The Contributions of Practice Pattern, Musical Training, and Development to Motor Sequence Learning

Tal Savion-Lemieux

A Thesis

in

The Department

of

Psychology

Presented in Partial Fulfillment of the Requirements
For the Degree of Doctor of Psychology at
Concordia University
Montreal, Quebec, Canada

July 2010

CONCORDIA UNIVERSITY
SCHOOL OF GRADUATE STUDIES

This is to certify that the thesis prepared

By: Tal Savion-Lemieux

Entitled: The Contributions of Practice Pattern, Musical Training, and Development to Motor Sequence Learning

and submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

complies with the regulations of the University and meets the accepted standards with respect to originality and quality.

Signed by the final examining committee:

Dr. Miranda D'Amico	Chair
Dr. Rachael Seidler	External Examiner
Dr. Christine Beckett	External to Program
Dr. Karen Li	Examiner
Dr. Diane Poulin-Dubois	Examiner
Dr. Virginia Penhune	Thesis Supervisor

Approved by

____
Chair of Department or Graduate Program Director

____
Dean of Faculty

ABSTRACT

The contributions of practice pattern, musical training, and development to motor sequence learning

Tal Savion-Lemieux, Ph.D.
Concordia University, 2010

The overall goal of the present thesis was to look at a selection of factors that affect fine motor sequence learning both within and across days of practice. The objective of study 1 was to examine factors related to motor training, specifically how practice pattern (or organization of practice) affects learning and transfer of multiple motor sequences. The objective of studies 2 and 3 was to investigate factors related to individual characteristics, specifically musical experience and development (i.e. age). First, findings from all three papers support the progression of sequence learning across time, characterized by rapid within-session improvements and slower incremental improvements across days of practice. Importantly, findings have shown that both adults and children show consolidation, defined as significant improvements in or maintenance of performance between the last block of practice on the initial practice session and the first block on the second session, after a period of rest of 24 hours with no additional practice. Second, a robust dissociation was found between the two behavioural measures used to assess learning, accuracy and response synchronization. Learning of the stimulus-response association, or finger-stimulus mapping, appeared to be a fast process, as significant improvements on the accuracy measure were often rapid and occurred within the first blocks of practice on day 1. This process seemed to require more effortful processing and attention initially; however, once the stimulus-response association was acquired, it seemed to be resistant to interference and transferrable to a novel sequence.

In contrast, learning of the sensorimotor integration and timing elements of the task appeared to be a slower and more difficult process to learn, as significant improvements on this measure persisted across days of practice. This more procedural process seemed to be under less cognitive control, be more susceptible to interference, and rely more heavily on ongoing practice. Finally, results from studies 2 and 3 provide new evidence that there may be a sensitive period in childhood where enriched motor training, through musical practice, results in long-lasting benefits for motor performance later in life.

Acknowledgments

This has been an incredible journey, both professionally and personally, and I would like to thank the many people that have helped me along the way and who have enriched my life in the process.

First, I would like to thank my research supervisor, Dr. Virginia Penhune, for her continuous support and guidance throughout my graduate career. Her faith in me and continuous encouragement (especially in the past two years) have been greatly appreciated. It has been an absolute privilege to be her graduate student. Most importantly, I would like to thank Virginia for showing me that it is possible to sanely balance a successful “scientist-practitioner” career and family life.

I would like to thank Drs. Karen Li, Diane Poulin-Dubois, Christine Beckett, and Rachael Seidler, my committee members, for their valuable feedback and providing me with an enriching (and pleasant) defense experience.

I would like to extend a heartfelt thank you to Clarisse Longo dos Santos for sharing this unique experience with me (you will be missed tremendously), Chris Steele for bringing music, food, and joy to the lab, Jennifer “Anne” Bailey for being the best “prodigy”, Sarah Fraser for inspiring me to finish this thesis, as well as Larry Baer, Kevin Trewartha, and all other past and present members of the Penhune-Li lab for making the lab a fun yet fruitful working place. I would also like to extend a heartfelt thank you to Alejandro Endo for his assistance with the design of the tasks and stimuli as well as data analysis software; Evan Zatorre for designing “Rolly the hamster” and “Bubbles the fish”; as well as Michael Spilka for helping with the completion and formatting of this thesis.

