denotes significance).

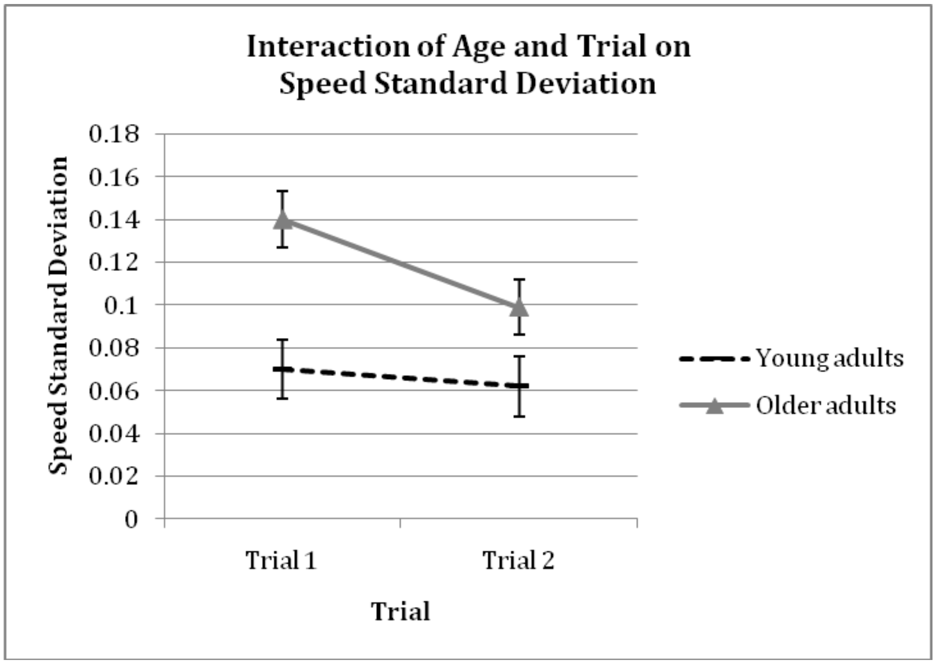


Figure 3.3. Interaction of age and trial on unimanual speed standard deviation. Symbols represent the means and error bars represent the standard error of the mean.

Measure	Main Effect/ Interaction	Older Adults	Young Adults	Partial η^2	Observed Power
		Mean (SE)	Mean (SE)		
Error Rate	Age Group	8.131 (.991)	3.509 (.913)	.210	.917
Speed	Age Group	.514 (.036)	.357 (.034)	.185	.870
Speed Standard Deviation	Age Group	.218 (.028)	.115 (.026)	.138	.737
Downbeat-Offbeat Ratio Standard Deviation	Age Group	.053 (.005)	.036 (.005)	.122	.675

Table 3.4. Means, effect sizes, and power of significant effects for bimanual movements. Mauchly's Test of Sphericity did not indicate a violation of sphericity, so no corrections were applied.

Bimanual Movements

For bimanual errors, the ANCOVA with years of music lessons as a covariate revealed a main effect of age, with older adults making significantly more errors than younger adults, $F(1,44)= 11.680$, $p=.001$ (Table 3.4).

For speed, the ANCOVA with years of music lessons as a covariate revealed a main effect of age, with older adults performing movements significantly slower than young adults, $F(1,44)= 9.974$, $p=.003$ (Table 3.4).

For standard deviation of speed, the ANCOVA with years of music lessons as a covariate revealed a main effect of age, with older adults performing movements with significantly higher standard deviation of speed than young adults, $F(1,44)= 7.038$, $p=.011$ (Table 3.4).

No significant effects were found for dominant-nondominant onset. For the standard deviation of dominant-nondominant onset, the ANCOVA with years of music lessons as a covariate revealed a main effect of age, with older adults exhibiting significantly higher standard deviation of dominant-nondominant onset than younger adults, $F(1,44)= 6.096$, $p=.018$ (Table 3.4).

Bimanual-Unimanual Ratios

Although several effects reached significance from the analysis; only those of interest are included (i.e. results related to the main effect of trial are not reported). For the error ratio, the ANOVA revealed a main effect of age; older adults had a significantly higher bimanual-unimanual error ratios than young adults, $F(1,54)=7.681$, $p=.008$ (Table 3.5).

For the speed ratio, the ANOVA revealed a main effect of music lessons; those with lessons had a significantly lower bimanual-unimanual speed ratio than those without, $F(1,54)=18.166$, $p<.001$ (Table 3.5). There was also a near-significant interaction of age group and music lessons in relation to the speed ratio, $F(1,54)=3.940$, $p=.052$. Though only exploratory, pairwise comparisons (with a Bonferroni correction) revealed a significant comparison between older adults with and without prior music lessons (mean difference= -.183, standard error= .041, $p<.001$). Older adults with prior music lessons had significantly lower ratios. The comparison failed to find a difference in terms of past lessons between young adults (mean difference= -.067, standard error= .041, $p=.113$).

For the standard deviation ratio of speed, the ANOVA revealed a main effect of age; older adults demonstrated significantly higher bimanual-unimanual standard deviation speed ratios than younger adults, $F(1,54)= 4.942$, $p=.030$ (Table 3.5). The ANOVA also revealed a main effect of music lessons on the speed standard deviation ratio; those with lessons had significantly lower speed standard deviation ratios than those without lessons, $F(1,54)=4.965$, $p=.030$ (Table 3.5).

Measure	Main Effect / Interaction		Mean (SE)	Partial η²	Observed Power
Error Ratios	Age Group	Older	.480 (.074)	.125	.777
		Young	.189 (.074)		
Speed Ratios	Music Lessons	No lessons	.266 (.021)	.252	.987
		Lessons	.142 (.021)		
Speed Standard Deviation Ratios	Age Group	Older	.304 (.040)	.084	.588
		Young	.176 (.040)		
	Music Lessons	No lessons	.304 (.040)	.084	.590
		Lessons	.176 (.040)		

Table 3.5. Means, effect sizes, and power of significant effects for bimanual-unimanual ratios.

Discussion

As predicted, older adults performed the keyboard task more slowly and with higher error rates for both unimanual and bimanual movements, which supports the *a priori* hypothesis of a global neurological decline associated with aging. In terms of bimanual performance, older adults demonstrated increased error rates and slower speed compared to young adults. Speed standard deviation and downbeat-offbeat ratio standard deviations were also moderately higher in older adults compared to young adults. This is consistent with reports of increased variability of movements due to aging (Bangert et al., Cooke et al., 1989; Danion et al., 2007).

Interactions of trial and age group for both speed and speed standard deviation and of trial and hand for speed in relation to unimanual movements were identified. While practice for older adults had a small effect, decreasing speed standard deviation over trial, the analysis failed to find a significant difference for younger adults. This suggests that although unimanual movements are more variable for older adults in terms of speed, practice partially ameliorates the effect of age. Indeed, the gap in performance between younger and older adults decreased from a moderate effect to a small effect size difference over trial (Cohen, 1988).

While younger adults were faster than older adults for unimanual movements for both trials, older adults improved similarly as a result of practice. This highlights the fact that although aging may be detrimental to unimanual performance, practice provides similar benefits for older adults. Although the study found large effects in favour of young adults for speed of both the dominant and nondominant hands, both young and older adults showed slower movement of the nondominant hand compared to the dominant hand corresponding to a small effect size. Thus, although nondominant movement is slower for older adults compared to young adults, nondominant hand function is not preferentially impacted by aging relative to dominant hand function.

Differences between performance of symmetrical and asymmetrical movements among older adults were not significantly different compared to young adults. Considering that the effects of aging likely compound with advancing years, the large age range of the older adult sample may have obscured discrete differences in effects to symmetrical and asymmetrical movements. However, it is possible that the reliance of symmetrical movements on inter-hemispheric connections, which differentially deteriorate with age, and the relatively larger neural demands of asymmetrical movements result in similar decrements of both types of bimanual movements as a result of aging (Bennett et al., 2010; De Weerd et al., 2003; Hasan et al., 2010; Lee et al., 2010; Maki et al., 2008). Delineation of the relative impact of these factors is important to the understanding of the effects of aging on bimanual movements.

Analysis of bimanual movements showed that older adults exhibited higher variability of downbeat-offbeat ratios. Downbeat-offbeat ratios provide a clue as to how rhythmically the movements are being performed. The fact that the analysis failed to find a significant difference between groups in relation to downbeat-offbeat ratios but older adults were more variable suggests that the two group use similar temporal strategies, but that execution of the strategy may be compromised among older adults.

The prediction of poorer performance of bimanual movements relative to unimanual movements is an extension of the hypothesis that differential deterioration of inter-hemispheric structures associated with aging results in decrements of bimanual performance. This prediction was tested with bimanual-unimanual ratios, which provide an indicator of relative proficiency with bimanual movements; lower ratios correspond to greater proficiency. In terms of error and speed standard deviation ratios, older adults had significantly higher values than young adults (partial η^2 of .125 and .084 respectively), suggesting less skill of bimanual movements relative to unimanual movements. This is consistent with the *a priori* hypothesis and reported deterioration of inter-hemispheric connections as a function of aging (Bennett et al., 2010; Hasan et al., 2010; Lee et al., 2007).

Individuals with prior music training had lower bimanual-unimanual speed ratios, suggesting greater speed of bimanual movements relative to unimanual movements (partial η^2 of .252). In addition, young adults with prior music training exhibited lower speed standard deviation ratios, suggesting greater stability of bimanual movements among this group. The near-significant interaction of lessons and age suggests that, in terms of speed, prior music lessons may be partially protective for older adults and moderate age-related declines in inter-hemispheric connectivity. The finding supports the hypothesis that music may be an effective treatment to attenuate age-related neural degradation (Wan & Schlaug, 2010).

The results of the study are consistent with previous studies investigating the impact of aging on motor movements. In general, aging is associated with increased variability, slower movement, and higher error rates. In addition to general deterioration of manual performance associated with aging, this study also identified a differential decline of bimanual performance relative to unimanual performance. The hypothesized global deterioration of neural structures superimposed by an accelerated decline of inter-hemispheric structures may be attributable to vascular effects associated with aging (Lee et al., 2010). As such, evaluation of vascular health in conjunction with motor performance would provide a clearer indication of how age and its physiological and vascular correlates interact with the variables investigated in this study.

The study highlights the beneficial effects of practice and prior musical training. The results suggest that the same techniques demonstrated to improve performance with young adults are also likely effective for older adults. Furthermore, the beneficial effect of music training on performance of bimanual movements relative to unimanual movements suggests that music training may be an effective therapy for ameliorating age-related motor decline and, specifically, a means to strengthen inter-hemispheric connectivity and minimize age-related deterioration of inter-hemispheric structures. Further research is required to address these issues.

CHAPTER 4:

MUSIC TRAINING AND SEX INFLUENCE THE EFFECT OF AUDITORY FEEDBACK ON MOTOR LEARNING

Introduction

Playing a musical instrument provides immediate auditory feedback about the success of the movement (Münte et al., 2002). It is not surprising, then, that learning to play a musical instrument results in co-activation of auditory and sensorimotor neural networks. With training, this co-activation occurs during motor performance in the absence of auditory feedback, and in the presence of auditory feedback without the corresponding motor performance (Bangert et al., 2006). Indeed, non-musicians fail to demonstrate this co-activation of auditory and sensorimotor networks in the absence of the auditory or motor features of music performance (Bangert et al., 2006).

The network activated by either the motor or auditory aspects of music performance with musicians includes the dorsolateral and inferior frontal cortices (including Broca's area), superior temporal gyrus (Wernicke's area), supramarginal gyrus, SMA, and premotor areas (Bangert et al., 2006). Activation of this extensive network also occurs when professional musicians observe others playing instruments, with or without auditory feedback (Haslinger et al., 2005), suggesting that musical training alters the auditory-sensory pathways in significant ways.

Musical training also reportedly alters the macrostructure of the brain. Measurable alterations to the anatomy of the brain that are attributed to musical training include the primary motor and somatosensory areas, inferior temporal gyri, anterior corpus callosum, and left cerebellum (Elbert et al., 1995; Gaser & Schlaug, 2003; Schlaug et al., 1995). In addition, the extent of these changes corresponds with an earlier onset of training as well as an increased intensity of training (Elbert et al. 1995; Gaser & Schlaug, 2003).

Although most research on music training focuses on comparisons between professional musicians and naïve controls, co-activation of bilateral frontolateral and temporal cortices was observed after five sessions of keyboard training during both a silent motor task and a passive listening task (Bangert & Altenmüller, 2003). A group of naïve musicians learned sequences on a keyboard using the right upper extremity with normal or random note-pitch associations. The group that learned with random-pitch associations improved markedly for certain aspects of performance such as modulation of pressure on the keys and timing, but exhibited *reduced* activation of the right anterior cortex over the course of training for both the silent motor and passive listening tasks (Bangert & Altenmüller, 2003). The results suggest that right anterior networks are particularly important for the recognition, recall, and performance of pitch sequences.

Following the first 20-minute practice session, the group that learned normal note-pitch associations exhibited decreased activation of the ipsilateral sensorimotor cortex during the silent motor task and increased activation around the central sulcus which was lateralized to the left during the passive listening task (Bangert & Altenmüller, 2003). Remarkably, co-activation of sensorimotor and auditory cortices in response to auditory stimuli occurred following a mere 20 minutes of practice. The effect was enhanced following five weeks of training (Bangert & Altenmüller, 2003). Similarly, increased motor cortex excitability was observed while listening to a piece that amateur pianists had rehearsed for 30 minutes, and cortico-spinal facilitation was found following five days of training (D'Ausilio et al., 2006).

Research also suggests that, with musical training, auditory information modifies motor performance. Artificially delaying a tone during keyboard performance with experienced musicians resulted in a compensatory increase in the speed of subsequent keystrokes (Furuya & Soechting, 2010). Alteration of the timing or pitch of a tone resulted in an increase of velocity (Furuya & Soetchting, 2010). Not surprisingly, artificial alterations of tones played by the dominant hand impacted performance parameters of the nondominant hand, confirming the bilateral influence of auditory feedback (Furuya & Soechting, 2010). In addition, irrelevant intervals introduced during keyboard performance impaired the performance of musicians, but not individuals without musical training (Drost, Rieger, Brass, Gunter, & Prinz, 2005). Moreover, the distractor tones induced the corresponding motor responses from musicians alone.

Considering that co-activation of sensorimotor and auditory cortices occurs rapidly with musical performance (Bangert & Altenmüller, 2003; D'Ausilio et al., 2006), it is conceivable that auditory feedback provides additional, immediate sensory information that may improve keyboard performance. Although altered auditory feedback modulates the performance of experienced musicians (Furuya & Soechting, 2010), the benefit of auditory feedback in learning different types of skilled movements for musically naïve individuals is unknown.

The purpose of this study is twofold: to confirm the findings of Study 1 (reported in Chapter 2), and to investigate the effects of feedback on motor performance. It is predicted that keyboard movements will be faster and more accurate with auditory feedback compared to when auditory feedback is not provided. Considering the macrostructural changes to the corpus callosum associated with musical training (Schlaug et al., 1995), it is hypothesized that individuals with music training develop more robust inter-hemispheric connections, which confers an advantage in the performance of bimanual movements. Further, it is predicted that individuals with music training will not only use feedback more effectively, but also perform bimanual movements relatively better than unimanual movements.

Materials and Methods

Subjects

University-age students (*n*=41, aged 18-35 years, mean age= 21.0 ± 3.5 years, 20 males, mean age= 21.4 ± 3.8 years, and 21 females, mean age= 20.6 ± 3.3 years) participated in the study for credit in undergraduate courses through the Department of Psychology's Human Subject Pool. Exclusion criteria included a prior history of playing the piano. However, four participants reported taking keyboard lessons in the remote past, with a range of two months to four years. Considering that motor measures correlated with years of music lessons for any instrument, the participants were not excluded and analysis were conducted accordingly (i.e. years of music lessons was entered as a covariate). Participants were seen at a laboratory. Two cases were excluded; data from one participant was excluded as the participant's age was far outside the range of the rest of the population sample. Data from the second participant was excluded because symmetrical and asymmetrical data from trial 2 was not useable, although the participant demonstrated an ability to do the movements competently at trial 1. Ethics approval for the study was obtained from the University of Lethbridge Human Subject Committee. The study procedures were explained, after which the participant signed a consent form.

Experimental Apparatus and Task

Hand dominance determination. Hand dominance was determined through a questionnaire, which consisted of questions related to which hand is used for specific tasks, and how consistently that hand is used (Elias et al., 1998). Responses were assigned values and summed to yield a score that indicated to hand dominance. Each participant completed the questionnaire at the beginning of the session and the questionnaire was scored prior to beginning the keyboard task.

Demographic questionnaire and vocabulary test. Participants were asked to report current medications, education level and handedness via a written questionnaire. To enable comparison with previous studies, a vocabulary test was used as an indirect measure of general intelligence (Ekstrom et al., 1976).

Keyboard task. The keyboard task is discussed in detail in Chapter 2 (pp. 20-22).

Feedback condition. For the feedback condition, participants were able to hear the electronic keyboard sounds through two speakers on either side of the participant. For the no feedback condition, the speakers were muted and the researcher listened to the keyboard output through earphones. The feedback condition was counterbalanced; 21 of the participants started with the sound condition, followed by the same task without sound, while 20 participants completed the tasks in the reverse order. Following an interval of approximately 15 to 20 minutes during which other tasks were performed, the participant completed the keyboard task again, but in the reverse order of the first trial. See Figure 4.1 for a flow map of the study procedures. The computer task is the weather prediction task, which is discussed in Chapter 5.

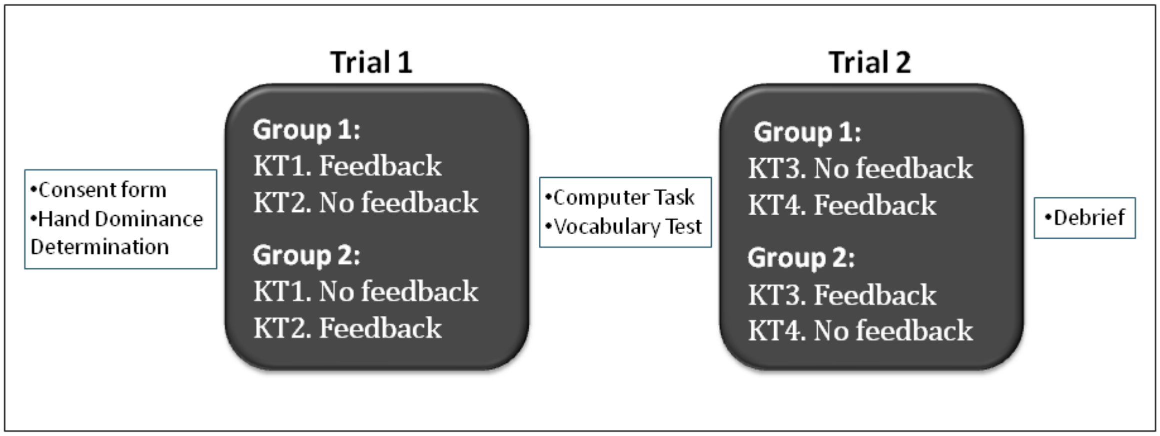


Figure 4.1. Procedures for Study 2 (KT: keyboard task).

Data Analysis

Data analysis is discussed in detail in Chapter 2 (pp. 23-25). For two cases, six and seven clean trials were available for analysis for the asymmetrical condition, and six and seven clean trials were available for the symmetrical condition (for one of the four trials from each participant). Eight clean trials were available for analysis for all movements and feedback conditions for the remaining 39 cases.

Statistical Analysis

Data were entered into PASWStatistics18.0 software for analysis. As discussed in Chapter 2, differences between the neural control of unimanual and bimanual movements justify separate analysis of these movements (Nicholson & Kimura, 1996; Swinnen, 2002; Walsh et al., 2008). A mixed factorial ANCOVA (2x2x2x2) was employed to analyze unimanual motor performance for within-subject factors of trial (1 and 2) and hand (dominant and nondominant), and between-subject factors of feedback condition (feedback, no feedback) and sex (male and female). Dependent measures entered into the ANCOVA included speed, speed standard deviation, and error rates. The number of years of music lessons was entered into the model as a covariate as it was in Study 1.

An additional mixed factorial ANCOVA (2x2x2x2) was used to compare bimanual motor performance for within-subject factors of trial and movement (symmetrical and asymmetrical), and between-subject factors of feedback condition and sex. Dependent measures of bimanual movement analyzed in the model included speed, speed standard deviation, error rates, dominant-nondominant onset, and dominant-nondominant onset standard deviation. The number of years of music lessons was entered into the model as a covariate as it was in Study 1.

A mixed factorial ANCOVA (2x2x6x2) was employed to compare downbeat-offbeat ratios for within-subject factors of trial and movement (dominant unilateral, nondominant unilateral, dominant symmetrical, nondominant symmetrical, dominant asymmetrical, and nondominant asymmetrical), and a between-subject factor of sex. The number of years of music lessons was entered into the model as a covariate as it was in Study 1. Significant interactions from the models were analyzed with pairwise comparisons with Bonferroni corrections.