I would like to acknowledge some very important individuals who are close to my heart and have been pivotal throughout this process: Dr. Dale Stack (and more recently Dr. Yves Beaulieu) for enriching my clinical career and providing me invaluable support and guidance (both professionally and personally); Naomi Grunzeweig for sharing brains, completing sentences when they needed to be completed, and being my best friend and colleague in graduate school (I can't wait to start a new journey with you); Kara Olineck for making graduate school (pre-wedding and kids) "a ball" by introducing Starbucks, Nachos, shoes, and purses, to study breaks (I miss you); Yolaine, Yohan, Sophie (more recently Eric), Arielle, and all my other friends, for helping put things in perspective and supporting me (and Darren) throughout this long and laborious process. Importantly, I wish to thank my family (Rachel, Gilbert, Ariel, Melissa) as well as the Reinblatt clan (particularly Sharon and Gerry) for their never-ending help and support (particularly taking care of our girls by providing them with lots of love, entertainment, and food). My greatest thank you goes to my parents for always believing in me and instilling me with the strength and confidence to follow my dreams. Graduate school would not have been possible without all the sacrifices my parents have done for me and my family. Toda raba! Finally, my warmest thank you goes to my husband Darren who has been unequivocally supportive, patient, calm, loving, and optimistic throughout this slightly longer than expected process. Darren, thank you for enriching my life!

I wish to dedicate this thesis to:

Rachel "My mother is a poem I will never be able to write, though everything I write is a poem to my mother." (*Sharon Dubiago*)

Noa and Maya, “You have brains in your head. You have feet in your shoes. You can steer yourself in any direction you choose. You’re on your own. And you know what you know. And YOU are the one(s) who’ll decide where to go. *Oh, the Places You’ll go*!... And will you succeed? Yes! You will indeed! (98 and ¾ percent guaranteed). (GIRLS), YOU’LL MOVE MOUNTAINS!” (*Dr. Seuss*).

CONTRIBUTIONS OF AUTHORS

This Ph.D. consists of three published manuscripts.

Study 1 (see chapter 2)

Savion-Lemieux and Penhune, V.B. (2010). The effect of practice pattern on the acquisition, consolidation, and transfer of visual-motor sequences. *Experimental Brain Research*, 204 (2): 271-81.

The first and second authors devised experimental methods and the research design collaboratively. The first author worked closely with computer programmer (Alejandro Endo) to develop the task and stimuli as well as tailoring the output produced by the scoring program. The first author wrote consent forms for this study and assisted Laura Fontil, Valerie Stitchman, and Anthony Hopley (undergraduate students) in the recruitment of participants. With the collaboration of these three undergraduate students, all participants were tested on two consecutive days in the Laboratory for Motor Learning and Neural Plasticity at Concordia University, Montreal. Following completion of the study, the first author was responsible for the data entry, statistical analyses, and interpretation of the data. The first author wrote all sections of the manuscript, with comments and revisions provided by the second author.

Study 2 (see chapter 3)

Watanabe, D., Savion-Lemieux, T., and Penhune, V.B. (2007). The effect of early musical training on adult motor performance: evidence for a sensitive period in motor learning. *Experimental Brain Research*, 176 (2): 332-40.

All three authors devised experimental methods and the research design collaboratively. The second author tailored the output produced by the scoring program.

The first and second authors wrote consent forms for this study. Both the first and second authors recruited and tested the musicians and non-musicians in the Laboratory for Motor Learning and Neural Plasticity at Concordia University, Montreal. Following completion of the study, the first and second authors were responsible for data entry, statistical analyses, and interpretation of the data. All three authors were involved in the writing of the manuscript.

Study 3 (see chapter 4)

Savion-Lemieux, T., Bailey, J.A., and Penhune, V.B. (2009). Developmental contributions to motor skill learning. *Experimental Brain Research,* 195 (2): 293-306.

The first and third authors devised experimental methods and the research design collaboratively. The first author worked closely with computer programmer (Alejandro Endo) to develop the task and stimuli as well as tailoring the output produced by the scoring program. The first author wrote consent forms for this study and assisted Jennifer Bailey, Andrea Lee, and Odelia Borten (undergraduate students and research assistant, respectively) in the recruitment of participants. With their collaboration, adult participants were tested on two consecutive days in the Laboratory for Motor Learning and Neural Plasticity at Concordia University, Montreal; child participants were tested at Lower Canada College (a local elementary school). Following completion of the study, the first author was responsible for the data entry, statistical analyses, and interpretation of the data, with the assistance of the second author. The first author wrote all sections of the manuscript, with comments and revisions provided by the third author.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Chapter 1

General Introduction

Motor skill learning is a critical aspect of our everyday lives, as we acquire and retain an extensive array of motor skills throughout the lifespan. Motor skill learning is a complex internal process (that is often taken for granted) by which motor skills become effortlessly performed through constant practice and experience over time (Willingham, 1998); it is a form of procedural learning, which refers to learning how to do what to do (Schmidt & Lee, 2005). For example, when first learning to play the piano, the ability to move the fingers across the keys (in coordination with reading the musical notes) is uncoordinated, but with repeated practice over time, this ability becomes more smooth, skillful, and refined. Since motor skills are ubiquitous in our everyday lives, considerable efforts have been made to determine the principal factors affecting their learning and retention. Such factors include, but are not limited to: amount of practice, distribution of practice, length of delay necessary for retention, contextual setting of learning (i.e. organization of practice), presence of interference, transfer of learning to other skills, as well as the effects of development and motor expertise on the learning of motor skills. Thus, the study of motor learning is centered around answering questions such as: "What factors affect learning?"; "How much practice is needed to show improvement over time?"; "How long can we retain a motor memory?"; "What is the best way to organize practice when faced with the task of learning multiple skills?"; "How generalizable and transferrable are learned motor skills?"; "Does motor learning capacity change across the lifespan?"; "Does musical training impact motor skill learning?", etc.

The overall goal of the present thesis was to examine a selection of factors that affect motor learning, specifically fine motor sequence learning. Fine motor sequence learning refers to learning to make a series of defined fine motor movements, typically involving the fingers in coordination with the eyes (e.g., typing the alphabet and playing "Frère Jacques" on the piano). Surprisingly, most studies on sequence learning focus on either within-day or across-day learning, but relatively few look at both aspects together or in relation to each other. Given that learning is a dynamic process that occurs over time, all three experiments included in this thesis explored both within-day and across-day changes. The objective of study 1 was to examine factors related to motor training, specifically how practice pattern affects learning and transfer of multiple motor sequences. The objective of studies 2 and 3 was to investigate factors related to individual characteristics, specifically experience and development (i.e. age, specifically childhood). Taken together, understanding the behavioural underpinnings of motor sequence learning is imperative for the development of practical theories that translate into essential applications in teaching and other learning environments (Schmidt & Lee, 2005).

Motor skill learning can be broken down into three behaviourally relevant stages (as referred to in the motor literature): early learning, late learning, and consolidation, which correspond to distinct points in the pattern of incremental changes observed in performance across sessions of practice (see Doyon and Benali, 2005; Karni, Meyer, Rey-Hipolito, Jezzard, Adams, Turner, & Ungerleider, 1998; Korman, Raz, Flash, & Karni, 2003, for reviews). The early learning stage is characterized by rapid improvements in performance, over relatively few trials, within the initial session of practice (e.g., Karni & Sagi, 1993; Bapi, Miyapuram, Graydon, & Doya, 2006). The late learning stage is characterized by slower and more gradual gains in performance, occurring over multiple days of practice, which lead to a plateau in performance (e.g., Korman, Raz, Flash, & Karni, 2003; Karni, Meyer, Jezzard, Adams, Turner, & Ungerleider, 1995; Savion-Lemieux & Penhune, 2005). The consolidation stage is an intermediate stage (between the early learning and late learning stage) that occurs across the first two sessions of practice. Consolidation is a specific concept that is commonly defined as either a significant improvement in performance following a period of rest with no additional practice (over and above what would be expected with continued practice) or a maintenance in performance after a period of rest, both of which are disrupted by learning a similar motor skill within a consolidation window of four to six hours (Robertson, Pascual-Leone, & Miall, 2004). Consolidation can also be considered as the across-day transition from early to late learning. Consolidation is thought to be sleep-dependent (e.g., Walker, Brakefield, Seidman, Morgan, Hobson, & Stickgold, 2003; Maquet, Schwartz, Passingham, & Frith, 2003). For example, Sejnowski and Destexhe (2000) have shown that spindle oscillations during the early stages of slow-wave sleep are important for opening molecular gates required for synaptic plasticity. Sleep spindles have also shown to be enhanced after training on a motor task (Fogel et al., 2001, cited in Walker et al., 2002). Based on previous work from our laboratory, we have hypothesized that consolidation may be the first step in laying down long-term motor memory (Savion-Lemieux & Penhune, 2005). Finally, once a motor skill is well learned and consolidated (i.e. performance has reached asymptote), few declines in performance are noted, even after extended delays with no additional practice (e.g., Hikosaka, Rand, Nakamura, Miyauchi, Kitaguchi, Sakai, Lu, Shimo, 2002; Korman et al., 2003; Savion-Lemieux & Penhune, 2005). Thus, it appears that motor skill learning is relatively permanent. It has been postulated that passage of time (or distribution of practice over several days) is essential for a maximum benefit of practice to be gained, as the time delay may allow for more time to process, encode, and consolidate the motor skill (Criscimagna-Hemminger and Shadmehr, 2008; Korman et al., 2003; Savion-Lemieux & Penhune, 2005).