To examine if individuals with music training had an advantage for the auditory feedback condition and performed bimanual movements relatively better than unimanual movements, participants were categorized into three groups: individuals with less than a year of music lessons, individuals with between one and two years of lessons, and individuals with more than two years of lessons. A ratio score was calculated for the measures of errors, speed, and speed standard deviation for each feedback condition and trial. For the ratio score, averaged unimanual scores were subtracted from averaged bimanual scores and then the resulting number was divided by the sum of the averaged unimanual and averaged bimanual scores. A mixed factorial ANOVA (2x2x3) was employed to compare ratios for the within-subject factor of trial and between-subject factors of feedback condition (feedback, no feedback) and music training group (less than a year of lessons, one to two years of lessons, and more than two years of lessons).

Results

Unimanual Movements

For unimanual errors, the ANCOVA with years of music lessons as a covariate revealed a main effect of trial, with error rates significantly decreasing from trial 1 to trial 2, $F(1,36)=35.251$, $p<.001$ (Table 4.1). This replicates a finding from the Study 1. No other main effects or interactions effects reached significance.

Measure	Main Effect / Interaction		Mean (SE)		Partial η^2	Observed Power
Error Rate	Trial	Trial 1	1.997 (.277)		.495	1.000
		Trial 2	.749 (.147)			
Speed	Trial	Trial 1	.229 (.009)		.208	.849
		Trial 2	.211 (.009)			
	Hand	Dominant	.212 (.009)		.408	.998
		Nondominant	.228 (.008)			
	Trial x Hand		Trial 1	Trial 2	.153	.698
		Dominant	.218 (.009)	.205 (.010)		
		Nondominant	.239 (.009)	.218 (.009)		
	Trial x Feedback x Sex		Trial 1	Trial 2	.189	.804
		Feedback, Males	.230 (.013)	.194 (.014)		
		No Feedback, Males	.207 (.014)	.203 (.013)		
		Feedback, Females	.236 (.013)	.226 (.014)		
		No Feedback, Females	.241 (.013)	.223 (.013)		
Speed Standard Deviation	Trial	Trial 1	.078 (.007)		.325	.982
		Trial 2	.056 (.004)			
	Hand	Dominant	.075 (.007)		.158	.715
		Nondominant	.060 (.004)			

Table 4.1. Means, effect sizes, and power of significant effects for unimanual movements. Mauchly's Test of Sphericity did not indicate a violation of sphericity, so no corrections were applied.

For unimanual speed, the ANCOVA with years of music lessons as a covariate found main effects of trial and hand. For the main effect of trial, speed increased significantly from trial 1 to trial 2, $F(1,36)=9.452$, $p=.004$ (Table 4.1). This replicates a finding from Study 1. For the main effect of hand, participants performed unimanual movements significantly faster with the dominant hand compared to the nondominant hand, $F(1,36)= 24.779$, $p<.001$ (Table 4.1). This replicates a finding from Study 1. No other main effects reached significance. However, two significant interactions were observed. There was a significant interaction for trial and hand, $F(1,36)=6.482$, $p=.015$ (Table 4.1). Pairwise comparisons (with a Bonferroni correction) showed that while speed significantly improved from trial 1 to trial 2, the nondominant hand was significantly slower than the dominant hand for both trials (Table 4.2).

The ANCOVA with years of music lessons as a covariate also found a significant interaction of trial, feedback, and sex on unimanual speed, $F(1,36)=8.374$, $p=.006$ (Table 4.1). Pairwise comparisons (with a Bonferroni correction) showed that males significantly increased speed of movement from trial 1 to trial 2 for the feedback condition (Table 4.3, Figures 4.2a, 4.2b). Other pairwise comparisons for trial failed to reach significance, although there was a trend for improved speed with females, but with the no feedback condition. Although the comparisons between males and females failed to reach significance, there was a trend for females to be slower than males at trial 1 for the no feedback condition (mean difference= -.034, standard error= .019, $p=.083$). Finally, the only detected difference in feedback condition was for males at trial 1, in which performance was significantly faster for the no feedback condition. No other interactions for unimanual speed reached significance.

For standard deviation of unilateral speed, the ANCOVA with years of music lessons as a covariate revealed main effects of trial and hand. For the main effect of trial, speed standard deviation significantly decreased from trial 1 to trial 2, $F(1,36)= 17.362$, $p<.001$ (Table 4.1). This replicates a finding from Study 1. For the main effect of hand, speed standard deviation was significantly lower for the nondominant hand compared to the dominant hand, $F(1,36)=6.750$, $p=.014$ (Table 4.1). No other main effects or interactions reached significance, although the main effect of feedback approached significance, $F(1,36)=3.394$, $p=.074$.

The ANCOVA failed to show significant main effects for the covariate, years of music lessons. However, two interactions reached significance. For unimanual errors, the ANCOVA showed a significant interaction of trial and lessons, $F(1,36)=4.110$, $p=.050$. For unimanual speed, the ANCOVA showed a significant interaction of feedback, hand, and lessons, $F(1,36)=8.369$, $p=.006$. No other interactions in relation to the covariate reached significance.

Comparisons for unimanual speed	Mean Difference	SE	Signi-ficance	Cohen’s *d*
Trial 1, Dominant – Nondominant Hand	-.021*	.004	<.001	-.349
Trial 2, Dominant – Nondominant Hand	-.012*	.003	.001	-.205
Dominant Hand, Trial 1 – Trial 2	.013*	.005	.013	.212
Nondominant Hand, Trial 1 – Trial 2	.021*	.006	.001	.356

Table 4.2. Pairwise comparisons of the interaction of trial and hand for unimanual speed (* denotes significance).

Comparisons for unimanual speed	Mean Difference	SE	Signi-ficance	Cohen’s *d*
Males, Feedback, Trial 1 – Trial 2	.036*	.008	<.001	.719
Males, No Feedback, Trial 1 – Trial 2	.003	.009	.715	N/A
Females, Feedback, Trial 1 – Trial 2	.011	.008	.189	N/A
Female, No Feedback, Trial 1 – Trial 2	.018	.009	.055	N/A
Males, Trial 1, Feedback – No Feedback	.024*	.008	.006	.434
Males, Trial 2, Feedback – No Feedback	-.009	.006	.136	N/A
Females, Trial 1, Feedback – No Feedback	-.004	.008	.585	N/A
Females, Trial 2, Feedback – No Feedback	.003	.006	.623	N/A

Table 4.3. Pairwise comparisons of the interaction of feedback, sex, and trial for unimanual speed (* denotes significance). Comparisons between males and females failed to reach significance and are not included in the table.

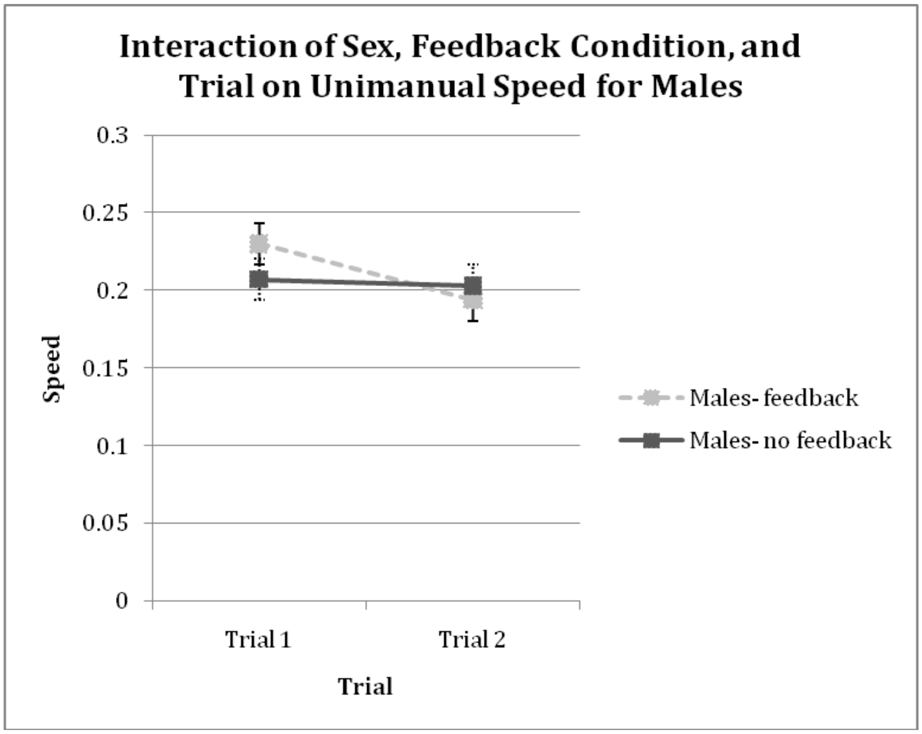


Figure 4.2a. Interaction of sex, feedback condition, and trial on unimanual speed for males. Symbols represent the means and error bars represent the standard error of the mean.

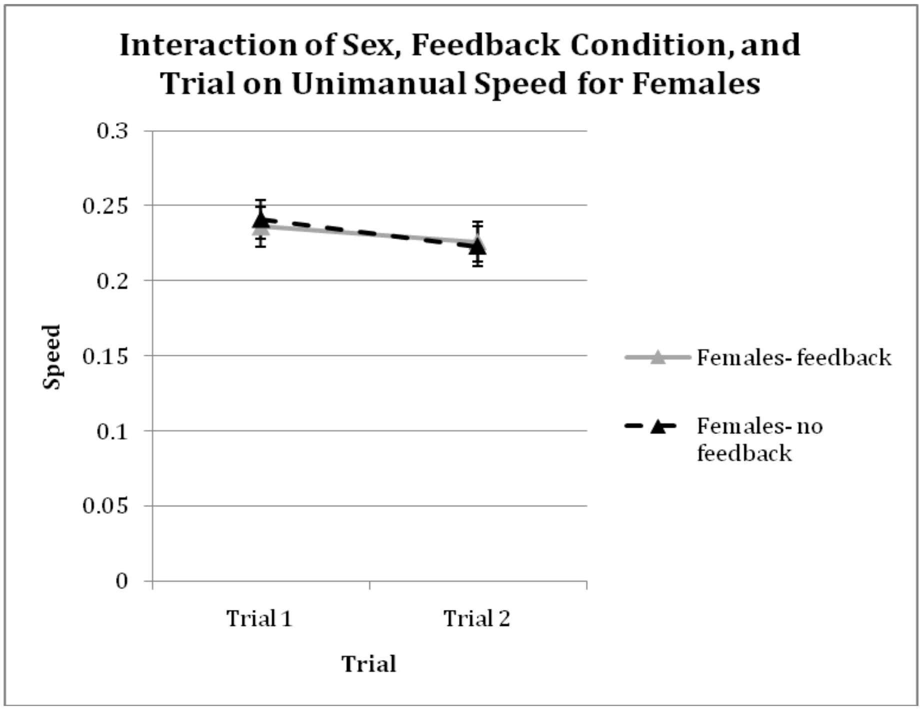


Figure 4.2b. Interaction of sex, feedback condition, and trial on unimanual speed for females. Symbols represent the means and error bars represent the standard error of the mean.

Bimanual Movements

For bimanual errors, the ANCOVA with years of music lessons as a covariate revealed main effects of trial and movement. For the main effect of trial, errors significantly decreased from trial 1 to trial 2, *F*(1,34)=32.648, *p*<.001 (Table 4.4). This replicates a finding from Study 1. For the main effect of movement, error rates were significantly lower for symmetrical movements compared to asymmetrical movements, *F*(1,34)=21.733, *p*<.001 (Table 4.4). This replicates a finding from Study 1. No other main effects reached significance.

However, there was a significant interaction of trial and movement on bimanual errors, *F*(1,34)=20.692, *p*<.001. Pairwise comparisons (with a Bonferroni correction) showed that error rates significantly decreased from trial 1 to trial 2, and that significantly more errors were made for asymmetrical movements than symmetrical movements (Table 4.5). This replicates a finding from Study 1.

Measure	Main Effect / Interaction		Means (SE)		Partial η^2	Observed Power
Error Rate	Trial	Trial 1	5.221 (.628)		.490	1.000
		Trial 2	2.349 (.387)			
	Movement	Symmetrical	2.304 (.291)		.390	.995
		Asymmetrical	5.266 (.745)			
	Trial x Movement		Trial 1	Trial 2	.378	.993
		Symmetrical	2.911 (.445)	1.697 (.260)		
		Asymmetrical	7.531 (1.010)	3.000 (.612)		
Speed	Trial	Trial 1	.371 (.026)		.524	1.000
		Trial 2	.303 (.017)			
	Movement	Symmetrical	.267 (.013)		.563	1.000
		Asymmetrical	.407 (.031)			
	Trial x Movement		Trial 1	Trial 2	.356	.988
		Symmetrical	.279 (.015)	.254 (.012)		
		Asymmetrical	.463 (.040)	.351 (.024)		
	Feedback x Movement		Feedback	No Feedback	.203	.816
		Symmetrical	.273 (.014)	.261 (.013)		
		Asymmetrical	.396 (.027)	.418 (.036)		
	Trial x Feedback x Sex		Trial 1	Trial 2	.125	.570
		Feedback, Males	.357 (.031)	.280 (.024)		
		Feedback, Females	.370 (.034)	.330 (.026)		
		No Feedback, Males	.347 (.043)	.289 (.024)		
		No Feedback, Females	.410 (.046)	.311 (.026)		
	Trial x Feedback x Movement		Trial 1	Trial 2	.113	.526
		Feedback, Symmetrical	.287 (.015)	.260 (.013)		
		Feedback, Asymmetrical	.440 (.033)	.351 (.023)		
		No Feedback, Symmetrical	.272 (.016)	.249 (.012)		
		No Feedback, Asymmetrical	.486 (.050)	.351 (.025)		
Speed Standard Deviation	Trial	Trial 1	.152 (.017)		.464	1.000
		Trial 2	.092 (.010)			
	Movement	Symmetrical	.079 (.008)		.537	1.000
		Asymmetrical	.165 (.019)			
	Trial x Movement		Trial 1	Trial 2	.269	.930
		Symmetrical	.092 (.010)	.066 (.007)		
		Asymmetrical	.211 (.025)	.119 (.015)		

Table 4.4. Means, effect sizes, and power of significant effects for bimanual movements. Mauchly's Test of Sphericity did not indicate a violation of sphericity, so no corrections were applied.

Comparisons for bimanual error rates	Mean Difference	SE	Signi-ficance	Cohen's *d*
Symmetrical Movement, Trial 1 – Trial 2	1.214*	.439	.009	.464
Asymmetrical Movement, Trial 1 – Trial 2	4.531*	.755	<.001	.808
Trial 1, Symmetrical – Asymmetrical	-4.620*	.927	<.001	-.893
Trial 2, Symmetrical - Asymmetrical	-1.303*	.534	.020	-.452

Table 4.5. Pairwise comparisons of the interaction of trial and movement for bimanual error rates (* denotes significance).

For bimanual speed, the ANCOVA with years of music lessons as a covariate revealed main effects of trial and movement. For the main effect of trial, speed significantly increased from trial 1 to trial 2, $F(1,34)= 37.496$, $p<.001$ (Table 4.4). This replicates a finding from Study 1. For the main effect of movement, symmetrical movement was performed significantly faster than asymmetrical movement, $F(1,34)=43.884$, $p<.001$ (Table 4.4). This replicates a finding from Study 1. No other main effects reached significance.

However, The ANCOVA found four significant interactions related to bimanual speed. There was a significant interaction of trial and movement on bimanual speed, $F(1,34)=18.757$, $p<.001$ (Table 4.4). Pairwise comparisons (with a Bonferroni correction) revealed a significant improvement from trial 1 to trial 2 for both symmetrical movements (mean difference= .025, standard error= .007, $p=.001$) and asymmetrical movements (mean difference= .112, standard error= .019, $p<.001$). In addition, pairwise comparisons indicated significantly slower speed for asymmetrical movements compared to symmetrical movements at both trial 1 (mean difference= -.184, standard error= .030, $p<.001$) and trial 2 (mean difference= -.096, standard error= .014, $p<.001$).

There was a significant interaction of feedback and movement on bimanual speed, $F(1,34)= 8.660$, $p=.006$ (Table 4.4). Pairwise comparisons (with a Bonferroni correction) showed that for symmetrical movements, speed was significantly slower for the feedback condition compared to the no feedback condition (mean difference= .013, standard error= .004, $p=.005$). However, the comparisons failed to find a significant difference for the asymmetrical condition, although the direction was for increased speed for the feedback condition (mean difference= -.023, standard error= .013, *p*=.100). Further, asymmetrical movement were significantly slower than symmetrical movements for both the feedback condition (mean difference= -.122, standard error= .017, *p*<.001) and the no feedback condition (mean difference= -.158, standard error= .026, *p*<.001).

There was a significant interaction of trial, feedback, and movement on bimanual speed, *F*(1,34)=4.343, *p*=.045 (Table 4.4, Figure 4.3). Pairwise comparisons (with a Bonferroni correction) showed that while there were significant improvements in speed from trial 1 to trial 2 for symmetrical and asymmetrical movements for the no feedback condition, only asymmetrical movements improved significantly over trial for the feedback condition (Table 4.6). Further, while symmetrical movements were significantly faster than asymmetrical movements during the no feedback condition for both trials, the difference between bimanual movements only reached significance at trial 1 for the feedback condition.

Comparisons for bimanual speed	Mean Difference	SE	Signi-ficance	Cohen's *d*
Feedback, symmetrical, trial 1 – 2	.616	.449	.179	N/A
Feedback, asymmetrical, trial 1 – 2	4.294*	.788	<.001	.548
No feedback, symmetrical, trial 1 - 2	1.811*	.724	.017	.263
No feedback, asymmetrical, trial 1 – 2	4.767*	1.151	<.001	.597
Trial 1, feedback, symmetrical – asymmetrical	-4.552*	.976	<.001	-1.077
Trial 1, no feedback, symmetrical – asymmetrical	-4.689*	1.374	.002	-1.086
Trial 2, feedback, symmetrical – asymmetrical	-.874	.481	.078	N/A
Trial 2, no feedback, symmetrical - asymmetrical	-1.733*	.818	.041	-.936

Table 4.6. Pairwise comparisons of the interaction of trial, feedback, and movement for bimanual speed (* denotes significance). Pairwise comparisons between the feedback and no feedback conditions failed to reach significance and are not included in the table.

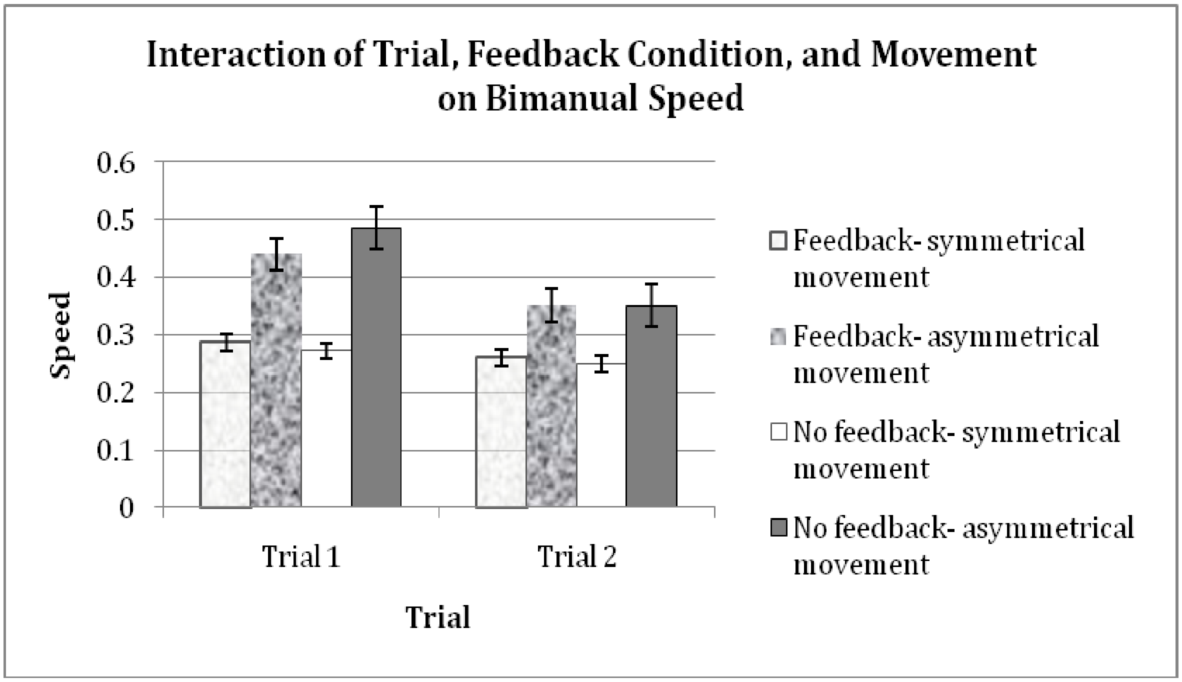


Figure 4.3. Interaction of trial, feedback condition, and movement on bimanual speed. Bars represent the means and error bars represent the standard error of the mean.

There was a significant interaction of trial, feedback, and sex on bimanual speed, *F*(1,34)= 4.838, *p*=.035 (Table 4.4, Figures 4.4a and 4.4b). Pairwise comparisons (with a Bonferroni correction) showed that while both males and females demonstrated significant improvements of speed over trial for both feedback conditions, males showed medium effect sizes for both conditions while females demonstrated a small effect size in relation to feedback and a medium effect size in relation to the no feedback condition (Cohen, 1988) (Table 4.7). Further, the only comparison in relation to feedback to reach significance was at trial 2 for females, in which bimanual speed was actually faster for the no feedback condition.