With the advent of neuroimaging technology, considerable support for the presence of separable stages of motor skill learning has been found. Functional imaging studies in adults have shown that different cortical and sub-cortical regions are preferentially recruited at the different stages of learning (Doyon and Benali, 2005; Doyon & Ungerleider, 2002; Hikosaka et al., 1999, 2002). For instance, it has been postulated that the cerebellum, rostral striatum, as well as motor, prefrontal, and parietal cortical regions are mainly active during early learning, while the caudal striatum, as well as motor and parietal cortical areas are involved in the later stage of learning (Doyon and Benali, 2005). This qualitative change from early to late learning is thought to be mediated through the consolidation stage. Crucially, following consolidation, activity in the striatum shifts from rostral to caudal regions and the cerebellum is no longer necessary for the production of skilled motor responses. Steele and Penhune (2010) recently found a functional connectivity between M1 and cerebellum in late learning that points to their interaction as a mechanism underlying the long-term representation and expression of a well-learned skill. Taken together, a growing body of evidence has demonstrated plastic neuronal changes in the adult human brain that are associated with the behavioural changes observed with learning of a motor skill. There is evidence for both early rapid changes occurring over minutes or hours and for relatively slowly developing changes occurring over multiple days or weeks.

Various experimental paradigms have been employed to study motor learning. Typically, motor skill tasks highly maximize motor control and minimize decision making abilities (Schmidt, 1991). There are two types of motor skill learning paradigms: adaptation and sequencing. The main difference between the two types of paradigms is that adaptation tasks probe our ability to learn from and adapt to different environments, while sequencing tasks force us to form new ordered memories. Classic adaptation tasks include target pointing or reaching within a dynamic force field (e.g., Shadmehr & Brashers-Krug, 1997) and pointing or reaching under visuomotor rotation (e.g., Mattar & Ostry, 2006). In these tasks, participants are required to adapt their movements while the environment is being altered or perturbed. Classic sequencing tasks include sequential pointing and serial reaction time tasks (SRT) with either one or several fingers (e.g., Karni et al., 1998; Nissen and Bullemer, 1987; Thomas & Nelson, 2001). In these tasks, participants are required to reproduce a well ordered set of movements. For example, in the classic SRT a stimulus appears in one of several locations and participants are required to press a button that corresponds to the spatial location of the stimulus. Typically, the dependent measures of learning consist of number of errors and mean response time or movement velocity, as participants are asked to respond "as fast and accurately as possible". Thus, reductions in dependent measures characteristically reflect enhanced performance. In the present thesis, we used sequencing tasks to investigate sequence learning within- and across multiple days of practice. In both the temporal motor sequencing task (TMST) and the multi-finger sequencing task (MFST), participants had to synchronize their motor response with a visual stimulus, using one or four fingers (respectively) of the right hand. The main difference between our tasks and other sequencing tasks is that participants were instructed to synchronize their response with the visual stimulus. As such, participants were not instructed to respond "as fast as possible". Learning was assessed by examining changes in accuracy and response synchronization over time. In all three experiments, accuracy required the association of the visual stimulus with the motor response, while response synchronization required fine-grained sensorimotor integration and timing (a more procedural component of the task).

One of the most important goals in the study of motor learning is to identify and understand which variables affect how individuals learn and retain motor skills. The current thesis was designed to examine a selection of factors that affect motor learning and retention. These factors were grouped into two broad categories. The first category encompassed factors related to how individuals are trained, such as amount, pattern (i.e. organization), and distribution of practice. The second category included factors that center around individual characteristics, such as experience and development (i.e. age, specifically childhood). Importantly, many studies in the literature focus on either within-day or across-day learning, but relatively few look at both aspects together or in relation to each other.

The first line of research in this thesis focused on examining factors related to how individuals are trained on motor sequences. The goal of this axis of research was to explore ways to optimize the organization or structure of practice. In a previous study, we investigated the effect of amount of practice on motor learning and retention (Savion-Lemieux & Penhune, 2005; Appendix A). In this study, we varied the amount of practice received over five consecutive days. Surprisingly, we found that total amount of practice per se did not affect motor learning and retention. Instead, we showed that distribution of practice over several days was a more influential factor. In other words, "passage of time", or training over multiple sessions, even if minimal, was sufficient to trigger learning and retention. From this study, we postulated that learning and consolidation are ongoing processes mediated by factors such as distribution of practice, and that once a skill is consolidated it is well retained (even after a period of a year without practice), possibly reflecting motor cortical plasticity. Support for this hypothesis also came from studies that have shown that spaced practice over several days augments subsequent performance on motor tasks, relative to massed or continuous practice within a single training session (e.g., Baddely & Longman, 1978; Shea et al., 2000).