Comparisons for bimanual speed	Mean Difference	SE	Signi-ficance	Cohen's *d*
Males, Feedback, Trial 1 – 2	.077*	.013	<.001	.725
Males, No Feedback, Trial 1 – 2	.059*	.023	.016	.541
Females, Feedback, Trial 1 – 2	.040*	.014	.010	.267
Females, No Feedback, Trial 1 – 2	.099*	.025	<.001	.514
Males, Trial 1, Feedback – No Feedback	.010	.021	.641	N/A
Males, Trial 2, Feedback – No Feedback	-.009	.008	.281	N/A
Females, Trial 1, Feedback – No Feedback	-.040	.023	.085	N/A
Females, Trial 2, Feedback – No Feedback	.019*	.009	.035	.120

Table 4.7. Pairwise comparisons of the interaction of feedback, sex, and trial for bimanual speed (* denotes significance). Pairwise comparisons between males and females failed to reach significance and are not included in the table.

For standard deviation of bimanual speed, the ANCOVA with years of music lessons as a covariate revealed main effects of trial and movement. For the main effect of trial, speed standard deviation significantly decreased from trial 1 to trial 2, $F(1,34)=29.496$, $p<.001$ (Table 4.4). This replicates a finding from Study 1. For the main effect of movement, speed standard deviation was significantly lower for symmetrical movement compared to asymmetrical movement, $F(1,34)=39.508$, $p<.001$ (Table 4.4). This replicates a finding from Study 1. No other main effects reached significance.

However, the ANOVA with years of music lessons as a covariate revealed a significant interaction of trial and movement on bimanual speed standard deviation, $F(1,34)= 12.507$, $p=.001$ (Table 4.4). Pairwise comparisons (with a Bonferroni correction) revealed that speed standard deviation significantly decreased over trial for both types of bimanual movements (Table 4.8). In addition, speed standard deviation for asymmetrical movements was significantly higher than symmetrical movements for both trials, although the effect size decreased from trial 1 to trial 2.

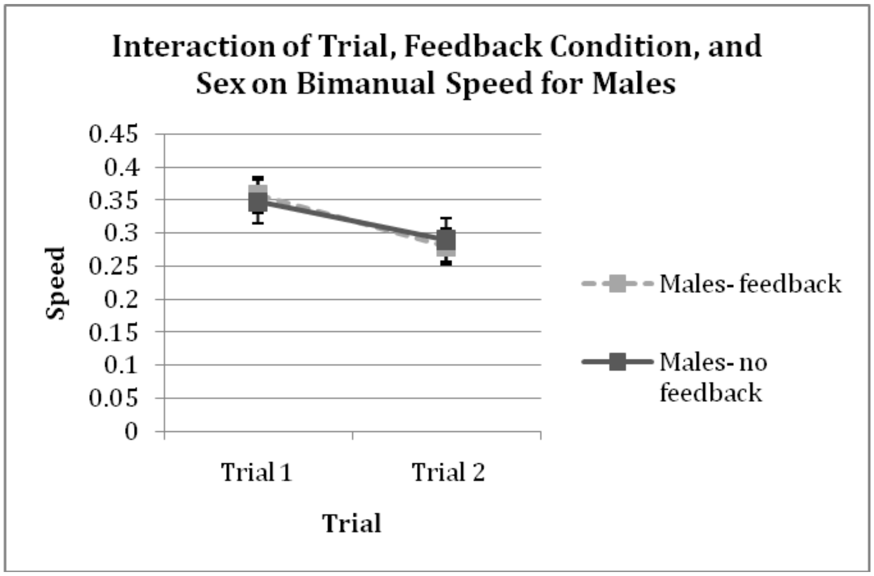


Figure 4.4a. Interaction of trial, feedback condition, and sex on bimanual speed for males. Symbols represent the means and error bars represent the standard error of the mean.

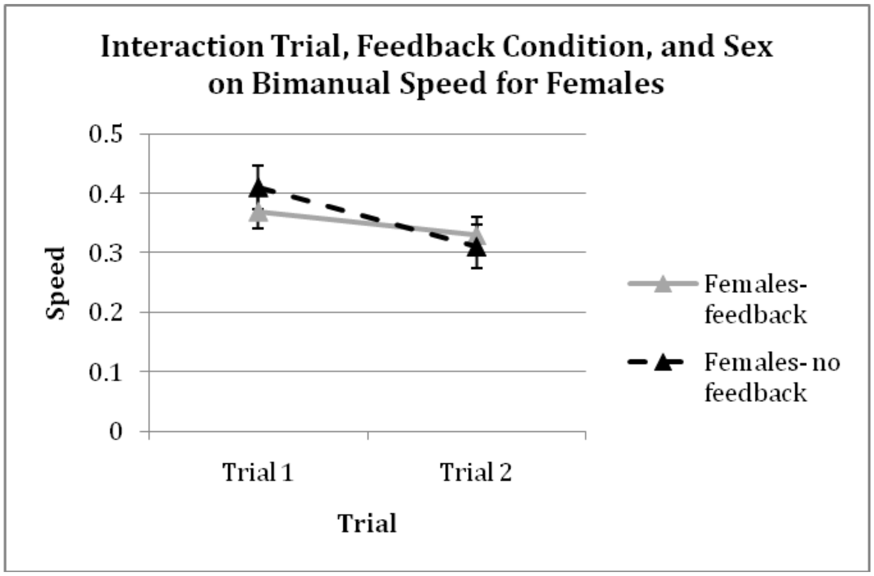


Figure 4.4b. Interaction of trial, feedback condition, and sex bimanual speed for females. Symbols represent the means and error bars represent the standard error of the mean.

Comparisons for bimanual speed standard deviation	Mean Difference	SE	Signi-ficance	Cohen's *d*
Symmetrical movement, Trial 1 – 2	.026*	.007	.001	.475
Asymmetrical movement, Trial 1 – 2	.092*	.018	<.001	.700
Trial 1, Symmetrical – Asymmetrical	-.119*	.019	<001	-1.032
Trial 2, Symmetrical – Asymmetrical	-.053*	.011	<.001	-.751

Table 4.8. Pairwise comparisons of the interaction of trial and movement for bimanual speed standard deviation (* denotes significance).

No other interactions for bimanual speed standard deviation reached significance, although there was a near-significant interaction of feedback, movement, and sex on bimanual speed standard deviation, *F*(1,34)= 3.719, *p*=.063 (Figure 4.5). Although only exploratory, pairwise comparisons (with a Bonferroni correction) demonstrated that speed standard deviation was significantly lower for symmetrical movements compared to asymmetrical movements for males and females, for both feedback conditions (Table 4.9). Pairwise comparisons for feedback conditions revealed a significant difference only for females, in which symmetrical movements were performed with significantly lower speed standard deviation for the no feedback condition. Finally, comparisons between males and females showed that females performed symmetrical movements with greater speed standard deviation during the feedback condition in comparison to males. The difference corresponds to a medium effect size (Cohen, 1988).

No main effects or interactions for dominant-nondominant onset or dominant-nondominant onset standard deviation reached significance. The ANCOVA showed significant a main effect for of covariate, years of music lessons, on the standard deviation of speed, *F*(1,34)= 4.654, *p*=.040. No other main effects in relation to the covariate reached significance, but two interactions reached significance. For bimanual speed, the ANCOVA showed a significant interaction of feedback and music lessons, *F*(1,34)=6.163, *p*=.018. For bimanual speed standard deviation, the ANCOVA showed a significant interaction of trial, movement, and music lessons *F*(1,34)= 4.395, *p*=.044. No other interactions in relation to the covariate reached significance.

Comparisons for bimanual speed standard deviation	Mean Difference	SE	Signi-ficance	Cohen's *d*
Males, Feedback, Symmetrical - Asymmetrical	-.092*	.018	<.001	-1.189
Males, No Feedback, Symmetrical – Asymmetrical	-.077*	.024	.002	-1.064
Females, Feedback, Symmetrical - Asymmetrical	-.064*	.019	.002	-.679
Females, No Feedback, Symmetrical – Asymmetrical	-.111*	.026	<.001	-.885
Males, Symmetrical, Feedback – No Feedback	-.011	.006	.100	N/A
Males, Asymmetrical, Feedback – No Feedback	.004	.020	.851	N/A
Females, Symmetrical, Feedback – No Feedback	.016*	.007	.032	.267
Females, Asymmetrical, Feedback – No Feedback	-.031	.022	.158	N/A
Feedback, Symmetrical, Male – Female	-.036*	.017	.037	-.659
Feedback, Asymmetrical, Male – Female	-.008	.035	.811	N/A
No Feedback, Symmetrical, Male – Female	-.010	.016	.555	N/A
No Feedback, Asymmetrical, Male – Female	-.044	.046	.349	N/A

Table 4.9. Pairwise comparisons of the interaction of feedback, movement, and sex for bimanual speed standard deviation (* denotes significance).

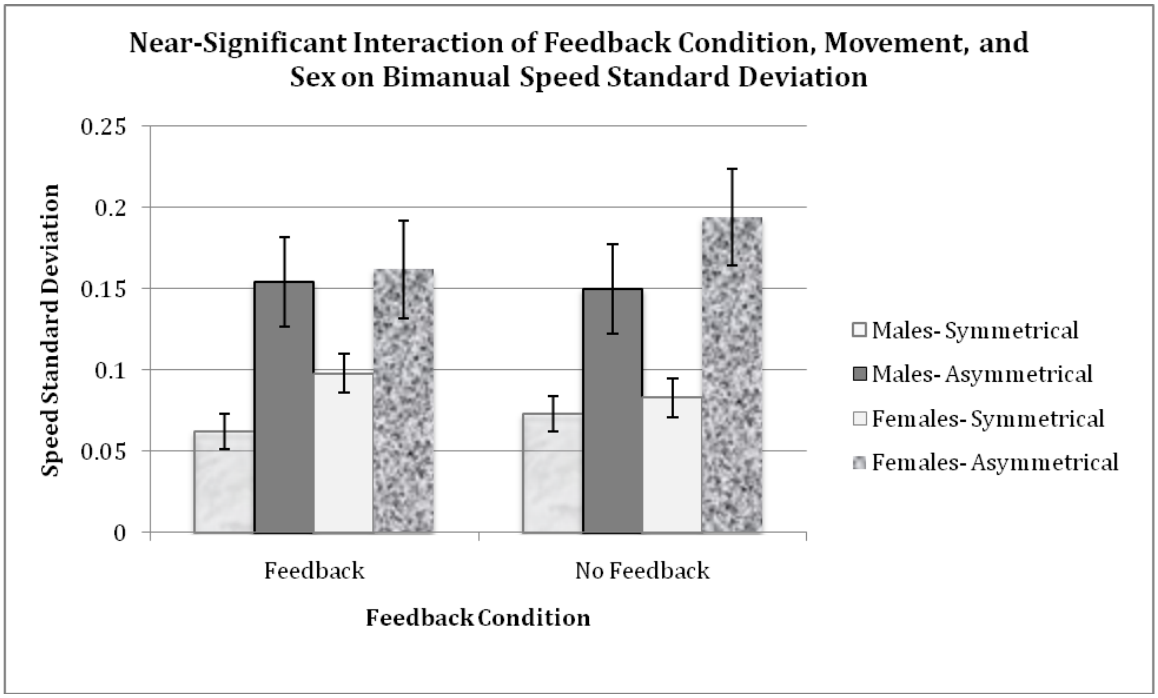


Figure 4.5. Near-significant interaction of feedback condition, movement, and sex on bimanual speed standard deviation. Bars represent the means and error bars represent the standard error of the mean.

Downbeat-Offbeat Ratios

For downbeat-offbeat ratios, the ANCOVA with years of music lessons as a covariate found a main effect of movement, $F(2.8,98.0)=7.593$, $p=<.001$, partial η^2 of .178, and power of .980 (Table 4.10). A Greenhouse-Geisser correction was applied as Mauchly's Test of Sphericity reached significance. Pairwise comparisons (with a Bonferroni correction) revealed that downbeat-offbeat ratios were significantly higher for nondominant symmetrical movements compared to dominant unilateral, dominant symmetrical and dominant asymmetrical movements (Table 4.11). The findings in relation to the dominant unimanual and dominant asymmetrical movements replicate findings from Study 1. In addition, nondominant asymmetrical movements were performed with significantly higher downbeat-offbeat ratios than dominant asymmetrical movements. No other effects, including those related to feedback, reached significance.

Movement	Dominant Unilateral	Nondominant Unilateral	Dominant Symmetrical	Nondominant Symmetrical	Dominant Asymmetrical	Nondominant Asymmetrical
Mean	.985	1.004	.989	1.012	.983	.998
SE	.006	.006	.007	.006	.006	.006

Table 4.10. Means and standard error of movements for downbeat-offbeat ratios.

Comparisons for downbeat-offbeat ratios	Mean Difference	SE	Signi-ficance	Cohen's *d*
Nondominant symmetrical – Dominant unilateral*	.027	.007	.012	.731
Nondominant symmetrical – Dominant symmetrical	.024	.007	.031	.614
Nondominant symmetrical – Dominant asymmetrical*	.030	.007	.002	.734
Nondominant asymmetrical – Dominant asymmetrical	.016	.005	.045	.367

Table 4.11. Statistically significant results of pairwise comparisons of the effect of movement for downbeat-offbeat ratios (* denotes replication of a finding from Study 1).

Bimanual-Unimanual Ratios

For the bimanual-unimanual speed ratio, the ANOVA revealed a main effect of trial, with the ratio significantly decreasing from trial 1 to trial 2, $F(1,31)=21.809$, $p<.001$ (Table 4.12). No other main effects reached significance.

There was a significant interaction of trial, feedback, and music lessons on speed ratios, $F(2,31)=3.5$, $p=.043$ (Table 4.12, Figures 4.6a and 4.6b). Pairwise comparisons (with a Bonferroni correction) revealed that although individuals with two or more years of lessons improved over trial for the no feedback condition, the change for the feedback condition failed to reach significance (Table 4.13). Further, this finding was reversed for individuals with less than a year of music lessons. This group improved over trial for the feedback condition, but the analysis failed to find a significant change over trial for the no feedback condition (Table 4.13). For pairwise comparisons that found a significant effect of trial, the ratio decreased from trial 1 to trial 2 (Table 4.13). Comparisons for feedback condition found that the speed ratio was significantly higher for the no feedback condition compared to the feedback condition for individuals with more than three years of music lessons at trial 1 (Table 4.13). No other interactions reached significance.

For speed standard deviation ratios, the ANOVA revealed a main effect of trial, with ratios significantly decreasing from trial 1 to trial 2, $F(1,31)=4.955$, $p=.033$ (Table 4.12). No other main effects or interactions reached significance for speed standard deviation ratios. For error ratios, no main effects or interactions reached significance.

Measure	Main Effect / Interaction		Means (SE)		Partial η^2	Observed Power
Speed	Trial	Trial 1	.223 (.018)		.413	.995
		Trial 2	.175 (.015)			
	Trial x Feedback x Music Lessons		Trial 1	Trial 2	.184	.610
	Feedback, <1 year lessons		.250 (.028)	.168 (.026)		
	No Feedback, <1 year lessons		.247 (.036)	.204 (.028)		
	Feedback, 2-3 years lessons		.225 (.027)	.190 (.169)		
	No Feedback, 2-3 years lessons		.249 (.034)	.169 (.027)		
	Feedback >3 years lessons		.146 (.033)	.179 (.030)		
	No Feedback >3 years lessons		.219 (.041)	.140 (.032)		
Speed Std. Deviation	Trial	Trial 1	.260 (.030)		.138	.578
		Trial 2	.171 (.042)			

Table 4.12. Means, effect sizes, and power of significant effects for bimanual-unimanual ratios.

Comparisons for bimanual-unimanual speed ratios	Mean Difference	SE	Significance	Cohen's *d*
<1 Year Lessons, Feedback, Trial 1 – 2	.082*	.021	<.001	.888
<1 Year Lessons, No Feedback, Trial 1 – 2	.043	.029	.150	N/A
2-3 Years Lessons, Feedback, Trial 1 – 2	.035	.020	.090	N/A
2-3 Years Lessons, No Feedback, Trial 1 – 2	.080*	.028	.008	.650
>3 Years Lessons, Feedback, Trial 1 – 2	-.033	.024	.185	N/A
>3 Years Lessons, No Feedback, Trial 1 – 2	.080*	.034	.025	1.008
<1 Year Lessons, Trial 1, Feedback – No Feedback	.003	.026	.912	N/A
<1 Year Lessons, Trial 2, Feedback – No Feedback	-.036	.024	.142	N/A
2-3 Years Lessons, Trial 1, Feedback – No Feedback	-.025	.025	.340	N/A
2-3 Years Lessons, Trial 2, Feedback – No Feedback	.021	.023	.373	N/A
>3 Years Lessons, Trial 1, Feedback – No Feedback	-.073*	.030	.023	-.656
>3 Years Lessons, Trial 2, Feedback – No Feedback	.039	.027	.162	N/A

Table 4.13. Pairwise comparisons of the interaction of trial, feedback condition, and music lessons for bimanual-unimanual speed ratios (* denotes significance). Pairwise comparisons in relation to years of lessons failed to reach significance and are not included in the table.

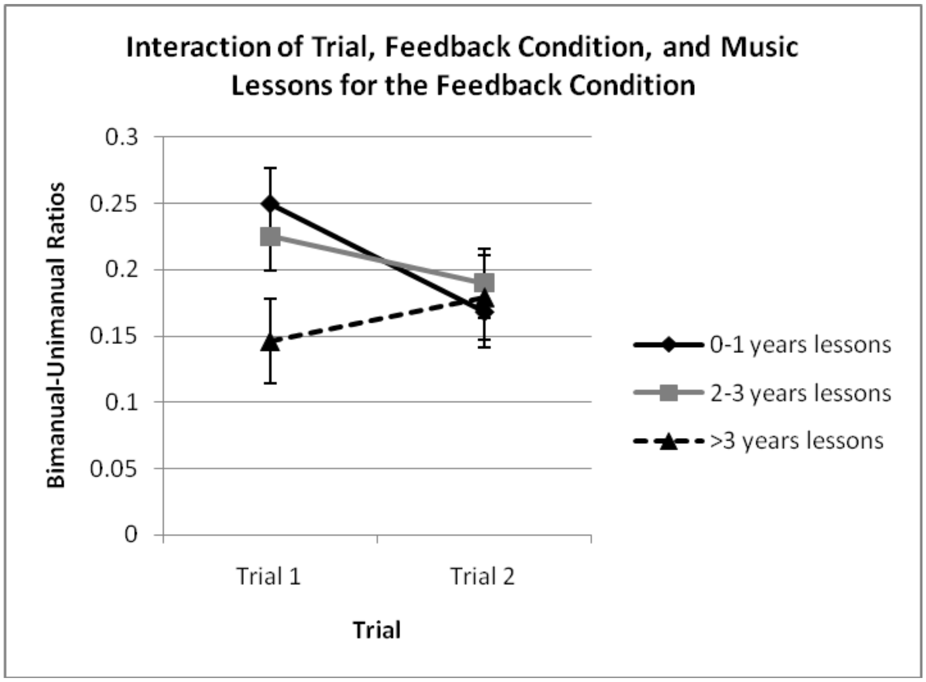


Figure 4.6a. Interaction of trial, feedback condition, and music lessons on bimanual-unimanual ratios for the feedback condition. Symbols represent the means and error bars represent the standard error of the mean.

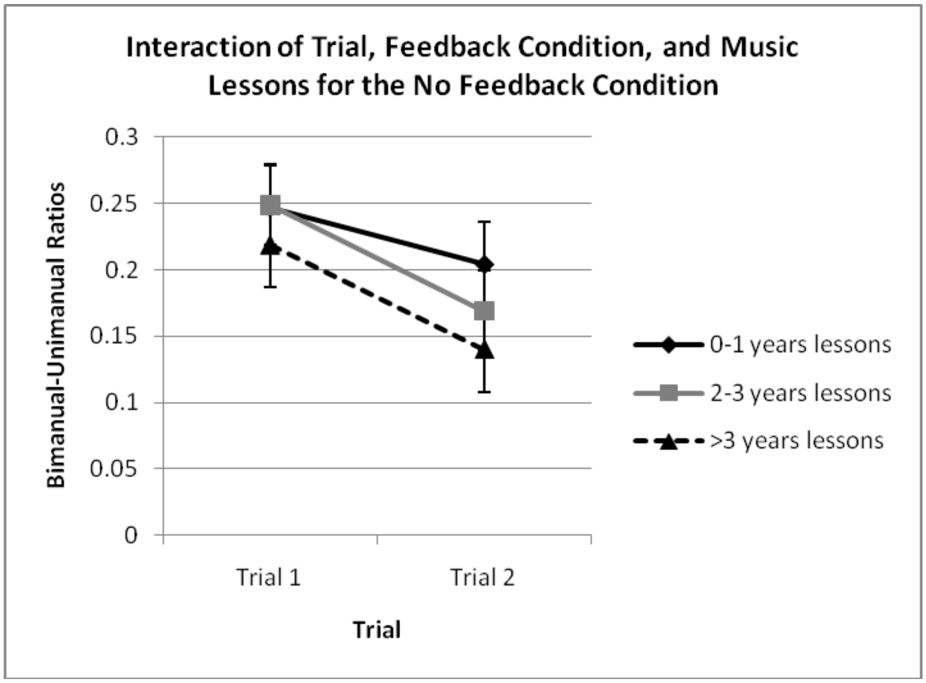


Figure 4.6b. Interaction of trial, feedback condition, and music lessons on bimanual-unimanual ratios for the no feedback condition. Symbols represent the means and error bars represent the standard error of the mean.

Discussion

Replication of Study 1

As with Study 1, an effect of trial with reduced unimanual error rates from trial 1 to trial 2 was observed. However, the analysis failed to find an interaction of trial, hand, and sex as observed in Study 1. The main effects of trial, with increased speed over trial, and hand, with increased speed for the dominant hand, were replicated, but in addition, an interaction of trial and hand was found. Further, the effect of trial for speed standard deviation, with decreasing values over trial, was replicated.

Consistent with Study 1, main effects of trial and movement on bimanual error rates were identified, as well as an interaction between the two factors. Bimanual errors decreased from trial 1 to trial 2, and errors rates were higher for asymmetrical movements compared to symmetrical movements. While main effects of trial and movement on bimanual speed were found with the same direction of effect as Study 1, an interaction of trial, movement, and sex on bimanual speed was not found.

Main effects of trial and movement on bimanual speed standard deviation were demonstrated as in Study 1. The present study failed to replicate the interaction of movement and sex on dominant-nondominant onset standard deviation. Note, however, that some of these divergent findings may result from sample differences; Study 1 included a portion of older adults while the present study included only younger adults.

This study failed to replicate the main effect of sex and the interaction of movement and sex on downbeat-offbeat ratios found in Study 1. However, a significant main effect of movement was identified. Although post-hoc analysis replicated only two of five significant comparisons of movement from Study 1, a clear theme emerged of increased downbeat-offbeat ratios of the nondominant hand, particularly for symmetrical movements. As postulated in Chapter 2, increased downbeat-offbeat ratios of the nondominant hand for symmetrical movements may relate to a strategy intended to increase coupling between the dominant and nondominant limbs.

The Effect of Auditory Feedback on Motor Performance

Several significant findings in relation to the effect of feedback on performance were identified. Further analysis of the interaction effect of trial, feedback, and sex on unimanual speed revealed that males demonstrated a large practice effect for the feedback condition, and performed significantly slower for the feedback condition at trial 1 compared to the no feedback condition. This effect, however, was not found at trial 2. This suggests that although males may have initially performed unimanual movements more slowly with feedback, practice ameliorated this effect. The finding cannot be attributed to more males starting with the feedback condition, as approximate half of males (11 of 20) started with the feedback condition. The finding suggests that feedback was detrimental to unimanual performance for males and is contrary to the *a priori* hypothesis.

The immediate detrimental effect of feedback on unimanual movement for males may relate to sex-specific competition for convergent neural pathways. Males exhibit increased lateralization to the right hemisphere during unimanual movement compared to females (Lissek et al., 2007; right-handed subjects). In addition, the electrophysiological response to music aberrations of musically naïve males is generated predominantly from the right hemisphere (Koelsch, Maess, Grossmann, & Friederici, 2003; right-handed subjects). Considering this evidence, pathways utilized by musically-naïve males to process auditory feedback may converge with pathways used to produce of unimanual movements, and the resulting competition results in decrements in motor performance. Note however, that males appeared to rapidly adapt to the presence of auditory feedback.

Symmetrical movements were performed significantly faster when feedback was absent, while asymmetrical movement tended to be performed faster with feedback. In addition, there was a blunted practice effect in relation to symmetrical movements with feedback compared to when feedback was absent. These findings suggest that auditory feedback is detrimental to performance of symmetrical movements for novice piano players. While not conclusive, there may be some benefit of auditory feedback in learning asymmetrical movements.

The interaction of feedback, gender, and trial revealed that females demonstrated significantly increased speed without feedback compared to the feedback condition at trial 2. In addition, females had a small effect of practice with feedback but a medium effect of practice without feedback. The interaction of sex, feedback, and movement revealed that females performed symmetrical movements with greater speed standard deviation with feedback compared to the no feedback condition. Further, with feedback, females performed symmetrical movements with greater speed standard deviation compared to males. Increased speed standard deviation is associated with decreased movement stability. Thus, the findings suggest that auditory feedback undermined the stability of symmetrical movements for females.

These apparent differences in the effect of auditory feedback on learning symmetrical movements, and for females in particular, may also relate to sex-specific competition for shared neural networks. Females use inter-hemispheric neural pathways relatively more than males to process auditory feedback (Koelsch et al., 2003). This is consistent with sexually dimorphic brain macrostructure; the anterior commissure is larger and the splenium is more bulbous in females (Kimura, 1999; Resnick & Driscoll, 2008). In addition, symmetrical movements are characterized by increased inter-hemispheric connectivity compared to other movements (Maki et al., 2008; Walsh et al., 2008). Conceivably, processing auditory feedback may compete for networks necessary to the production and monitoring of symmetrical movements for musically naïve females. This theory also explains why the effect does not extend to asymmetrical movements, which are characterized by reduced inter-hemispheric activity (Maki et al., 2008).

Contrary to the *a priori* hypothesis, feedback did not improve motor performance; rather feedback was detrimental to performance under specific conditions. Considering that years of music lessons was entered as a covariate into the statistical models revealing these findings, variance related to prior music training was minimized. As such, the findings reflect the response of neural systems to auditory feedback as a novel event. Prior research demonstrated that musically naïve individuals who trained with random key-pitch associations over 10 sessions exhibited superior temporal accuracy and velocity control compared to individuals who learned normal pitch associations (Bangert & Altenmüller, 2003). Thus, although co-activation of auditory and motor networks occurs rapidly with training (Bangert & Altenmüller, 2003), it does not necessarily confer an immediate advantage to motor performance. It appears that co-activation is a precursor to the ability to exploit auditory feedback for superior motor performance, but the amount of training needed to confer this benefit is unclear.

The prediction that individuals with music training would use auditory feedback more effectively was confirmed. The interaction of trial, feedback, and sex on bimanual-unimanual speed ratios showed that participants with less than a year of music training demonstrated a practice effect for the feedback condition while participants with more than a year of training demonstrated a practice effect for the no feedback condition. Further, the group with more than three years of music training demonstrated significantly lower bimanual-unimanual speed ratios at trial 1 for the feedback condition.

These results suggest that music training leads to faster bimanual movements compared to unimanual movements when auditory feedback is available. However, a rapid practice effect was observed for all groups across feedback conditions. It is tempting to suggest that the rapid co-activation of auditory and motor cortices observed after only 20 minutes of practice resulted in the group with less than a year of music lessons being able to integrate auditory feedback effectively for improved performance (Bangert & Altenmüller, 2003), but this is not necessarily the case. Considering that trial 2 consisted of the same task as trial 1, and that at trial, 1 the task was done both with and without feedback, it may be that individuals with less than a year of lessons demonstrated a practice effect rather than integration of auditory feedback at trial 2.

The results did not support the prediction that individuals with music training would perform bimanual movements better relative to unimanual movements. Pairwise comparisons of the interaction of feedback condition, music lessons, and trial failed to find significant differences between groups with music training on bimanual-unimanual speed ratios. However, Study 1 found lower speed ratios (partial η^2 of .252) and speed standard deviation ratios (partial η^2 of .084) for individuals with a year or more of music training compared those with less than a year. Categorization of participants into three groups rather than two may have obscured effects. In addition, the categorization of individuals according to music lessons did not consider average practice time or if the instrument learned required skilled use of both hands. For example, violinists skilfully use the dominant hand to finger the strings while the other hand grasps the bow. In such cases, training may not result in better sequential bimanual skills.

In conclusion, the majority of the findings of Study 1 were replicated and novel findings of the effect of auditory feedback were found. Analysis corrected for years of musical training showed that males performed unimanual movement more slowly in the presence of feedback, although this effect diminished with practice.

Symmetrical movement speed decreased when auditory feedback was present. In addition, females not only performed bimanual movements more slowly with feedback, but also demonstrated increased speed deviation for symmetrical movements, and thus reduced stability of movement. These sex and movement differences revealed by auditory feedback point to sexually divergent patterns of neural activation for the processing of auditory feedback and production of movement. Finally, individuals with music training demonstrated increased efficiency in the use of feedback to produce novel bimanual movements.

CHAPTER 5:

WEATHER PREDICTION TASK PERFORMANCE CORRELATES WITH SYMMETRICAL MOVEMENT

Introduction

It is generally accepted that anatomically distinct memory systems are responsible for dissociable learning and memory behaviours (Sweatt, 2010). Explicit, or declarative, memory requires the ability to consciously recall information, of which semantic memory, defined as recall of "world knowledge," and episodic memory, defined as recall of past life events, are dissociable (Gazzaniga et al., 2009). The anatomical structure most consistently implicated with explicit memory is the medial temporal lobe (Sweatt, 2010).

Conversely, implicit, or non-declarative, memory arises from unconscious processes and may involve learning simple behaviours or sequences of many smaller components that comprise whole behaviours (Sweatt, 2010). Implicit behaviours are often thought of in terms of motor behaviours, such as the act of dressing, but may also include cognitive components and processes (Gazzaniga et al., 2009). Anatomical structures implicated in implicit learning include the motor cortex, premotor cortex, basal ganglia, thalamus, cerebellum, and brain stem (Sweatt, 2010). The body of literature related to implicit learning is of particular interest to the study of bimanual learning as it provides a framework to examine motor learning. Further, the relationship between memory systems and their contribution to bimanual skill acquisition is important to delineate.

The weather prediction task is purported to reflect implicit processes (Knowlton et al., 1994). The task requires choosing one of two outcomes, sunny or rainy weather, based on the presentation of combinations of one to three cards from an array of four cards containing geometric shapes (Figure 5.1). Outcomes for each pattern are based on a predetermined probability ranging 62.5 to 88.9% for the original version; each outcome, rain or sun, is correct 50% of the time over all of the trials (Knowlton et al., 1994). The weather prediction task is presented as an implicit task because individuals are unable to identify the most probable outcomes associated with card patterns, despite an improvement in performance over successive trials.

To test the notion of the task relying on implicit processes, participants completed a questionnaire following the weather prediction task in its standard format (50 trials per block for 4 blocks) (Gluck, Shohamy, & Myers, 2002). Average reported strategies were not consistent with ideal strategies, reported perception of strategy effectiveness did not correspond to performance, and reported strategy use was inconsistent with outcomes expected if the participant had actually followed those strategies. However, with probing, subjects did tend to associate the square card with sun and the triangle card with rain (Gluck et al., 2002). If participants had responded with rain when the triangle card was present or with sun when the square card was present, responses would be 75.6% accurate. In this particular study, participants started near chance for block 1 (50%), and improved to over 70% accuracy by block 4 (Gluck et al., 2002). Participants’ difficulty with accurately describing their strategies was cited as evidence of the implicit nature of the task (Gluck et al., 2002).

Neural Correlates Associated With the Weather Prediction Task

Several attempts have been made to identify neural correlates of the weather prediction task. While some evidence suggests that individuals with frontal lesions perform the weather prediction task normally (Knowlton et al., 1996), others found that individuals with orbitofrontal cortex lesions demonstrate mild deficits in the first 50 trials of the task, but perform normally overall compared to controls (Chase et al., 2008). In keeping with this, inhibitory (theta) TMS over the dorsolateral prefrontal cortex did not significantly compromise learning the weather prediction task (Wilkinson, Teo, Obeso, Rothwell, & Jahanshahi, 2009). However, inhibitory TMS over M1, but not the SMA, prevented performance improvements associated with learning the task (Wilkinson et al., 2009).

Pertinent to this present study, the effect of age on performance of the weather prediction task was investigated by monitoring brain activation with fMRI (Fera et al., 2005). No significant differences were found between older and young adults in relation to learning over time, performance strategies, or activation of neural networks (Fera et al., 2005). However, there were significant differences in proportional neural activation between the two groups. Young adults demonstrated relatively more activation of the prefrontal cortex and caudate nuclei and less activation of the parietal cortex compared to older adults (Fera et al., 2005). In addition, better performance correlated with greater activation of the prefrontal cortex and caudate nuclei in young adults, and greater activation of prefrontal and parietal cortices in older adults. The results led to the supposition that increased parietal activation was a compensatory mechanism for inadequate prefrontal cortex and caudate activation among older adults (Fera et al., 2005).

Participants with and without Alzheimer disease were scanned with magnetic resonance spectroscopic imaging while performing the weather prediction task (Colla et al., 2003). The study failed to find a significant difference in performance between the two groups, but males with Alzheimer disease performed significantly poorer than male controls. In addition, elevation of trimethylamine signal in the basal ganglia correlated with poor performance. Trimethylamine compound concentration is thought to reflect membrane turnover, an indicator of cell loss associated with reactive gliosis (Miller et al., 1996). No significant differences were observed between male and female participants with Alzheimer disease for age, age of onset, Mini-Mental State Exam score, or measures of declarative memory.

In a different study, individuals with moderate Alzheimer disease performed significantly better on the weather prediction task compared to individuals with mild Alzheimer disease and controls (Klimkowicz-Mrowiec, Slowik, Krzywoszanski, Herzog-Krzywoszanska, & Szczudlik, 2008). The results were purported to support the idea of competition between declarative and non-declarative memory systems (Klimkowica-Mrowiec et al., 2008). Other reports related of the impact of temporal lobe lesions have been conflicting. An early study found participants with amnesia performed the task normally (Knowlton et al., 1996). In contrast, another study found that participants with bilateral hippocampal damage due to hypoxia performed significantly worse than controls (Hopkins, Myers, Shohamy, Grossman,

& Gluck, 2004). Strategy analysis suggested that participants with amnesia used degraded strategies, and controls demonstrated increased activation of the medial temporal lobe even in the early stages of the task (Hopkins et al., 2004).

Individuals with Parkinson's disease reportedly fail to improve on the weather prediction task (Knowlton et al., 1996). Further, individuals with Parkinson's disease exhibit decreased activation of the caudate nucleus and greater activation of the prefrontal cortex and medial temporal lobe during task performance compared to controls (Moody, Bookheimer, Vanek, & Knowlton, 2004). Recent studies have challenged the notion of impaired performance associated with deterioration of the neostriatum. In a recent study, only individuals with Parkinson's disease taking levodopa had impaired performance on the weather prediction task compared to controls without neurological conditions and individuals with Parkinson's not taking levodopa (Jahanshahi, Wilkinson, Gahir, Dharminda, & Lagnado, 2010). The authors purport that the deluge of systemic levodopa obscured subtle phasic dopaminergic changes necessary for learning (Jahanshahi et al., 2010). Further, when a paired associate version of the task is used, participants with Parkinson's disease do not perform significantly differently than controls (Wilkinson et al., 2008).

In considering past research as a whole, the weather prediction task does not appear to rely exclusively on structures associated with implicit memory. The role of the medial temporal lobe in the weather prediction task is clouded by issues related to incomplete impairment of medial temporal lobe function and potential confounds associated with dysfunction of other regions. For example, the finding that poorer performance by participants with Alzheimer disease correlated with markers of basal ganglia damage suggests that concomitant disease processes contributed to poor performance rather than selective medial temporal lobe damage (Colla et al., 2003). However, the association between medial temporal lobe damage and the selection of degraded strategies implicates explicit systems in execution of the weather prediction task (Hopkins et al., 2004).

Performance of the weather prediction task does not appear to rely on frontal lobe function (Knowlton et al., 1996; Wilkinson et al., 2009). However, increased activation of the prefrontal cortex does correlate with improved performance, with the addition of the caudate nuclei for young adults and the parietal cortex for older adults (Fera et al., 2005). A single but convincing study suggests that M1 is critical in task performance (Wilkinson et al., 2009). While challenging the notion that the weather prediction task relies solely on implicit learning, previous research into neural correlates of the task suggest that it relies on parallel functioning of implicit and explicit memory systems. Importantly, patterns of activation associated with optimal performance may change as a result of aging or disease (Fera et al., 2005; Hopkins et al., 2004; Moody et al., 2004). A related consideration is that diverse strategies may be successfully applied to the task and strategies may be unconsciously selected with deference to intact and comparatively efficient neural pathways.

Performance Strategies Associated With the Weather Prediction Task

Strategy analysis has been applied to weather prediction task performance. Gluck et al. (2002) analyzed responses by block for best fit with three reported strategies: 1) a multi-cue strategy associating patterns of cards with outcome, which would result in the best performance, 2) a one-cue strategy associating outcome with the presence or absence of one of the highly predictive cues (square or triangle cards for the version used), which would result in 87.5% of responses being correct, and 3) a singleton strategy associating only single cards with an outcome, which would yield a correct response rate of 66%. With mathematical models, a general shift from a singleton strategy in block 1 to a multi-cue strategy by block 4 was reported (Gluck et al., 2002).

Performance of the weather prediction task by individuals with Parkinson's disease was analyzed by the same method of strategy analysis (Shohamy, Myers, Onlaor, & Gluck, 2004). Results suggest that individuals with Parkinson's disease exhibit different patterns of strategy use; individuals with Parkinson's disease tended to use a singleton strategy while controls integrated singleton strategies into a multi-cue strategy (Shohamy et al., 2004). An important consideration is that all participants were taking levodopa at the time of the study (Jahanshahi et al., 2010).

More sophisticated approaches to strategy analysis have been applied. Based on the previously described strategies, a computer program used Monte Carlo simulations to search across all trials and identify strategy switches within a few trials (Meeter, Myers, Shohamy, Hopkins, & Gluck, 2006). The original three strategies were expanded to 11 strategies, including a random strategy. Using data from a previously published study, individuals with hippocampal damage were found to make fewer strategy switches and were as likely to switch to an inferior strategy as an optimal strategy (Meeter et al., 2006).

Challenges to the Non-Declarative Label of the Weather Prediction Task

Considering that memory systems may work in parallel, caution is warranted when labeling strategies as solely implicit or explicit (Gluck et al., 2002). It has been argued that the weather prediction task actually relies on explicit memory processes (Newell, Lagnado, & Shanks, 2007). This position is supported by evidence that a competing memory task performed concurrently with the feedback version of the weather prediction task impairs task performance (Newell et al., 2007). In addition, participants had comparable insight into strategies and outcomes for both the feedback and observation versions of the weather prediction task.

Young adults, older adults, and individuals with Parkinson's disease were compared on performance of the weather prediction task and an information integration task (Price, 2005). The information integration task is similar to the weather prediction task in that there are cues in various combinations on the screen (between one to five of six possible cues), but the outcome is based on mathematically assigned values associated with the cues. Performance on the weather prediction task correlated with hypothesis testing ability and working memory capacity. Further, both older adults and patients with Parkinson's disease performed significantly worse on the weather prediction task, but only individuals with Parkinson’s disease were impaired on the information integration task (Price, 2005).

Price (2009) later asserted that weather prediction task performance relies on both implicit and explicit learning. Implicit learning has been demonstrated to rely on immediate feedback, whereas explicit learning is not impacted by delayed feedback. To manipulate implicit learning for the task, feedback was delayed by five seconds, which did not alter classification success or the strategies used by participants. However, when explicit learning of the task was minimized by reducing the time to respond to one second, classification accuracy and the adoption of successful strategies by participants was significantly impaired (Price, 2009).

Correlation of Weather Prediction Task Performance and Motor Learning

Learning of a pursuit-rotor task, a mirror tracing task, and the weather prediction task among individuals with Gilles de la Tourette syndrome and matched controls has been examined (Marsh, Alexander, Packard, Zhu, & Peterson, 2005). Although individuals with Gilles de la Tourette syndrome demonstrated impaired performance on the weather prediction task, performance of the sequential motor tasks failed to show similar decrements. The authors concluded that the results reflect the sensitivity of the weather prediction task to striatal damage, while motor skill learning relies on multiple neurological systems (Marsh et al., 2005). However, considering evidence that the weather prediction task is sensitive to damage of the basal ganglia (Knowlton et al., 1996; Moody et al., 2004; Shohamy et al., 2004), presumably an important structure for motor learning, weather task performance may correspond to more skilled motor measures. If weather prediction task performance corresponds to the ability to learn motor tasks, it may provide a means to measure the viability of neural structures underpinning motor learning without the repeated administration of a standardized motor task. Further, aging is implicated in deterioration of implicit learning and memory systems (Salthouse, McGuthry, & Hambrick, 1999).

The possible relationship between implicit processes and degradation of motor acquisition associated with aging has yet to be examined. The purpose of this study is to examine the relationship between weather prediction task performance and the keyboard task described in Chapter 2. It is hypothesized that non-declarative learning systems underpin aspects of manual motor performance. Consequently, it is predicted that performance on the weather prediction task will correlate with learning of skilled manual movements. It is also predicted that age will detrimentally impact performance of the weather prediction task.