It is worth noting that our study looked at how adults learned one motor sequence, whereas in real-life situations we are often faced with the challenge of learning multiple skills simultaneously. Therefore, other important factors to consider, besides the amount of practice, are the pattern of practice as well as the ability to transfer learning from one motor skill to another. Consequently, the first paper included in this thesis focused on the effect of practice pattern on motor learning, retention, and transfer. This work was fuelled by research on the contextual interference effect which postulates that when learning multiple skills, massing practice leads to better within-day acquisition, whereas random practice leads to better across-day consolidation and transfer (see Brady, 2004; Magill & Hall, 1990 for reviews). On day 1, participants were randomly assigned to the massed, alternating, or random condition. The massed condition received blocks of sequence A followed by blocks of sequence B; the alternating condition received alternating blocks of A and B; and the random condition received blocks in which A and B were quasi-randomly presented within each block. On day 2, all participants received one block of A and one of B (to test for consolidation) as well as one block of a novel sequence C (to test for transfer). We hypothesized that if the contextual interference effect is supported, participants in the Massed condition would perform better than participants in the two other conditions on the first day of learning, whereas participants in the Alternating and Random conditions would perform better at consolidation and on transfer to a novel motor sequence presented on day 2.

The second line of research in this thesis focused on investigating how individual characteristics, such as musical training and developmental changes across childhood, affect motor sequence learning. The primary goal of this axis of research was to explore the possibility of a putative sensitive period for motor learning, similar to that observed for language acquisition. A sensitive period refers to a window of time in development during which “the effects of experience on the brain are unusually strong” (Knudsen, 2004, p. 1412). For example, it has been shown that learning a second language is easier if a child is exposed to it before adolescence (e.g., Weber-Fox and Neville, 2001). Despite the widespread belief that early training is a precursor to expert motor performance (e.g., Michael Phelps started swimming at age 7 and Yo-Yo Ma started playing the cello at age 4), very little is known experimentally about this effect. A sensitive period in the motor domain would suggest that during a sensitive period in development, neural systems are particularly responsive to motor stimuli and are more susceptible to change when stimulated. For instance, structural and functional neuroimaging studies in musicians have shown that musical training can lead to neural changes, and that this neural plasticity is greater for musicians who began their training early in life (e.g., Elbert et al., 1995; Gaser and Schlaug, 2003; Schlaug et al., 1995). In a preliminary study using the TMST (Watanabe, 2003), we compared early- and late-trained musicians matched for age, but not years of experience, and found that early-trained musicians performed better than late-trained musicians on a timed visual-motor task. However, we also found a significant correlation between years of experience and performance, indicating that those who had played longer performed better. This suggested that the most important predictor of performance was not age at the start of training, but simple years of experience. Thus, in the second paper included in this thesis, the two groups of musicians were matched for years of musical experience, to control for differences in the total number of years of musical training. We hypothesized that if there was a putative sensitive period for motor learning, musical training early in life would lead to improved motor performance later in life.

Another important factor to consider in the concept of a sensitive period in motor learning is the effect of development. Pediatric structural neuroimaging studies have found ongoing changes in brain systems important for motor learning (e.g., Paus et al., 1999; Sowell et al., 1999, 2004; Mackie et al., 2007; Wilke et al., 2007), suggesting that maturational changes in the child brain coincide with and likely underlie changes in motor abilities across development. Surprisingly, there is a paucity of research on motor learning in children. Moreover, most developmental studies in the literature focused on the learning of basic motor skills (e.g., Badan et al., 2000), reaching (e.g., Takahashi et al., 2003) and aiming (e.g., Contreras-Vidal et al., 2005), but very few have looked at sequence learning across days. Thus, the final paper in this thesis assessed motor sequence learning across two days in three samples of school-aged children aged 6, 8, and 10 and a control sample of adults. A two-year separation between the child participants was used in order to be able to identify any incremental changes that might occur. Although the design of this study did not allow us to directly evaluate the presence of a sensitive period in motor learning, it allowed us to assess the presence of a possible developmental progression in motor learning, which in turn will guide future investigations in this area (to be further addressed in the discussion section of this thesis).

Taken together, the three behavioural experiments presented in this thesis provide an important window into the understanding of the behavioural sequels of motor sequence learning. Understanding motor learning at the behavioural level offers practical applications in various domains including, but not limited to, music and sports training as well as rehabilitation training after stroke or injury. Ultimately, understanding motor learning at the behavioural level helps to elucidate the bidirectional relationship between motor skill learning and brain plasticity, and facilitates the design of neuropsychological studies based on behavioural outcomes.