Materials and Methods

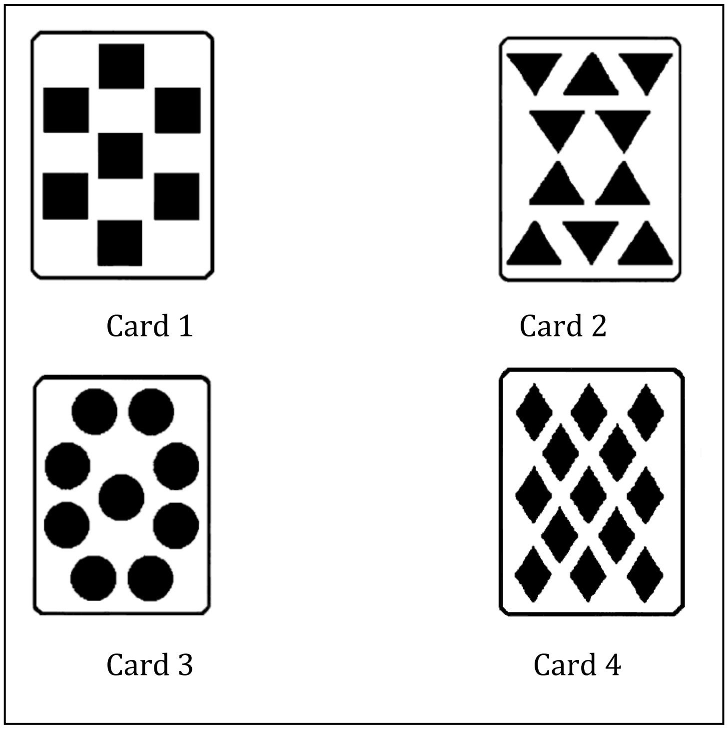
Subjects

Study 1. University-age students (*n*=31, aged 18-28 years, mean age= 21.2 ± 2.5 years, 14 males) participated in the study for credit in undergraduate courses through the Department of Psychology's Human Subject Pool. Older adults (*n*=34, aged 55-95 years, mean age= 73.0 ± 9.6 years, 14 males) were recruited through a local senior centre and word of mouth. Participants were seen at a laboratory at the university or a local senior centre organization. Four cases were excluded due to movement disorders resulting from neurological or orthopaedic conditions with older adults; one subject withdrew from the study. Ethics approval for the study was obtained from the University of Lethbridge Human Subject Committee. The study procedures were explained, after which the participant signed a consent form.

Study 2. University-age students (*n*=41, aged 18-35 years, mean age= 21.0 ± 3.5 years, 20 males) participated in the study for credit in undergraduate courses through the Department of Psychology's Human Subject Pool. Participants were seen at a laboratory. Two cases were excluded; data from one participant was excluded as the participant's age was far outside the range of the rest of the population sample. Data from the second participant was excluded because motor data from trial 2 was not useable. Ethics approval for the study was obtained from the University of Lethbridge Human Subject Committee. The study procedures were explained, after which the participant signed a consent form.

Experimental Apparatus and Task

For the weather prediction task, participants were given multidimensional stimuli and asked to classify them into one of two categories (rain or sun). The stimuli were four cards (Figure 5.1), each containing a unique geometric pattern. Table 5.1 shows the 14 patterns that were used in the Knowlton et al. (1994) weather prediction study. Each pattern is represented as a numeric four-digit sequence corresponding to whether each of the four cards is present (1) or absent (0). The feedback given to the participant is determined by a probabilistic rule based on the individual cards, and as such each pattern is a partially accurate predictor of the weather. Although feedback is determined by the probability attached to each pattern, correct responses are those that correspond to the most probable outcome. For example, if pattern B was presented and the participant selected “sun” the response was considered correct, even if the feedback on the screen indicated that the outcome was rain.



Card 1

Card 2

Card 3

Card 4

Figure 5.1. Cards used for the weather prediction task. The cards were presented on the computer monitor as they are positioned in the table.

Participants were instructed that the purpose of the task was to learn which of two outcomes is best predicted by the pattern of cards on the monitor. Participants viewed between one and three cards on a 17 inch computer monitor in any one trial. There were 204 trials in total. The cards were presented with instructions to press “Z” for “rainy” in the left hand bottom corner and to press “M” for “sunshine” in the bottom right hand corner. Participants had three seconds to respond. If no response was made within three seconds, red font appeared in the middle of screen stating, “Please respond faster next time.” If the correct response assigned to that particular trial was made, “You are correct. The answer is SUNSHINE/RAIN” appeared in green font in the middle of the screen. If an incorrect response was made, “You are incorrect. The answer was SUNSHINE/RAIN” appeared in the middle of the screen in red font. There was a one-second inter-trial interval, and trials were grouped into blocks of 51 trials. Participants were permitted to take a break between blocks and press the space bar to continue with the next block of trials.

Pattern	Card Presentation				Probability (%)	Most Probable Outcome	Pattern Exposure
	Card 1	Card 2	Card 3	Card 4			
A	0	0	0	1	88.24	Sun	17
B	0	0	1	0	64.71	Sun	17
C	0	0	1	1	82.35	Sun	0
D	0	1	0	0	64.71	Rain	17
E	0	1	0	1	82.35	Sun	17
F	0	1	1	0	50	N/A	0
G	0	1	1	1	82.35	Sun	34
H	1	0	0	0	88.24	Rain	17
I	1	0	0	1	50	N/A	0
J	1	0	1	0	82.35	Rain	17
K	1	0	1	1	64.71	Sun	17
L	1	1	0	0	88.24	Rain	17
M	1	1	0	1	64.71	Rain	17
N	1	1	1	0	76.47	Rain	17

Table 5.1. Card patterns, associated probabilities, and frequencies. The all present and all absent patterns were never used, nor was pattern C. Absent cards are denoted with a “0” and present cards are denoted with a “1.”

Only patterns with a correct response were presented, so patterns F and I were not included. Within in the 204 trials, all patterns were presented 17 times, except pattern C. Due to an error carried from the ethics application to the programming, pattern G was administered twice as often and pattern C was not administered. The overall outcomes remain the same as the original task; the overall probability of rain was 50% while the overall probability of sun was 50%. The presentation of trials within each block was random, but patterns and their outcomes were assigned relatively evenly to each block from the total of 204 trials. Feedback was based on probabilities ranging from approximately 65 to 88% for this study.

Data Analysis

From E-Prime, data were written to an Excel spreadsheet for each possible response (sun or rain), for the number of correct responses, and the reaction time for correct responses by block. Responses made in 100 ms or less were excluded from the analysis. The percent correct and average response rate for each block was then computed within Excel. To analyze performance by probability pattern, data were written to an Excel spreadsheet for correct responses attributed to each of the possible patterns for each of the blocks. Again, responses made in 100 ms or less were excluded from the analysis. Data from patterns with the same percent probability were compiled by block, with the exception of pattern G. Pattern G data remained separate as it occurred twice as frequently during the task.

Statistical Analysis

Study 1. Percent correct and reaction times for valid responses for Study 1 were analyzed in a mixed factorial ANOVA (4x2x2) with a within-subject factor of block (blocks 1 to 4) and between-subject factors of age (young and older), and sex (male and female). To investigate the effect of probability pattern, a mixed factorial ANOVA (4x4x2x2) was used to analyze within-subject factors of probability pattern (88.2%, 82.4%, 76.5%, and 64.7%) and block, and between-subject factors of age and sex. To investigate the effect of exposure, a mixed factorial ANOVA (2x4x2x2) was executed to examine within-subject factors of exposure (17 times versus 34 times over the course of the task) for the 82.4% pattern and block, and between-subject factors of age and sex. To examine if weather prediction task performance corresponded to motor performance, bivariate correlations were employed with weather task measures (percent correct and reaction time) and motor measures (overall speed, speed standard deviation, and error rates for the unimanual and bimanual movement conditions).

Study 2. Percent correct and reaction times for valid responses for Study 2 were analyzed in a mixed factorial ANOVA (4x2) with a within-subject factor of block and a between-subject factor of sex. An additional mixed factorial ANOVA (4x4x2) was used to compare probability pattern, block, and sex. To investigate the effect of exposure, a mixed factorial ANOVA (2x4x2) was employed to compare exposure for the 82.4% pattern, block, and sex. Finally, bivariate correlations were calculated with weather task measures and motor measures as for Study 1.

Results

Study 1

For percentage of correct responses, the ANOVA examining the impact over block revealed a main effect of block, $F(3,162)=10.004$, $p<.001$ (Table 5.2, Figure 5.2). Planned comparisons (with a Bonferroni correction, 95% confidence intervals) showed a significant improvement from block 1 to block 2, and block 2 to block 3, but not from block 3 to block 4 (Table 5.3). Further, the effect size between blocks 1 and 2 was greater than that between blocks 2 and 3, explaining 9.0 and 5.5% of the variance respectively. The analysis also showed a main effect of age. Percentage of correct responses were significantly higher for young adults compared to older adults, $F(1,54)= 9.483$, $p=.003$ (Table 5.2). No other main effects and no interactions reached significance.

For reaction time, the ANOVA examining the impact over block revealed a main effect of block, $F(2.5,135.4)=15.808$, $p<.001$ (Table 5.2). Pairwise comparisons (with a Bonferroni correction) showed significantly longer reaction times for blocks 2, 3, and 4 compared to block 1 (mean difference= 249.3, 308.9, and 317.2 respectively, standard error= 54.8, 64.4, and 62.5 respectively, $p<.001$ for all comparisons). Other comparisons failed to reach significance. The analysis also showed a main effect of age; reaction time was significantly faster for young adults for correct responses compared to older adults, $F(1,54)= 9.334$, $p=.003$ (Table 5.2). No other main effects and no interactions reached significance.

Measure	Main Effect	Means (SE)				Partial η^2	Observed Power	Sphericity Correction
Percent Correct	Block	1	2	3	4	.156	.998	SA
		51.963 (1.315)	54.592 (1.343)	57.987 (1.228)	58.761 (1.461)			
	Age	Young		Older		.149	.856	N/A
		58.983 (1.390)		52.668 (1.508)				
Reaction Time	Block	1	2	3	4	.226	1.000	HF
		1681.386 (62.071)	1432.098 (59.667)	1372.461 (65.345)	1364.233 (63.762)			
	Age	Young		Older		.147	.851	HF
		1298.482 (72.780)		1626.607 (78.985)				

Table 5.2. Means, effect sizes, power, and sphericity corrections of significant effects for block for Study 1 (SA: sphericity assumed, N/A: not applicable, HF: Huynh-Feldt).

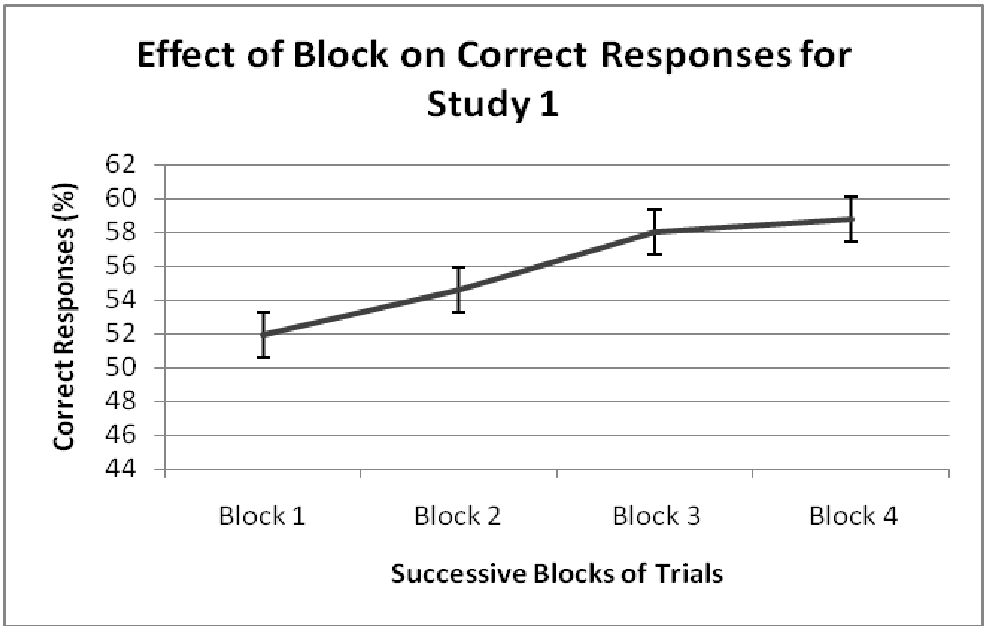


Figure 5.2. Effect of block on percent correct responses for Study 1. The line represents the means and error bars represent the standard error of the mean.

Planned contrasts for percent correct	*F*	*p* value	Mean Difference	SE	η^2
Block 1 – Block 2	16.8421	<.001	-4.10391*	1.04157	.08966
Block 2 – Block 3	9.91027	.003	-3.14806*	.96012	.05478
Block 3 – Block 4	.41721	.521	-.64592	.92623	N/A

Table 5.3. Planned contrasts of the effect of block for percent correct for Study 1 (* denotes significance). Sphericity corrections were not applied as Mauchly's Test of Sphericity did not reach significance.

For percentage of correct responses, the ANOVA examining the impact of probability revealed a main effect of probability, *F*(2.0,71.5)= 36.892, *p*<.001 (Table 5.4, Figure 5.3). Pairwise comparisons (with a Bonferroni correction) failed to find significant differences between the 88.2, 82.4, and 76.5% probability patterns, but these three probabilities were all significantly higher in terms of correct responses than the 64.7% probability patterns (mean difference= 28.9, 33.1, and 28.8 respectively, standard error= 3.8, 4.8, and 4.1 respectively, *p*<.001 for these comparisons). No other main effects and no interactions reached significance.

For reaction time, the ANOVA examining the impact of probability revealed a main effect of probability, *F*(3,108)=8.383, *p*<.001 (Table 5.4). Pairwise comparisons (with a Bonferroni correction) showed that reaction times were lower for the 82.4% probability patterns compared to the 76.5 and 64.7% probability patterns (mean difference= -140.7 and -217.0 respectively, standard error= 39.5 and 43.3 respectively, *p*=.006 and <.001 respectively). Other comparisons, including the comparisons with the 88.2% patterns, failed to reach significance. No other main effects reached significance.

Measure	Main Effect / Interaction		Mean (SE)				Partial η^2	Observed Power	Sphericity Correction
Percent Correct	Probability		88.2%	82.4%	76.5%	64.7%	.506	1.000	GG
			67.743 (2.625)	71.940 (2.638)	67.659 (2.627)	38.860 (2.560)			
Reaction Time	Probability		88.2%	82.4%	76.5%	64.7%	.189	.992	SA
			1457.788 (69.068)	1365.511 (71.255)	1506.180 (71.871)	1582.496 (80.530)			
	Probability x Block x Age						.063	.823	GG
			88.2%	82.4%	76.5%	64.7%			
	Young	Block 1	1519.34 (111.88)	1422.00 (117.19)	1389.35 (108.14)	1691.63 (134.30)			
		Block 2	1185.23 (109.83)	1044.04 (96.75)	1509.80 (136.95)	1520.96 (126.70)			
		Block 3	1170.33 (102.68)	1206.31 (118.73)	1153.44 (112.34)	1357.38 (130.85)			
		Block 4	1122.14 (109.17)	1102.84 (108.35)	1383.55 (163.46)	1293.37 (123.00)			
	Older	Block 1	1872.15 (132.09)	1726.02 (138.35)	2041.26 (127.67)	1906.88 (158.55)			
		Block 2	1608.55 (129.67)	1562.50 (114.22)	1499.76 (161.68)	1687.21 (149.57)			
		Block 3	1531.06 (121.22)	1429.16 (140.17)	1418.69 (132.63)	1683.98 (154.48)			
		Block 4	1653.52 (128.88)	1431.21 (127.92)	1653.61 (192.98)	1518.55 (145.21)			

Table 5.4. Means, effect sizes, power, and sphericity corrections of significant effects for probability for Study 1 (GG: Greenhouse-Geisser, SA: sphericity assumed).

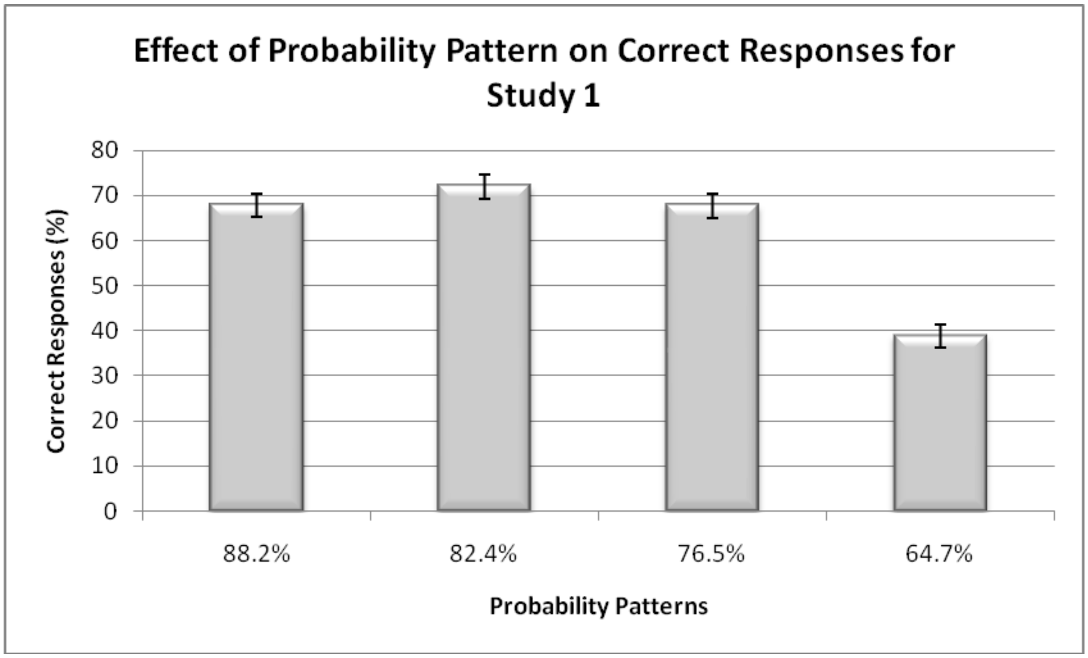


Figure 5.3. Effect of probability pattern on correct responses for Study 1. Bars represent the means and error bars represent the standard error of the mean.

The ANOVA examining the impact of probability showed an interaction of age, probability pattern, and block for reaction time, *F*(6.2, 223.2)=2.404, *p*=.027 (Table 5.4, Figures 5.4a-d). Pairwise comparisons (with a Bonferroni correction) revealed that young adults responded with significantly shorter reaction times for the 88.2% probability patterns over all four blocks (Table 5.5). However, the analysis failed to find significant differences for most blocks of the remaining probability patterns. In addition, reaction times for young adults improved significantly from block 1 in comparison to the subsequent blocks for the 88.2% probability patterns, and improved from block 1 in comparison to blocks 2 and 4 for the 76.5% patterns. The comparisons failed to find significant changes in reaction time in relation to the 76.5% probability patterns, and found a significant difference between the first and fourth block only for the 64.7% probability patterns. Meanwhile, older adults demonstrated significant improvements in reaction time only for the 76.5% probability patterns between blocks 1 and 2 and blocks 1 and 3 (Table 5.5). No other interactions reached significance.

Pairwise comparisons for reaction time	Mean Difference	SE	Significance
88.2% pattern, block 1, young – older adults	-352.814	173.102	.049
88.2% pattern, block 2, young – older adults	-423.327	169.929	.017
88.2% pattern, block 3, young – older adults	-360.731	158.866	.029
88.2% pattern, block 4, young – older adults	-531.378	168.899	.003
82.4% pattern, block 2, young – older adults	-518.461	149.687	.001
76.5% pattern, block 1, young – older adults	-651.910	167.316	<.001
Young adults, 88.2% pattern, block 1 – 2	334.109	101.949	.014
Young adults, 88.2% pattern, block 1 – 3	349.008	111.117	.020
Young adults, 88.2% pattern, block 1 – 4	397.196	119.715	.012
Young adults, 82.4% pattern, block 1 – 2	377.964	104.749	.006
Young adults, 82.4% pattern, block 1 – 4	319.163	111.129	.041
Young adults, 64.7% pattern, block 1 – 4	398.261	125.113	.018
Older adults, 76.5% pattern, block 1 – 2	541.499	173.115	.021
Older adults, 76.5% pattern, block 1 – 3	622.569	163.231	.003

Table 5.5. Statistically significant results of pairwise comparisons of the interaction of age, probability pattern, and block for reaction time for Study 1. Few comparisons of probability patterns in each block reached significance, so those comparisons were excluded from the table.

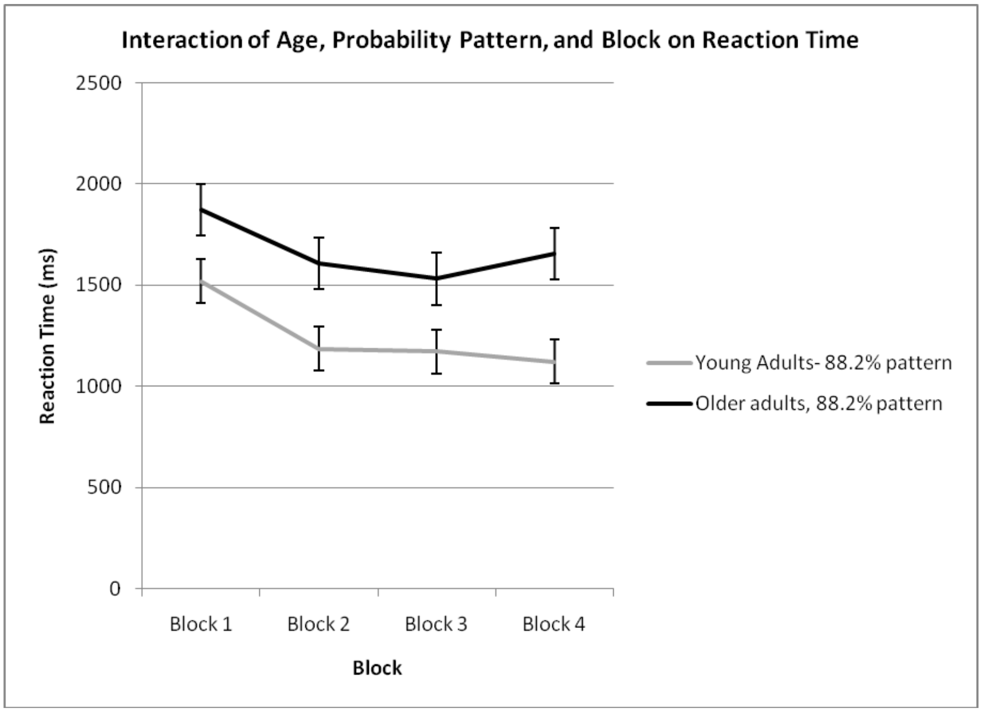


Figure 5.4a. Interaction of age, probability pattern, and block on reaction time for the 88.2% probability pattern (Study 1). Lines represent the means and error bars represent the standard error of the mean.

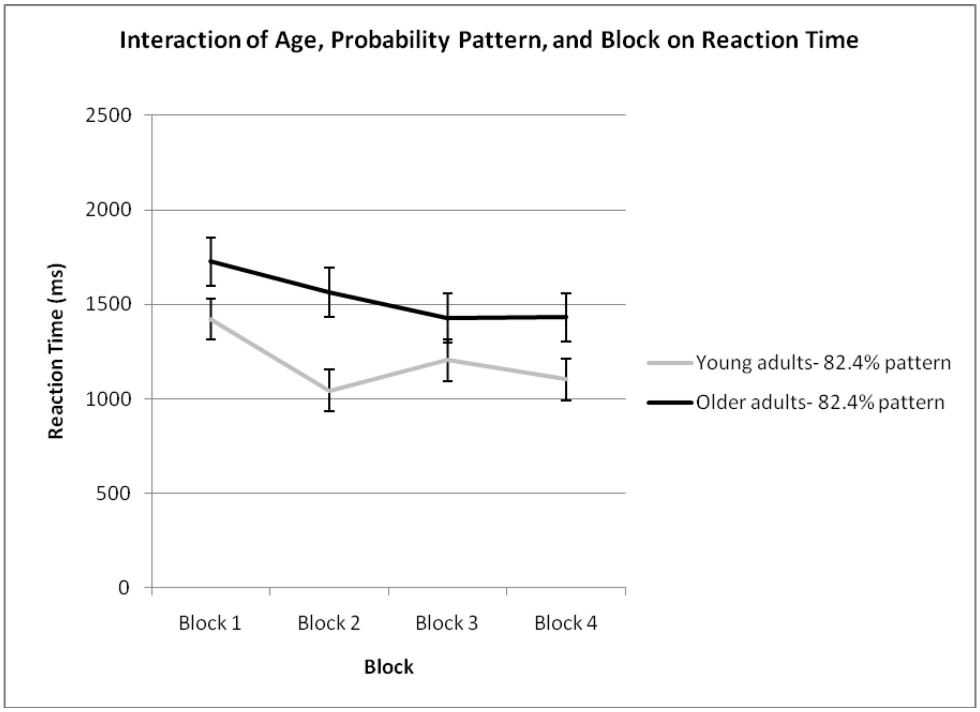


Figure 5.4b. Interaction of age, probability pattern, and block on reaction time for the 82.4% probability pattern (Study 1). Lines represent the means and error bars represent the standard error of the mean.

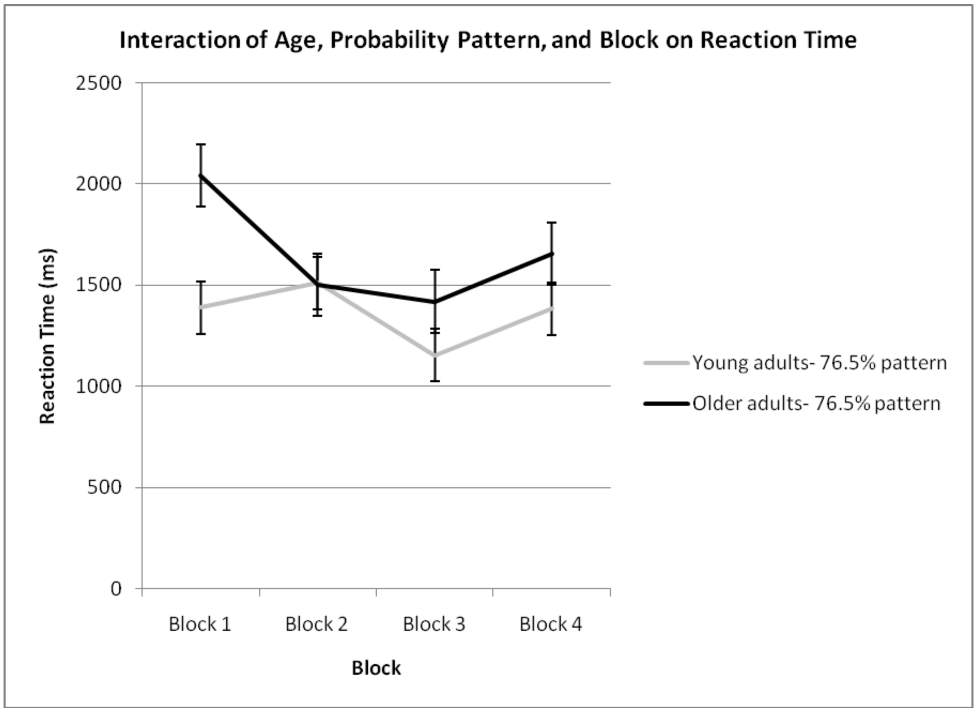


Figure 5.4c. Interaction of age, probability pattern, and block on reaction time for the 76.5% probability pattern (Study 1). Lines represent the means and error bars represent the standard error of the mean.

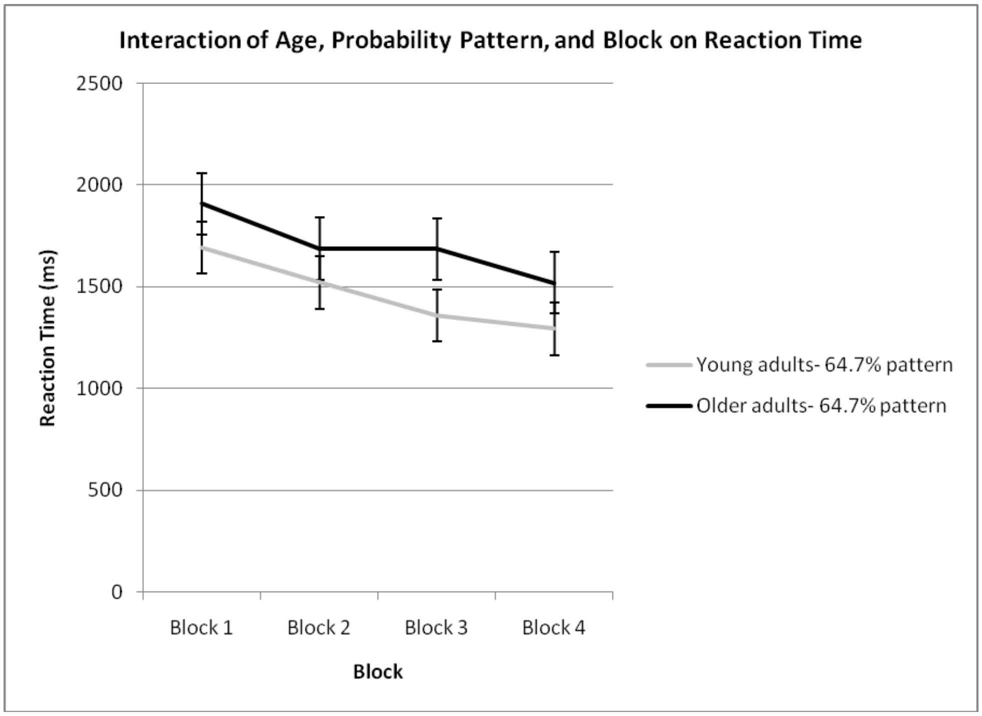


Figure 5.4d. Interaction effect of age, probability pattern, and block on reaction time for the 64.7% probability pattern (Study 1). Lines represent the means and error bars represent the standard error of the mean.

The ANOVA examining the impact of exposure to patterns failed to find any main effects or interactions in relation to percentage of correct responses or reaction time.

Bivariate correlations between the overall percent correct and reaction time with the weather prediction task and measures of motor performance with the keyboard task revealed several significant correlations (Table 5.6). All measures related to asymmetrical and symmetrical movements correlated significantly and negatively with percentage of correct responses on the weather prediction task, along with a few measures of unimanual movement (P of -.260 to -.418, p=.049 to .001). Therefore, faster speed, decreased speed standard deviation, and lower error rates all correlated with a larger percentage of correct responses on the weather prediction task. Some unimanual measures and one symmetrical measure correlated significantly and positively with reaction time on the weather prediction task (P of .266 to .309, p=.044 to .018). Therefore, faster speed and lower speed standard deviation correlated with faster reaction time.

		Weather Prediction Task Measures	
		Percent Correct	Reaction Time
Movement Measures	Asymmetrical speed	*P*= -.285*, *p*=.030	*P*=.198, *p*=.136
	Asymmetrical speed standard deviation	*P*= -.356*, *p*=.006	*P*=.208, *p*=.118
	Asymmetrical error rates	*P*= -.382*, *p*=.003	*P*=.189, *p*=.155
	Symmetrical speed	*P*= -.305*, *p*=.020	*P*=.242, *p*=.067
	Symmetrical speed standard deviation	*P*= -.295*, *p*=.024	*P*=.266*, *p*=.044
	Symmetrical error rates	*P*= -.371*, *p*=.004	*P*=.230, *p*=.082
	Unimanual dominant speed	*P*=-.252, *p*=.056	*P*=.309*, *p*=.018
	Unimanual dominant standard deviation	*P*=-.306*, *p*=.019	*P*=.105, *p*=.431
	Unimanual dominant error rates	*P*=-.418*, *p*=.001	*P*=.044, *p*=.743
	Unimanual nondominant speed	*P*=-.253, *p*=.055	*P*=.283*, *p*=.031
	Unimanual nondominant speed standard deviation	*P*=-.210, *p*=.114	*P*=.303*, *p*=.021
	Unimanual nondominant error rates	*P*=-.260*, *p*=.049	*P*=.078, *p*=.559

Table 5.6. Correlations between the weather prediction task and the keyboard task for Study 1 (*denotes significance).

Study 2

For percentage of correct responses, the ANOVA examining the impact over block failed to find any main effects or interactions. For reaction time, the ANOVA examining the impact of block revealed a significant main effect of block (corrected using Greenhouse-Geisser), *F*(2.2,107.0)=21.591, *p*<.001 (Table 5.7, Figure 5.5). Pairwise comparisons (with a Bonferroni correction) revealed significantly higher reaction time in block 1 compared to blocks 2, 3, and 4 (mean difference= 268.1, 353.7, and 405.6 respectively, standard error= 52.8, 68.8, and 66.1 respectively, *p*<.001 for these comparisons). All other comparisons failed to reach significance. No other main effects or interactions reached significance.

For percentage of correct responses, the ANOVA examining the impact of probability revealed a main effect of probability, *F*(2.2,65.0)= 26.184, *p*<.001 (Table 5.8, Figure 5.6). Consistent with Study 1, pairwise comparisons (with a Bonferroni correction) failed to find significant differences between the 88.2, 82.4, and 76.5 percent probability patterns, but these probability patterns were all significantly higher than the 64.7 percent probability patterns (mean difference= 21.6, 26.4, and 22.6 respectively, standard error= 3.9, 4.0, and 3.9 respectively, *p*<.001 for these comparisons). No other main effects and no interactions reached significance.

Measure	Main Effect / Interaction		Mean (SE)	Partial η^2	Observed Power	Sphericity Correction
Reaction Time	Block	Block 1	1411.573 (70.624)	.356	1.000	GG
		Block 2	1143.460 (71.673)			
		Block 3	1057.871 (63.800)			
		Block 4	1005.932 (56.745)			

Table 5.7. Means, effect sizes, power, and sphericity corrections of significant effects for block for Study 2 (GG: Greenhouse-Geisser).

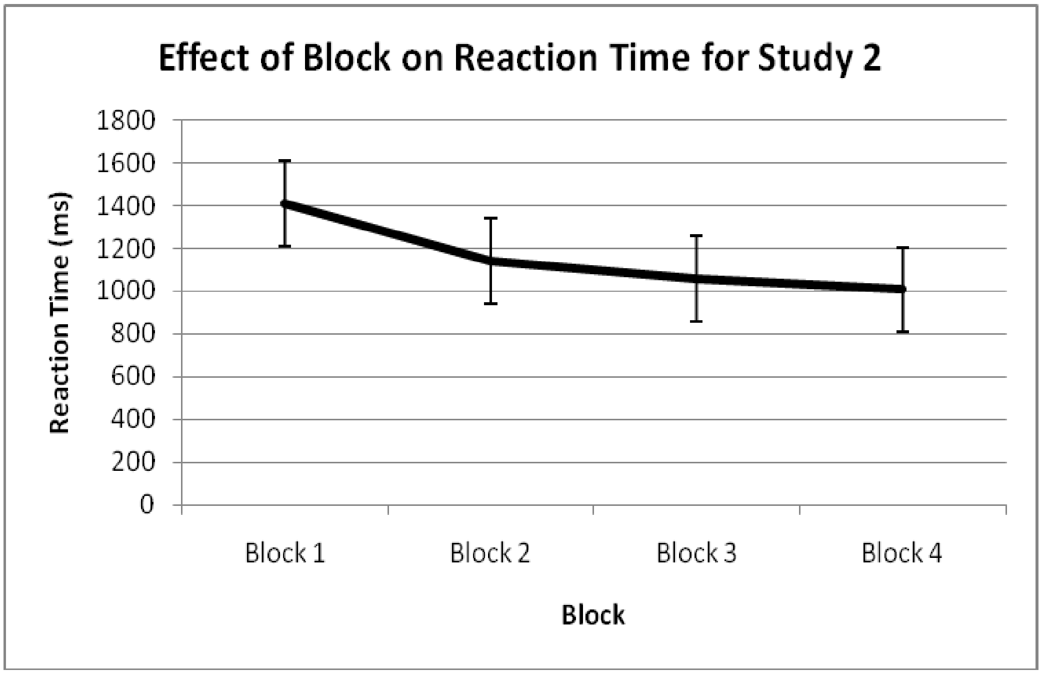


Figure 5.5. Effect of block on reaction time for Study 2. The line represents the means and error bars represent the standard error of the mean.

Measure	Main Effect / Interaction	Mean (SE)				Partial η^2	Observed Power	Sphericity Correction
Percent Correct	Probability Pattern	88.2%	82.4%	76.5%	64.7%	.474	1.000	GG
		65.952 (2.436)	70.754 (2.436)	67.016 (2.934)	44.387 (2.575)			
Reaction Time	Probability Pattern	88.2%	82.4%	76.5%	64.7%	.156	.923	SA
		1147.282 (55.327)	1180.904 (72.448)	1283.904 (86.849)	1276.009 (69.328)			

Table 5.8. Means, effect sizes, power, and sphericity corrections of significant results for probability for Study 2 (GG: Greenhouse-Geisser, SA: sphericity assumed).

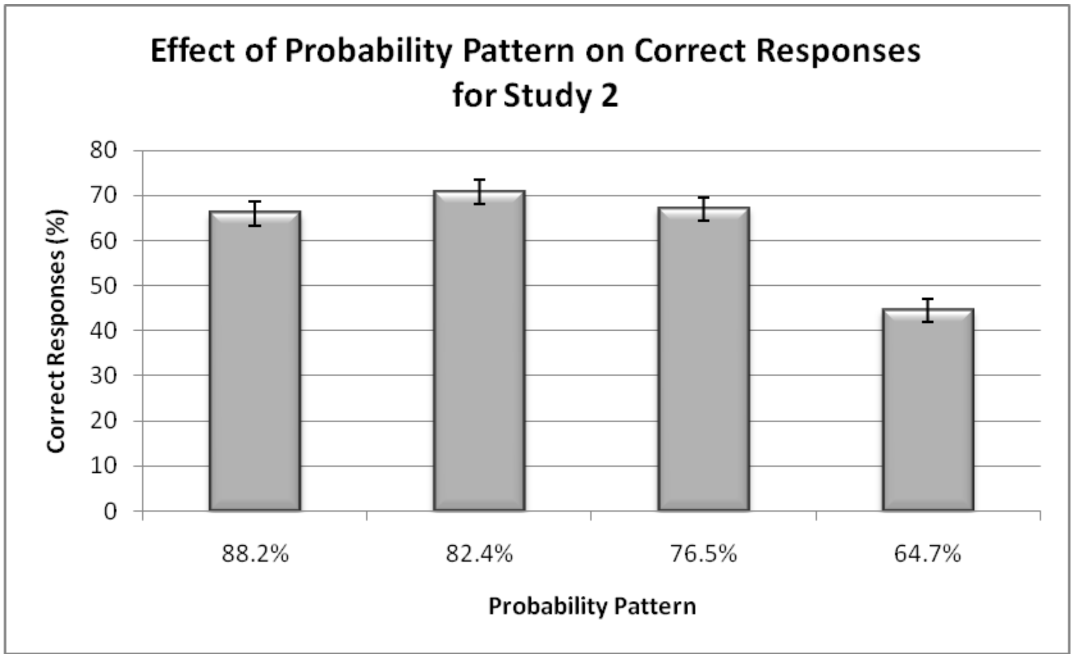


Figure 5.6. Effect of probability pattern on correct responses for Study 2. Bars represent the means and error bars represent the standard error of the mean.

For reaction time, the ANOVA examining the impact of probability revealed a main effect of probability, *F*(3,87)=5.346, *p*=.002 (Table 5.8, Figure 5.6). Pairwise comparisons (with a Bonferroni correction) showed that reaction times were lower for the 88.2% probability patterns compared to the 64.7% patterns (mean difference= -128.7, standard error= 41.3, *p*=.025). There was also a near-significant comparison for shorter reaction times for the 88.2% probability pattern compared to the 76.5% pattern (mean difference= -95.1, standard error= 34.0, *p*=.055). Other comparisons, including the comparisons with the 88.2% patterns, failed to reach significance. No other main effects and no interactions reached significance.

The ANOVA examining the impact of exposure to patterns failed to find any main effects or interactions in relation to percentage of correct responses or reaction time.

Bivariate correlations between percent correct responses on the weather prediction task and keyboard measures revealed a significant correlation with symmetrical speed standard deviation for both the feedback condition, *P*=-.324, *p*=.039, and the no feedback condition, *P*=-.354, *p*=.023. Correlations among the other motor measures and percent correct and reaction time on the weather prediction task failed to reach significance.

Discussion

Study 1

Percentage of correct responses on the weather prediction task improved rapidly over the first few blocks and then plateaued between blocks 3 and 4. The analysis failed to find a significant difference between the 88.2, 82.4, and 76.5% probability patterns, but performance for these probability patterns was significantly higher than for the 64.7% patterns. Performance of the 64.7% patterns was worse than chance.

The latter results may in part be due to less consistent feedback with the 64.7% probability pattern as to the most probable outcome, but the use of specific strategies has been reported to influence performance, including use of a one-cue strategy (Gluck et al., 2002). For this version of the weather task, card one (squares) was highly predictive of rain and card four (diamonds) was highly predictive of sun (Table 5.1, Figure 5.1). Choosing the outcome based on the presence or absence of one of these cards would result in 83.3% of responses being correct (i.e. the most probable response). However, this strategy would result in incorrect responses for two of the four 64.71% probability patterns.

Preference for this strategy may in part account for the gap between the 64.7% patterns and others; however, the overall percentage of correct responses falls well below the 83.3% expected if a one-cue strategy had been followed consistently, ranging from 52.0% for block 1, to 58.8% for block 4. Therefore, the selection of specific strategies may not solely explain performance, but feedback probabilities may moderate responses as well.

A surprising finding was that while exposure to pattern G was double that of the other 82.4% probability patterns, the analysis failed to find a difference in percent correct or reaction time for pattern G compared to the other 82.4% probability patterns. This is despite the fact that the 82.4% probability patterns all fit a one-cue strategy (using either card one or card four) and a multi-cue strategy (basing a response on the combination of cards presented). None of the 82.4% probability patterns fit a singleton strategy (basing a response on patterns with single cards). Using a singleton strategy and guessing randomly on the remaining patterns would result in a 66.7% accuracy rate, but the percent correct for the 82.4% probability patterns was 71.9%, suggesting more effective strategies were used for at least a portion of the task.