Chapter 2

The Effect of Practice Pattern on the Acquisition, Consolidation and Transfer of Visual-Motor Sequences

ABSTRACT

The effect of practice pattern on the acquisition, consolidation and transfer of visual-motor sequences

The contextual interference hypothesis proposes that when learning multiple skills, massing practice leads to better within-day acquisition, whereas random practice leads to better retention and transfer. In this experiment, we examined the effect of practice pattern on the learning, consolidation, and transfer of visual-motor sequences. On day 1, participants were randomly assigned to the massed, alternating, or random condition. On day 2, all participants were tested for consolidation and transfer. Learning was assessed by measuring changes in accuracy and response synchronization. We found that massed practice led to enhanced sensorimotor integration and timing (as measured by response synchronization), whereas random practice led to better stimulus-response association (as measured by accuracy). On day 2, all groups showed consolidation for both measures, as well as transfer for accuracy but not response synchronization. Overall, this pattern of results provides limited support for the contextual interference hypothesis. Our findings are consistent with differential encoding of specific domains of motor performance. We propose that learning of the stimulus-response association is a fast process that benefits from random practice because it requires the acquisition of this association in multiple contexts. Once the association is learned, it seems resistant to interference and transferrable to a novel sequence. In contrast, learning of the sensorimotor integration and timing is a slower process that benefits from blocked practice because practice in a single context allows fine-tuning of the response. Lastly, we postulate that learning that occurs in the context of interference can show consolidation.

Introduction

In everyday life, a vast array of motor skills can be learned simultaneously. A central question in the study of motor learning is how to structure practice of multiple skills in order to facilitate learning and retention. For instance, when a pianist is faced with learning Rachmaninoff's four piano concertos, what is the optimal way to organize their practice sessions? Should she learn one concerto before proceeding to the next one, or alternatively, should she learn all four concertos concurrently? Previous work has shown that when more than one motor skill is learned in a single session, massed patterns of practice lead to better within-day acquisition, but random patterns of practice lead to better retention and transfer. This effect was first termed "contextual interference" by Battig in describing the results of verbal memory experiments (1972), and was then applied to the domain of motor learning by Shea and Morgan in 1979 (see Brady, 2008 for reviews; Magill & Hall, 1990; Schmidt & Bjork, 1992). The current study examined the effect of three different practice patterns on visual-motor sequence learning over two consecutive days. The three practice patterns were tested: Massed, Random, and an intermediate Alternating condition in which blocks of the same sequence were alternated during practice.

Many studies of motor sequence learning have looked at how a single novel sequence is acquired and retained over several training sessions (Doyon et al., 2002; Karni et al., 1998; Nissen & Bullemer, 1987; Savion-Lemieux & Penhune, 2005; Seidler et al., 2005; Willingham, 1998). Commonly, learning has been characterized by three stages that correspond to specific points in the pattern of incremental changes that occur while practicing a new sequence (Doyon, Penhune, & Ungerleider, 2003; Hikosaka et al., 1999; Karni, 1996; Korman, Raz, Flash, & Karni, 2003b; Willingham, 1998). Within the first training session, fast and significant improvements in performance are observed, typically over a relatively small number of practice trials. This stage is followed by slower and more gradual gains that take place over a number of days or weeks, leading to an eventual plateau in performance (Hikosaka, Nakamura, Sakai, & Nakahara, 2002; Karni et al., 1998; Korman et al., 2003b; Savion-Lemieux & Penhune, 2005). A third, intermediate stage, referred to as consolidation, has been the focus of much recent interest. This stage occurs between the first and second training sessions and is thought to be sleep-dependent (Brashers Krug, Shadmehr, & Bizzi, 1996; Criscimangna-Hemminger & Shadmehr, 2008; S Fischer, Nitschke, Melchert, Erdmann, & Born, 2005; Walker et al., 2003). Consolidation has been measured in a number of different ways (Krakauer & Shadmehr, 2006 for review; see Robertson, Pascual-Leone, & Miall, 2004). One is improvement in performance after a period of rest or a night of sleep, with no additional practice. Another is resistance to interference by learning of a second sequence or task. The last is the ability to transfer learning to another sequence or task.

Support for the presence of separable stages of motor learning comes from functional imaging studies showing that different cortical and subcortical regions are preferentially activated at different stages of learning (Doyon & Benali, 2005; Floyer-Lea & Matthews, 2005; Penhune & Doyon, 2002, 2005). For instance, it has been postulated that while the cerebellum, rostral striatum, as well as motor, prefrontal, and parietal cortical regions are mainly active during early learning, the caudal striatum, as well as motor and parietal cortical areas are involved in consolidation and the later stage of learning (Doyon & Benali, 2005). It has been suggested that distribution of practice over time is important for a maximum benefit of practice to be gained, as the time delay allows for these neural changes to occur (Criscimangna-Hemminger & Shadmehr, 2008; Korman et al., 2003b; Savion-Lemieux & Penhune, 2005). This stage has been argued to be sleep-dependent, with a number of studies showing consolidation effects after a night of sleep compared with simple passage of time (Fischer, Hallschmid, Elsner, & Born, 2002; Krakauer & Shadmehr, 2006; Robertson et al., 2004; Walker et al., 2003).

Another important factor influencing how well a motor sequence is acquired and consolidated is the pattern of practice. This factor may be particularly relevant when learning more than one sequence, as is commonly the case in real-life situations. Early studies of verbal memory in the 1960s revealed that practice in which learning trials were presented in a blocked order, where all trials of one task are learned together before those of a second one are introduced, resulted in better within-day acquisition but poorer retention and transfer to a novel task, compared to practice in which learning trials were presented in a random order (Battig, 1966, 1972). This effect has been termed “contextual interference,” as it was postulated that high degrees of interference during initial learning enhance across-day retention and transfer of learned skills to a novel task (Battig, 1972; Magill & Hall, 1990). Potential factors contributing to the contextual interference effect include, but are not limited to, the task and the practice schedule (Magill & Hall, 1990; Schmidt & Bjork, 1992).

Two principal theories have been put forward to explain the contextual interference effect: the elaboration hypothesis (Shea & Zimny, 1988; Shea & Zimny, 1983) and the action plan reconstruction hypothesis (Lee & Magill, 1985). The elaboration hypothesis suggests that learning skills in a random fashion leads to more elaborative processing and therefore more comprehensive and retrievable memories in the long term. The reconstruction hypothesis postulates that learning skills in a random manner requires the learner to actively reconstruct many action plans, which in turn leads to more effortful processing and a more permanent memory (for a more detailed review of the two hypotheses see, Brady, 2008). Support for this latter theory comes from an fMRI study of contextual interference on motor sequence learning (Cross, Schmitt, & Grafton, 2007). Their results showed that random practice slowed initial performance, but improved retention. Consistent with the proposed mechanisms underlying contextual interference, they showed that during acquisition, the random-practice group took more time to plan their movements, and showed greater activity in motor regions associated with movement planning and response selection.

Since Shea and Morgan's original experiment (1979), numerous studies in the motor skill domain have investigated the contextual interference effect (see Brady, 2008 for reviews; Magill & Hall, 1990). However, results have been somewhat inconclusive. As Brady (2004) noted in his meta-analytic study "the literature on contextual interference contains many studies performed with different groups, different tasks, small sample sizes, and low power, thus rendering generalizations based solely on probability misleading" (p. 117). In fact, many recent studies conducted in both laboratory (e.g., bimanual coordination, sequential aiming, pursuit-tracking) and applied settings (e.g., pistol-shooting, endoscopic surgery, volleyball; Keller, Li, Weiss, & Relyea, 2006; Kurahashi, Leming, Carnahan, & Dubrowski, 2008; Maslovat, Chua, Lee, & Franks, 2004; Russell & Newell, 2007; Sekiya, 2006; Zetou, Michalopoulou, Giazitzi, & Kioumourtzoglou, 2007) have yielded inconsistent evidence. For example, Maslovat et al. (2004) found that the random group outperformed the blocked group on the learning and retention of bimanual coordination patterns, and no group effects were found during the transfer test.