The prediction that older adults would perform more poorly compared to young adults was validated. This diverges from a prior study by Fera et al. (2005), which found that young and older adults used similar strategies and exhibited similar learning curves. However, the participants in the present study are considerably older than in the previous study, 73.0 ± 9.6 years and 67.1 ± 5.3 years respectively (Fera et al., 2005). In addition, a prior study with a sample of older adults, aged 68.2 ± 10.3 years, also reported decrements with the weather prediction task (Price, 2005). This study failed to find an interaction of probability pattern and age, but presumably selection of less efficient strategies or delayed selection of better strategies is responsible for the differences between groups in this study.

In terms of reaction time, the interaction of age, block, and probability pattern reveals an intriguing finding. While younger adults responded more quickly to the 88.2% probability patterns, this pattern was not consistently observed with the lower probability patterns. In addition, young adults' reaction time improved significantly from block 1 to block 2 for the 88.2% probability pattern and then plateaued. Again, this effect was not consistently observed for the other probability patterns. Older adults appeared to show this pattern of decreased response time from block 1 to block 2, but only for the 76.5% probability pattern. This suggests that the younger and older adults may have used different strategies to complete the weather prediction task, and that the younger adults may have used strategies that resulted in better overall performance.

The prediction of correlation between weather prediction task and keyboard task performance was confirmed. Faster speed, lower speed variance, and lower error rates for asymmetrical and symmetrical movements consistently correlated with a higher percentage of correct responses on the weather prediction task. Lower unimanual error rates also correlated with a higher percentage of correct responses on the weather prediction task. In addition, increased unimanual speed and variance correlated with faster reaction times on the weather prediction task. While the findings suggest that the weather prediction task may provide a means of investigating the integrity of neural structures necessary for manual movements, the results may simply reflect a global decline of neural systems associated with aging. Further investigation is required to determine if the weather prediction task selectively identifies neural deficits necessary to skilled manual movement.

Study 2

As with Study 1, the analysis failed to find a significant difference between the 88.2, 82.4, and 76.5% probability patterns, but performance in relation to these patterns were significantly higher than for the 64.7% patterns. Performance of the 64.7% patterns was again worse than chance. As with Study 1, no effect of exposure to the 82.4% probability patterns was observed. While reaction time decreased significantly from block 1 to block 2 and then plateaued, this study failed to replicate the interaction of probability and block for reaction time. This may result from the smaller and more homogenous group in this study compared to Study 1.

While all of the measures of keyboard performance correlated significantly with either percent correct or reaction time on the weather prediction task in Study 1, only symmetrical speed standard deviation correlated with percent correct in Study 2. Consequently, it appears that either age may confound the correlations between the weather prediction task and keyboard measures or the larger differences observed between younger and older adults correspond with differences in the integrity of neural systems crucial to skilled motor performance. These results require replication, particularly considering that previous investigation failed to find a correlation between the weather prediction task and motor tasks, despite impaired performance on the weather prediction task (Marsh et al., 2005).

While some assessments used in the clinical setting must be sensitive to small changes in order to measure improvements resulting from rehabilitation, other assessments are used to detect clinically significant impairments. Although the weather prediction task does not demonstrate sensitivity to small changes in motor performance (considering the lack of correlations in Study 2), the task may identify impairment of underlying neural systems that corresponds to motor function decrements. As mention previously, it is important to identify if the findings of Study 1 relate to global deterioration of neural systems associated with aging, or if selective neural impairments contributed to poor weather prediction task performance and corresponded with poor motor performance.

The underlying learning systems employed in performing the weather prediction task remain under debate. Given current research, it appears unlikely that the task relies solely on explicit or implicit learning systems. However, it is also unlikely that the keyboard task relies solely on implicit systems. Conceivably, certain aspects of keyboard performance, such as initial hand placement, rely on declarative memory. As such, parallel operation of implicit and explicit memory systems for the weather prediction task may resemble the complement of skills required for skilled manual movements. However, this may confound identification of the specific systems that contribute to poor function and require intervention.

Structures associated with declarative systems (i.e. the medial temporal lobe) are implicated in the selection of strategies for the weather prediction task (Hopkins et al., 2004). This function may be comparable to aspects of the keyboard task such as the initial selection of motor programs. Further, virtual lesions of M1, an essential structure in motor performance, significantly impairs performance on the weather prediction task (Wilkinson et al., 2009). Structures associated with implicit memory systems, specifically the striatum, are implicated in performance of the weather prediction task (Miller et al., 1996; Moody, 2004). Conceivably the striatum is crucial to the execution of finger sequences for the keyboard task. While weather prediction task performance correlated with keyboard performance among a heterogeneous sample (in Study 1), contributions of these various learning systems and associated neural structures must be defined. Further, the probable interaction between implicit and explicit memory systems in successful performance of these tasks deserves further investigation.

CHAPTER 6:
IMPLICATIONS AND FUTURE DIRECTIONS

Introduction

Bimanual movement is crucial to normal daily function for humans and as such, elucidating the factors that influence bimanual motor learning is important. A piano keyboard task was used to assess motor skill of unimanual, bimanual symmetrical, and bimanual asymmetrical movements. The influence of sex, age, and feedback on acquisition of motor skill, and in particular bimanual movement, was investigated.

Testing of Thesis Hypotheses

The research affirmed the usefulness of the keyboard task in studying bimanual movement, and effectively tested the *a priori* hypotheses. See Table 6.1 for outcomes related to testing of predictions associated with the hypotheses.

Novel Findings

Sex Differences

There was a trend for females to initially perform asymmetrical movements more quickly than males. Additionally, females demonstrated significantly higher dominant-nondominant onset standard deviation solely for the asymmetrical condition. Asymmetrical movements are characterized by decreased inter-hemispheric connectivity (Maki et al., 2008; Walsh et al., 2008) and increased dominant-nondominant onset standard deviation may correspond with neural strategies to reduce “limb locking.” Use of such neural strategies by females may account for the initial trend for faster asymmetrical performance than males. It also suggests that females may be better able to inhibit inter-hemispheric connectivity.

Hypothesis	Prediction	Finding
Dominant unimanual movements require relatively fewer neural resources than nondominant unimanual movements.	1. Dominant unimanual movements will be performed faster and with fewer errors than nondominant unimanual movements.	Dominant unimanual movements were faster than nondominant movements. Differences in error rates failed to reach significance.
Symmetrical movements require fewer neural resources relative to asymmetrical movements.	2. Symmetrical movements will be performed faster and with fewer errors than asymmetrical movements.	Symmetrical movements were performed faster, with fewer errors, and with more stability than asymmetrical movements.
Males have a basic motor speed advantage for less skilled movements.	3. Males will perform unimanual movements more quickly than females.	Not supported.
Stronger inter-hemispheric pathways among females confers an advantage for the increased motor programming demands associated with bimanual performance.	4. Females will perform bimanual movements with greater speed and accuracy than males.	Trend for females to initially perform asymmetrical movements faster than males.
Global neurological decline associated with older age will result in poorer performance of skilled manual movements.	5. Older adults will perform all movements with decreased accuracy and speed compared to young adults.	Older adults performed slower and with more errors for both unimanual and bimanual movements.
Differential deterioration of inter-hemispheric structures with aging will result in greater deficits for bimanual movements relative to other movements.	6. Older adults will perform bimanual movements with less skill relative to unimanual movements in comparison with young adults.	Older adults performed bimanual movements with greater errors and speed standard deviation relative to unimanual movements.
Neural networks rapidly adapt to and exploit auditory feedback as a means to superior motor performance.	7. Skilled manual movements will be faster and more accurate when auditory feedback is given.	Under specific conditions, auditory feedback was detrimental to performance.
Music training strengthens inter-hemispheric pathways and consequently results in better performance of bimanual movements relative to unimanual movements.	8. Individuals with past music lessons will use feedback more effectively.	Individuals with prior music training performed better in the presence of feedback.
	9. Individuals with past music lessons will perform bimanual movements better than unimanual movements.	Music training resulted in better bimanual movement relative to unimanual movement in Study 1, but not in Study 2.
Non-declarative learning systems underlie components of manual motor performance.	10. Performance on the weather prediction task will correlate with manual movements.	Motor and weather prediction task performance correlated for Study 1, but not Study 2.
	11. Older adults will show decrements with the weather prediction task.	Older adults made fewer correct responses and were slower to respond on the weather prediction task.

Table 6.1 Comparisons of findings with hypotheses and predictions.

Males initially performed unimanual movements more slowly with feedback. It is plausible that male-specific neural lateralization for unimanual movement (Lissek et al., 2007) and processing of auditory information (Koelsch et al., 2003) result in competition for shared neural networks. Note however, that males showed a rapid practice effect.

Females performed bimanual movements significantly faster without feedback at trial 2, suggesting that feedback is actually detrimental to bimanual performance for females. In addition, exploratory analyses revealed that, with feedback, females performed symmetrical movements with increased standard deviation of speed. This suggests that symmetrical movements were less stable in the presence of feedback.

It is hypothesized that female-specific preference for use of inter-hemispheric connections in the production of bimanual movements and processing of auditory information (Koelsch et al., 2003) may result in competition for shared neural networks. It has yet to be shown, however, that females display more symmetrical activation than males during bimanual movements. Symmetrical movements may be more sensitive than asymmetrical movements to these sex differences as symmetrical movements are characterized by increased inter-hemispheric activity compared to asymmetrical movements (Maki et al., 2008; Walsh et al., 2008).

Rhythmic Movement Strategies

Higher downbeat-offbeat ratios correspond to greater emphasis on the rhythmic aspects of movement. Downbeat offbeat ratios of the nondominant hand were higher for symmetrical movements for both studies. Higher values for symmetrical movements may correspond with increased reliance of the nondominant hand on the dominant hemisphere for input, and specifically for the temporal aspects of movement.

Effect of Age on Bimanual Performance

Older adults performed bimanual movements with less proficiency relative to unimanual movements in terms of errors and speed standard deviation, suggesting that bimanual movements are relatively more sensitive to the detrimental effects of aging than unimanual movements. The finding supports the hypothesis that age-related deterioration of inter-hemispheric connections results in greater deficits for bimanual movements relative to other movements (Bennett et al., 2010; Hasan et al., 2010; Lee et al., 2007).

Exploratory analysis showed that older adults with prior music training had significantly lower bimanual-unimanual speed ratios ($p<.001$), demonstrating a protective effect of prior music lessons. The findings also support the hypothesis that age-related degeneration of inter-hemispheric structures differentially affects bimanual movement. Music training results in structural changes to the anterior aspect of the corpus callosum (Gaser & Schlaug, 2003; Schlaug et al., 1995), and may offset age-related deterioration.

Effect of Auditory Feedback on Bimanual Performance

Participants with less than a year of music training demonstrated a learning effect with auditory feedback for bimanual-unimanual speed ratios, while those with more than a year of training demonstrated a learning effect when feedback was absent. In addition, those with more than three years of music training exhibited faster bimanual movements compared to unimanual movements in the presence of feedback.

Presumably, macrostructual neural changes that result from music training provide an advantage to motor performance when auditory feedback is available (Elbert et al., 1995; Gaser & Schlaug, 2003; Schlaug et al., 1995). While co-activation of motor and auditory networks occurs rapidly with playing a musical instrument (Bangert & Altenmüller, 2003; D'Ausilio et al., 2006), the amount of training required to confer a benefit of auditory feedback to motor performance is unclear.

Individuals with more than three years of training performed better with auditory feedback and those with less than a year performed better when feedback was absent. However, the study did not control for the type of instrument trained or the intensity of training. Clarification of these issues is important to determine the stage of training and relative neural plasticity necessary to confer a benefit of auditory feedback to motor performance.

The Role of the Non-Declarative Systems in Motor Performance

Reduced accuracy and increased reaction times among older adults for the weather prediction task is in keeping with decline of non-declarative systems with aging (Salthouse et al., 1999). Significant correlations between the weather prediction task and motor performance in Study 1 suggest that the tasks rely on similar underlying neural networks. Although impaired motor performance in relation to impaired weather task performance was not found among individuals with Gilles de la Tourette syndrome (Marsh et al., 2005), the keyboard task assesses relatively more complex motor movements. The weather prediction task may be a sensitive means of identifying clinically important dysfunction of non-declarative systems and consequent impairment of skilled motor performance. However, elucidation of relative contributions of underlying systems to both the weather prediction and keyboard task is needed.

While the weather prediction task does not solely assess non-declarative systems (Gluck et al., 2002; Newell et al., 2007; Price, 2005, 2009), aspects of motor performance also likely rely on declarative systems. Reaction times differences among young and older adults for different probability patterns suggest the use of different strategies, and that younger adults employ better strategies. Strategy selection likely involves declarative systems (Hopkins et al., 2004; Meeter et al., 2006), and is arguably similar to the selection of motor programs or schemas.

Limitations and Caveats

It is important to point out limitations related to this work. The keyboard task provided several reliable and sensitive measures related to motor performance; however, it does not provide kinematic measures of joint position, delineate inter-joint contributions to force, or clearly identify initiation of movements. Further research pairing the keyboard task with movement analysis would eliminate these limitations.

Although Study 1 identified several significant findings related to sex, Study 2 failed to replicate many of these findings. These findings may be spurious, but the large portion of older adults in Study 1 may have magnified sex-related differences as sex differences may compound with age (Bayer & Hausmann, 2010; Lacreuse et al., 2005; Ruff & Parker, 1993).

Vascular health may be a more important determinant of motor proficiency than age *per se*; consequently, the failure to quantify vascular health may be a significant limitation of this study. In addition, linking neural changes associated with aging, such as deterioration of inter-hemispheric connections with behavioral data, is important in order to generalize study findings and identify plausible interventions.

Most analyses for the effects of feedback on motor performance were corrected for music training by entering years of music lessons as a covariate into the models. As a result, important effects related to music training may not have been identified. However, elucidating the impact of feedback was considered paramount, so analyses were conducted accordingly. Further, this study did not address the long-term effects of music training on motor movement, which has obvious ramifications in terms of clarifying the benefits of musical training to bimanual performance.

Implications

The study results reveal the importance of grading activities within a rehabilitation program. Therapy programs typically target the client's current level of ability; the program begins with a challenging and yet achievable goal and gradually increases task difficulty in small increments to improve performance over time. Dominant unimanual movements were relatively easier than nondominant unimanual movements and symmetrical movements were relatively easier than asymmetrical movements. As such, the study suggests that therapy progression should take into account that difficulty increases from dominant unimanual, to nondominant unimanual, to symmetrical, to asymmetrical movements. In addition, because of varying neural demands associated with symmetrical and asymmetrical movements, it cannot be assumed that skills learned in a symmetrical format will generalize to asymmetrical movements.

Several sex-related differences were identified. It is important to determine if these findings are genuine as there are important implications for rehabilitation of neuro-degenerative disorders and brain injury. For example, this research suggests that bimanual movements are relatively easier for females compared to males. As a consequence, a graded program may initially use a less complex bimanual sequences for males. The detrimental effect of auditory feedback on bimanual performance for females may warrant practicing complex bimanual sequences without auditory feedback initially with females without prior music training, and then gradually introducing feedback as a means of increasing task complexity.

The present findings confirm the usefulness of the piano keyboard task as a means to study motor learning. Not only is the task sensitive, gradable, and adaptable to research needs, but it also is a socially valued and functional activity. Further, the keyboard task allows for manipulation of the temporal aspects of motor coordination as well. Considering these features, the task may have application to the clinical setting for the purposes of retraining functional manual movements.

While the study identified age-related decrements in motor performance, it also identified the beneficial effect of practice and prior musical training for older adults. These results suggest that the same methods demonstrated to improve performance with young adults are also valid for use with older adults. Older adults also demonstrated reduced proficiency with bimanual movements relative to unimanual movements. It follows that therapies that maintain the integrity of neural systems associated with bimanual movements are important to healthy aging.

The results of this study suggest that the weather prediction task may be a means of assessing the integrity of neural structure underpinning manual motor skills. The task shows age-related decrements, but relative contributions of specific systems engaged for the task must be delineated. Further, use of more detailed assessment techniques in conjunction with the weather prediction task (such as strategy analysis and manipulation of task parameters) may enhance the usefulness of the task in assessing neural systems implicated in performance of the task.

Future Directions

Replication of sex differences in terms of manual movement acquisition and the impact of feedback on motor learning is important as there are broad potential clinical ramifications. It may be that other factors, such as age, modulate the impact of sex differences and quantification of these effects may explain sex differences in recovery from neural injury such stroke (Di Carlo et al., 2003), and lead to more tailored neuro-rehabilitation interventions.

Findings related to age require replication prior to application to preventative interventions and treatment of age-related motor disorders. Further, it would be prudent to quantify vascular health of the older participants. Motor decrements associated with age may be more strongly associated with the vascular health of neural systems than age in terms of chronological years. Considering that the present work demonstrates behavioural effects with training and differences between age groups, the next logical step is to correlate motor learning measures with neural plastic changes, in particular of inter-hemispheric structures.

Interventions that induce neural plastic changes of inter-hemispheric structures are crucial to prevention and treatment of bimanual movement dysfunction. Although auditory feedback was initially detrimental under specific conditions, rapid adaptation to feedback was observed, in accord with reports of co-activation of motor and auditory networks after just 20 minutes of practice (Bangert & Altenmüller, 2003). Past research demonstrates that the neural plastic response to music training engages a broad network, including the corpus callosum (Elbert et al., 1995; Gaser & Schlaug, 2003; Schlaug et al., 1995). Consequently, playing an instrument may be a beneficial treatment modality, and a means of targeting inter-hemispheric structures essential to proficient bimanual movement. A nonrandomized, non-controlled study that examined this activity as a therapeutic medium after stroke reported positive effects (Schneider et al., 2007); however, the use of music training as a therapeutic intervention deserves further investigation.

Conclusions

In conclusion, the findings of this thesis demonstrate that the keyboard task is a sensitive and practical method of studying complex bimanual learning in the general population. Further, the results provide insights into the effects of sex on motor performance, namely that females may have an advantage in performance of bimanual movements. This work also demonstrated that aging results in decrements of motor performance, differentially affecting bimanual movements. However, older adults demonstrated similar improvements with practice as young adults and music training may offer some protection against age-related motor decline. The research revealed some sex-specific differences in the utility of auditory feedback for motor learning in the short term. Although further investigation is needed prior to application of findings, this research identifies a key role for interventions that target bimanual movement.

REFERENCES

Altenmüller, E. O. (n.d.). *From laetoli to Carnegie: Music making as a paradigm for the wonders of neuroplasticity.* Institute of Music Physiology and Musician's Medicine. Hanover University for Music and Drama.

Bangert, A. S., Reuter-Lorenz, P. A., Walsh, C. M., Schachter, A. B., & Seidler, R. D. (2010). Bimanual coordination and aging: Neurobehavioral implications. *Neuropsychologia, 48*(4), 1165-1170.

Bangert, M., & Altenmüller, E. O. (2003). Mapping perception to action in piano practice: A longitudinal DC-EEG study. *BMC Neuroscience, 4*, 26.

Bangert, M., Peschel, T., Schlaug, G., Rotte, M., Drescher, D., Hinrichs, H., … Altenmüller, E. (2006). Shared networks for auditory and motor processing in professional pianists: Evidence from fMRI conjunction. *NeuroImage, 30*, 917-926.

Bayer, U., & Hausmann, M. (2010). Hormone therapy in postmenopausal women affects hemispheric asymmetries in fine motor coordination. *Hormones and Behavior, 58*(3), 450-456.

Bennett, I. J., Madden, D. J., Vaidya, C. J., Howard, D. V., & Howard, J. H., (2010). Age-related differences in multiple measures of white matter integrity: A diffusion tensor imaging study of healthy aging. *Human Brain Mapping, 31*(3), 378-390.

Bodwell, J. A., Mahurin, R. K., Waddle, S., Price, R., & Cramer, S. C. (2003). Age and features of movement influence motor overflow. *Journal Of The American Geriatrics Society, 51*(12), 1735-1739.

Brown, R. G., Jahanshahi, M., & Marsden, C. D. (1993).The execution of bimanual movements in patients with Parkinson's, Huntington's and cerebellar disease. *Journal of Neurology, Neurosurgery & Psychiatry, 56*(3), 295–297.

Cardoso de Oliveira, S., Gribova, A., Donchin, O., Bergman, H., & Vaadia, E. (2001). Neural interactions between motor cortical hemispheres during bimanual and unimanual arm movements. *European Journal of Neuroscience, 14*(11), 1881–1896.

Casadio, M., Sanguineti, V., Squeri, V., Masia, L., & Morasso, P. (2010). Inter-limb interference during bimanual adaptation to dynamic environments. *Experimental Brain Research, 202*(3), 693-707.

Cesqui, B., Macrì, G., Dario, P., & Micera, S. (2008). Characterization of age-related modifications of upper limb motor control strategies in a new dynamic environment. *Journal Of Neuroengineering And Rehabilitation, 5*, 31-31.

Chase, H. W., Clark, L., Myers, C. E., Gluck, M. A., Sahakian, B. J., Bullmore, E. T., & Roggins, T. W. (2008). The role of the orbitofrontal cortex in human discrimination learning. *Neuropsychologia, 46*(5), 1326-1337.

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences, 2nd ed*. Lawrence Erlbaum Associates.

Colla, M., Ende, G., Bohrer, M., Deuschle, M., Kronenberg, G., Henn, F., & Heuser, I. (2003). MR spectroscopy in Alzheimer's disease: Gender differences in probabilistic learning capacity. *Neurobiology Of Aging, 24*(4), 545-552.

Cooke, J.D., Brown, S.H., & Cunningham, D.A. (1989). Kinematics of arm movements in elderly humans. *Neurobiology Of Aging, 10*, 159-165.

D'Ausilio, A., Altenmüller, E., Olivetti Belardinelli, M., & Lotze, M. (2006). Cross-modal plasticity of the motor cortex while listening to a rehearsed musical piece. *European Journal of Neuroscience, 24*, 955-958.

Danion, F., Descoins, M., & Bootsma, R. J. (2007). Aging affects the predictive control of grip force during object manipulation. *Experimental Brain Research, 180*(1), 123-137.

De Weerd, P., Reinke, K., Ryan, L., McIsaac, T., Perschler, P., Schnyer, D., … Gmitro, A. (2003). Cortical mechanisms for acquisition and performance of bimanual motor sequences. *NeuroImage, 19*, 1405-1416.

Di Carlo, A., Lamassa, M., Baldereschi, M., Pracucci G., Basile, A. M., Wolfe, C. D. A., … Inzitari, D. (2003). Sex differences in the clinical presentation, resource use, and 3-month outcome of acute stroke in Europe: Data from a multicenter multinational hospital-based registry. *Stroke, 34*, 1114-1119.

Drost, U. C., Rieger, M., Brass, M., Gunter, T. C., & Prinz, W. (2005). When hearing turns into playing: Movement induction by auditory stimuli in pianists*. The Quarterly Journal of Experimental Psychology, 58A*(8), 1376-1389.

Duque, J., Davare, M., Delaunay, L., Jacob, B., Saur, R., Hummel, … Olivier, E. (2009). Monitoring coordination during bimanual movements: Where is the mastermind? *Journal of Cognitive Neuroscience, 22*(3), 16.

Ekstrom, R. B., French, J. W., & Harman, H. H. (1976). *Manual for kit of factor-referenced cognitive tests*. Princeton, NJ: Educational Testing Service.

Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B., & Taub, E. (1995). Increased cortical representation of the fingers of the left hand in string players. *Science, 270*, 305-307.

Elias, L. J., Bryden, M. P., & Bulman-Fleming, M. B. (1998). Footedness is a better predictor than is handedness of emotional lateralization. *Neuropsychologia, 36*(1), 37–43.

Eliassen, J. C., Baynes, K., & Gazzaniga, M. S., (2000). Anterior and posterior callosal contributions to simultaneous bimanual movements of the hands and fingers. *Brain, 123*(12), 2501–2511.

Essers, L., & Adam, J. J. (2010). Response preparation with static and moving hands: Differential effects of unimanual and bimanual movements. *Human Movement Science, 29*(2), 187-199.

Falkenstein, M., Yordanova, J., & Kolev, V. (2006). Effects of aging on slowing of motor-response generation. *International Journal Of Psychophysiology, 59*(1), 22-29.

Fathi, D., Ueki, Y., Mima, T., Koganemaru, S., Nagamine, T., Tawfik, A., & Fukuyama, H. (2010). Effects of aging on the human motor cortical plasticity studies by paired associative simulation. *Clinical Neurophysiology, 121*, 90-93.

Fera, F., Weickert, T. W., Goldberg, T. E., Tessitore, A., Hariri, A., Das, S., … Mattay, V. S. (2005). Neural mechanisms underlying probabilistic category learning in normal aging. *The Journal Of Neuroscience, 25*(49), 11340-11348.

Fradet, L., Lee, G., & Dounskaia, N. (2008). Origins of submovements in movements of elderly adults. *Journal Of Neuroengineering and Rehabilitation, 5*, 28-28.

Franz, E.A., Ivry, R.B., & Helmuth, L.L. (1996). Reduced timing variability in patients with unilateral cerebellar lesions during bimanual movements. *Journal of Cognitive Neuroscience 8*(2), 107–118.

Furuya, S., & Kinoshoita, H. (2008). Organization of the upper limb movement for piano key-depression differs between expert pianists and novice players. *Experimental Brain Research, 185*, 581-593.

Furuya, S., & Soechting, J. F. (2010). Role of auditory feedback in the control of successive keystrokes during piano playing. *Experimental Brain Research, 204*(2), 223-237.

Gaser, C., & Schlaug, G. (2003). Brain structures differ between musicians and non-musicians. *Journal Of Neuroscience, 23*(28), 9240-9245.

Gazzaniga, M. S., Ivry, R. B., & Mangun, G. R. (2009). *Cognitive neuroscience: The biology of the mind, 3rded*. New York: W.W. Norton & Company.

Gluck, M. A., Shohamy, D., & Myers, C. (2002). How do people solve the "weather prediction" task?: Individual variability in strategies for probabilistic category learning. *Learning & Memory, 9*(6), 408-418.

Goble, D. J., Coxon, J. P., Van Impe, A., De Vos, J., Wenderoth, N., & Swinnen, S. P. (2010). The neural control of bimanual movements in the elderly: Brain regions exhibiting age-related increases in activity, frequency-induced neural modulation, and task-specific compensatory recruitment. *Human Brain Mapping, 31*, 1281-1295.

Gorus, E., De Raedt, R., & Mets, T. (2006). Diversity, dispersion, and inconsistency of reaction time measures: Effects of age and task complexity. *Aging Clinical And Experimental Research, 18*(5), 407-417.

Hasan, K. M., Kamali, A., Abid, H., Kramer, L. A., Fletcher, J. M., & Ewing-Cobbs, L. (2010). Quantification of the spatiotemporal microstructural organization of the human brain association, projection and commissural pathways across the lifespan using diffusion tensor tractography. *Brain Structure & Function, 214*(4), 361-373. doi: 10.1007/s00429-009-0238-0

Haslinger, B., Erhard, P., Altenmüller, E., Schroeder, U., Boecker, H., & Ceballos-Baumann, A. O. (2005). Transmodal sensorimotor networks during action observation in professional pianists. *Journal of Cognitive Neuroscience, 17*(2), 282-293.

Hopkins, R. O., Myers, C. E., Shohamy, D., Grossman, S., & Gluck, M. (2004). Impaired probabilistic category learning in hypoxic subjects with hippocampal damage. *Neuropsychologia, 42*(4), 524-535.

Hughes, C. M. L., & Franz, E. A. (2008). Goal-related planning constraints in bimanual grasping and placing of objects. *Experimental Brain Research, 188*(4), 541-550.

Jabusch, H.-C., Vauth, H., & Altenmüller, E. (2004). Quantification of focal dystonia in pianists using scale analysis. *Movement Disorders, 19*(2), 171-180.

Jahanshahi, M., Wilkinson, L., Gahir, H., Dharminda, A., & Lagnado, D. A. (2010). Medication impairs probabilistic classification learning in Parkinson's disease. *Neuropsychologia, 48*(4), 1096-1103.

Janssen, L., Beuting, M., Meulenbroek, R., & Steenbergen, B. (2009). Combined effects of planning and execution constraints on bimanual task performance. *Experimental Brain Research, 192*(1), 61-73.

Johansen-Berg, H., Della-Maggiore, V., Behrens, T. E. J., Smith, S. M., & Paus, T. (2007). Integrity of white matter in the corpus callosum correlates with bimanual co-ordination skills. *NeuroImage, 36*, T16-T21.

Kastman, E. K., Willette, A. A., Coe, C. L., Bendlin, B. B., Kosmatka, K. J., McLaren, D. G., … Johnson, S. C. (2010). A calorie-restricted diet decreases brain iron accumulation and preserves motor performance in old rhesus monkeys. *The Journal Of Neuroscience, 30*(23), 7940-7947.

Kelso, J. A. S. (1981). On the oscillatory basis of movement. *Bulletin of the Psychonomic Society, 18*, 63.

Kelso, J. A. S. (1984). Phase transitions and critical behavior in human bimanual coordination. *American Journal of Physiology: Regulatory, Integrative and Comparative Physiology, 15*, R1000-R1004.

Ketcham, C. J., Dounskaia, N. V., & Stelmach, G. E. (2004). Age-related differences in the control of multijoint movements. *Motor Control, 8*(4), 422-436.

Kimura, D. (1999). *Sex and cognition*. Cambridge: Massachusetts Institute of Technology.

Klimkowicz-Mrowiec, A., Slowik, A., Krzywoszanski, L., Herzog-Krzywoszanska, R. Ç., & Szczudlik, A. (2008). Severity of explicit memory impairment due to Alzheimer's disease improves effectiveness of implicit learning. *Journal of Neurology, 255*(4), 502-509.

Knowlton, B. J., Mangels, J. A., & Squire, L. R. (1996). A neostriatal habit learning system in humans. *Science, 273*(5280), 1399-1402.

Knowlton, B. J., Squire, L. R., & Gluck, M. A. (1994). Probabilistic classification learning in amnesia. *Learning and Memory, 1*(2), 106-120.

Koelsch, S., Maess, B., Grossmann, T., & Friederici, A. D. (2003). Electric brain responses reveal gender differences in music processing. *NeuroReport, 14*(5), 709-713.

Kurniawan, I. T., Seymour, B., Talmi, D., Yoshida, W., Chater N., & Dolan, R. J. (2010). Choosing to make an effort: The role of striatum in signaling physical effort of a chosen action. *Journal of Neurophysiology, 104*, 313-321.

Lacreuse, A., Diehl, M. M., Goh, M. Y., Hall, M. J., Volk, A. M., Chhabra, R. K., & Herndon, J. G. (2005). Sex differences in age-related motor slowing in the rhesus monkey: Behavioral and neuroimaging data. *Neurobiology Of Aging, 26*(4), 543-551.

Lang, C. E., Wagner, J. M., Edwards, D. F., & Dromerick, A. W. (2007). Upper extremity use in people with hemiparesis in the first few weeks after stroke. *Journal of Neurologic Physical Therapy, 31*(2), 56-63.

Lee, D. Y., Fletcher, E., Marinez, O., Zozulya, N., Kim, J., Tran, J., … & DeCarli, C. (2010). Vascular and degenerative processes differentially affect regional interhemispheric connections in normal aging, mild cognitive impairment, and Alzheimer disease. *Stroke, 41*, 1791-1797.

Lee, G., Fradet, L., Ketcham, C. J., & Dounskaia, N. (2007). Efficient control of arm movements in advanced age. *Experimental Brain Research, 177*(1), 78-94.

Leonard, G., Milner, B., & Jones, L. (1988). Performance on unimanual and bimanual tapping tasks by patients with lesions of the frontal or temporal lobe. *Neuropsychologia, 26*(1), 79–91.

Lezak, M. D., Howieson, D. B., & Loring, D. W. (2004). *Neuropsychological Assessment, 4th ed.* New York: Oxford University Press.

Lissek, S., Hausmann, M., Knossalla, F., Peters, S., Nicolas, V., Güntürkün, O., & Tegenthoff, M. (2007). Sex differences in cortical and subcortical recruitment during simple and complex motor control: An fMRI study. *NeuroImage, 37*, 912-926.

Loehr, J. D., & Palmer, C. (2007). Cognitive and biomechanical influences in pianists' finger tapping. *Experimental Brain Research, 178*(4), 518-528.

Maki, Y., Wong, K. F. K., Sugiura, M., Ozaki, T., & Sadato, N. (2008). Asymmetric control mechanisms of bimanual coordination: An application of directed connectivity analysis to kinematic and functional MRI data. *NeuroImage, 42*, 1295-1304.

Marsh, R., Alexander, G. M., Packard, M. G., Zhu, H., & Peterson, B. S. (2005). Perceptual-motor skill learning in Gilles de la Tourette syndrome: Evidence for multiple procedural learning and memory systems. *Neuropsychologia, 43*, 1456-1465.

Matthews, A. J., Martin, F. H., Garry, M., & Summers, J. J. (2009). The behavioural and electrophysiological effects of visual task difficulty and bimanual coordination mode during dual-task performance. *Experimental Brain Research, 198*(4), 477-487.

Meeter, M., Myers, C. E., Shohamy, D., Hopkins, R. O., & Gluck, M. A. (2006). Strategies in probabilistic categorization: Results from a new way of analyzing performance. *Learning & Memory, 13*(2), 230-239.

Miller, B., Chang, L., Booth, R., Ernst, T., Cornford, M., & Nikas, D. (1996). In vivo H-1 MRS choline: Correlation with in vitro chemistry histology. *Life Sciences, 58*(22), 1929-1935.

Moody, T. D., Bookheimer, S. Y., Vanek, Z., & Knowlton, B. J. (2004). An implicit learning task activates medial temporal lobe in patients with Parkinson's disease. *Behavioral Neuroscience, 118*(2), 438-442.

Münte, T. F., Altenmüller, E., & Jäncke, L. (2002). The musician’s brain as a model of neuroplasticity. *Nature Reviews: Neuroscience, 3*, 473-478.

Naccarato, M., Calautti, C., Jones, P. S., Day, D. J., Carpenter, T. A., & Baron, J. C. (2006). Does healthy aging affect the hemispheric activation balance during paced index-to-thumb opposition task? An fMRI study. *NeuroImage, 32*(3), 1250-1256.

Newell, B. R., Lagnado, D. A., & Shanks, D. R. (2007). Challenging the role of implicit processes in probabilistic category learning. *Psychonomic Bulletin & Review, 14*(3), 505-511.

Nicholson, K.G. & Kimura, D.(1996). Sex differences for speech and manual skill. *Perceptual and Motor Skills, 82*, 3–13.

Obhi, S. S., Haggard, P., Taylor, J., & Pascual-Leone, A. (2002). rTMS to the supplementary motor area disrupts bimanual coordination. *Motor Control 6*(4), 319–332.

Poston, B., Van Gemmert, A. W. A., Barduson, B., & Stelmach, G. E. (2009). Movement structure in young and elderly adults during goal-directed movements of the left and right arm. *Brain And Cognition, 69*(1), 30-38.

Potter, L. M., & Grealy, M. A. (2006). Aging and inhibitory errors on a motor shift of set task. *Experimental Brain Research, 171*(1), 56-66.

Price, A. L. (2005). Cortico-striatal contributions to category learning: Dissociating the verbal and implicit systems. *Behavioral Neuroscience, 119*(6), 1438-1447.

Price, A. L. (2009). Distinguishing the contributions of implicit and explicit processes to performance of the weather prediction task. *Memory & Cognition, 37*(2), 210-222.

Rabbitt, P. M. A. (1989). Sequential reactions. In Holding, D. H. (Ed.), *Human Skills, 2nd ed*. London: John Wiley & Sons Ltd.

Resnick, S., & Driscoll, I. (2008). Sex differences in brain aging and Alzheimer’s disorders. In J. B. Becker, K. J. Berkley, N. Geary, E. Hampson, J. P. Herman, & E. A. Young (Eds.), *Sex differences in the brain* (pp. 427-454). New York: Oxford University Press.

Riecker, A., Gröschel, K., Ackermann, H., Steinbrink, C., Witte, O., & Kastrup, A. (2006). Functional significance of age-related differences in motor activation patterns. *NeuroImage, 32*(3), 1345-1354.

Rodriguez, T. M., Buchanan, J. J., & Ketcham, C. J. (2010). Identifying leading joint strategies in a bimanual coordination task: Does coordination stability depend on leading joint strategy? *Journal of Motor Behavior, 42*(1), 11.

Rosano, C., Brach, J., Studenski, S., Longstreth, W. T., Jr., & Newman, A. B. (2007). Gait variability is associated with subclinical brain vascular abnormalities in high-functioning older adults. *Neuroepidemiology, 29*(3-4), 193-200.

Rossit, S., & Harvey, M. (2008). Age-related differences in corrected and inhibited pointing movements. *Experimental Brain Research, 185*(1), 1-10.

Rowe, J. B., Siebner, H., Filipovic, S. R., Cordivari, C., Gerschlager, W., Rothwell, J., & Frackowiak, R. (2006). Aging is associated with contrasting changes in local and distant cortical connectivity in the human motor system. *NeuroImage, 32*(2), 747-760.

Ruff, R. M., & Parker, S. B. (1993). Gender-specific and age-specific changes in motor speed and eye-hand coordination in adults- Normative values for the finger tapping and grooved pegboard tests. *Perceptual and Motor Skills, 76*(3), 1219-1230.

Ruiz, P. J. G., Bernardos, V. S., Bartolomé, M., & Torres, A. G. (2007). Capit timed tests quantify age-related motor decline in normal subjects. *Journal Of The Neurological Sciences, 260*(1-2), 283-285.

Sachdev, P. S., Wen, W., Christensen, H., & Jorm, A. F. (2005). White matter hyperintensities are related to physical disability and poor motor function. *Journal of Neurology Neurosurgery and Psychiatry, 76*(3), 362-367.doi: 10.1136/jnnp.2004.042945

Sarlegna, F. R. (2006). Impairment of online control of reaching movements with aging: A double-step study. *Neuroscience Letters, 403*(3), 309-314.

Salthouse, T. A., McGuthry, K. E., & Hambrick, D. Z. (1999). A framework for analyzing and interpreting differential aging patterns: Application to three measures of implicit learning. *Aging, Neuropsychology, and Cognition, 6*(1), 1-18.

Schlaug, G., Jäncke, L., Huang, Y., Staiger, J. F., & Steinmetz, H. (1995). Increased corpus callosum size in musicians. *Neuropsychologia, 33*(8), 1047-1055.

Schneider, S., Schönle, P. W., Altenmüller, E., & Münte, T. F. (2007). Using musical instruments to improve motor skill recovery following a stroke. *Journal of Neurology, 254*, 1339-1346.

Serrien, D. J., Nirkko, A. C., Lovblad, K. O., & Wiesendanger, M. (2001). Damage to the parietal lobe impairs bimanual coordination. *NeuroReport, 12*(12), 2721–2724.

Shohamy, D., Myers, C. E., Onlaor, S., & Gluck, M. A. (2004). Role of the basal ganglia in category learning: How do patients with Parkinson's disease learn? *Behavioral Neuroscience, 118*(4), 676-686.

Soumare, A., Elbaz, A., Zhu, Y. C., Maillard, P., Crivello, F., Tavernier, B., … Tzourio, C. (2009). White matter lesions volume and motor performances in the elderly. *Annals of Neurology, 65*(6), 706-715.doi: 10.1002/ana.21674

Spilt, A., Weverling-Rijnsburger, A. W. E., Middelkoop, H. A. M., van Der Flier, W. M., Gussekloo, J., de Craen, A. J. M., … Westendorp, R. G. J. (2005). Late-onset dementia: Structural brain damage and total cerebral blood flow. *Radiology, 236*(3), 990-995.

Starr, J. M., Leaper, S. A., Murray, A. D., Lemmon, H. A., Staff, R. T., Deary, I. J., & Whalley, L. J. (2003). Brain white matter lesions detected by magnetic resonance imaging are associated with balance and gait speed. *Journal of Neurology Neurosurgery and Psychiatry, 74*(1), 94-98.

Stephan, K. M., Binkofski, F., Halsband, U., Dohle, C., Wunderlich, G., Schnitzler, A., … Freund, H.-J. (1999). The role of ventral medial wall motor areas in bimanual co-ordination. A combined lesion and activation study. *Brain, 122*(2), 351–368.

Sterr, A., & Dean, P. (2008). Neural correlates of movement preparation in healthy ageing. *European Journal of Neuroscience, 27*(1), 254-260.doi: 10.1111/j.1460-9568.2007.05975.x

Sweat, J. D. (2010). *Mechanisms of memory, 2nd ed*. Amsterdam: Elsevier.

Swinnen, S. P. (2002). Intermanual coordination: From behavioural principles to neural-network interactions. *Nature Reviews Neuroscience, 3*, 350-361.

Swinnen, S. P., Verschueren, S. M. P., Bogaerts, H., Dounskaia, N., Lee, T. D., Stelmach, G. E., & Serrien, D. J. (1998). Age-related deficits in motor learning and differences in feedback processing during the production of a bimanual coordination pattern. *Cognitive Neuropsychology, 15*(5), 439-466.

Trewartha, K. M., Endo, A., Li, K. Z. H., & Penhune, V. B. (2009). Examining prepotent response suppression in aging: A kinematic analysis. *Psychology And Aging, 24*(2), 450-461.

Walsh, R. R., Small, S. L., Chen, E. E., & Solodkin, A. (2008). Network activation during bimanual movements in humans. *NeuroImage, 43*, 540-553.

Wan, C. Y., & Schlaug, G. (2010). Music making as a tool for promoting brain plasticity across the life span. *Neuroscientist, 16*(5), 566-577.doi: 10.1177/1073858410377805

Wilkinson, L., Lagnado, D. A., Quallo, M., & Jahanshahi, M. (2008).The effect of feedback on non-motor probabilistic classification learning in Parkinson's disease. *Neuropsychologia, 46*(11), 2683-2695.

Zhuang, J., LaConte, S., Peltier, S., Zhang, K., & Hu, X. (2005). Connectivity exploration with structural equation modeling: An fMRI study of bimanual motor coordination. *NeuroImage, 25*, 462-470.