The majority of studies looking at contextual interference have focused on the learning of gross motor skills, whereas very few studies have looked at fine motor skill learning. Studying contextual interference may be especially relevant in settings in which optimal performance of fine motor movement is required, such as playing a musical instrument. In addition, studies investigating the influence of contextual interference on motor learning have typically used an interference condition involving a high degree of contextual interference, in which three or more tasks are presented in an unsystematic or random order. However, many day-to-day fine motor tasks are not acquired in an unsystematic or random order, but rather are learned in a controlled and predictable manner (e.g., practicing the piano, learning to type). Therefore, in the present experiment we used the multi-finger sequencing task (MFST), a variant of the classical serial reaction time task (SRT; Nissen & Bullemer, 1987), to study the effect of the pattern of practice on fine motor sequence learning, across two consecutive days. In the MFST, participants had to reproduce sequences of key presses on an electronic keyboard, using four fingers of their right hand. The MFST is thought to be more naturalistic and similar to learning a tune on the piano. Two sequences were presented in a blocked, alternating, or random fashion on the first day of testing. On the second day, participants were either presented with the last block they practiced on Day 1 (to test for consolidation) or a novel transfer sequence. Given that recent research in both animals and humans has suggested that specific aspects of motor skill are learned and retained differently, and that learning of these parameters may be sub-served by different brain networks (Ghilardi, Moisello, Silvestri, Ghez, & Krakauer, 2009; Hikosaka et al., 2002; Savion-Lemieux & Penhune, 2005), we examined the effect of patterns of practice on two different aspects of performance. The first aspect is sequence accuracy, a component of the task that requires the association of the visual stimulus with the motor response. The second aspect is response synchronization, a more procedural component that requires fine-grained sensorimotor integration and timing. Overall, we hypothesized that if the contextual interference effect was operative, participants in the Massed condition would perform better than those in the two other conditions on the first day of learning, whereas participants in the Alternating and Random conditions would perform better at consolidation and transfer to Day 2.

Method

Participants

The total sample was comprised of 81 healthy undergraduates (27 males and 54 females). All participants were between the ages of 18 and 35 years. All participants were neurologically healthy and right-handed, as assessed using an adapted version of Crovitz and Zener's (1962) handedness questionnaire. Given that a previous study in our laboratory found behavioural differences in motor skill performance between adult musicians and non-musicians, participants in the present study were selected to have less than 3 years of musical training and experience, as measured using a modified version of the Global Index of Musical Training and Experience questionnaire (Watanabe, Savion-Lemieux, & Penhune, 2007). Participants were requested to refrain from drinking alcohol prior to each testing session. Three additional participants were tested, but were excluded from the final sample due to experimental error. The experimental protocol was approved by the Concordia University Human Research Ethics Committee, Montreal, Quebec. Participants provided written informed consent and were compensated for their time.

Multi-finger sequence task and stimuli

The Multi-finger sequence task (MFST) is a variant of the classical Serial Reaction Time (SRT) task originally designed by Nissen and Bullemer (1987). In the MFST, participants reproduced 13-element sequences of key presses on a MIDI-compatible electronic keyboard (Yamaha P-90), using four fingers of their right hand (i.e., index, middle, ring, and pinkie). Participants were cued to press one of the four marked keys by visual stimuli presented on the computer monitor (21-inch Sony Trinitron Multiscan G520 computer monitor, running at 100 Hz). The visual display consisted of four rectangular gray bars (11.5 cm X 3 cm) which remained on the screen for the entire duration of each trial. During a trial, the gray bars each turned red in a given order. The red illumination of a gray bar indicated that the corresponding key was to be pressed. The total inter-tap interval was 750 ms, during which the red bar was lit for 500 ms and the interval between the end of one stimulus and the beginning of the next was 250 ms. Additionally there was a 2000 ms delay between trials.

Each trial of the MFST consisted of a 13-element sequence and each block of practice included 12 trials. Three sequences were employed which were all designed to be of equal difficulty (sequence A: 1, 2, 4, 3, 1, 4, 2, 3, 2, 1, 3, 4, 1; sequence B: 2, 4, 1, 3, 2, 1, 4, 3, 1, 2, 3, 4, 2; and sequence C; 3, 1, 4, 2, 1, 3, 4, 1, 2, 4, 3, 2, 3). In addition, the same key was never pressed twice in succession and the same transition between two fingers never occurred twice consecutively. Breaks were provided between blocks to prevent fatigue and optimize performance.

A computer (Windows 2000) recorded all generated responses from the midi-compatible electronic keyboard. In-house custom software written in C++ was used to create and control the presentation of the visual stimuli and automatically recorded the onset and offset of participants' key presses, which were subsequently used to calculate the indices of learning.

Procedure

Testing included two learning sessions on two consecutive days, approximately 24 hours apart. On Day 1, participants were randomly assigned to one of three conditions (Fig. 1): a massed condition (n = 23), an alternating condition (n = 24), or a random condition (n = 23). In the massed condition, participants received four blocks of sequence A followed by four blocks of sequence B. In the alternating condition, participants received eight alternating blocks of sequences A and B. In the random condition, participants received eight blocks in which both sequences A and B were quasi-randomly presented within each block. On Day 2, within each condition, participants were divided into two groups (with 11 to 12 participants per group). The groups received either: one block of sequence B followed by one block of sequence A (i.e. consolidation group); or one block of a novel sequence C (i.e., transfer group; Fig. 1). Of note, participants in the random condition received two blocks in which both sequences A and B were quasi-randomly presented within each block. An additional control group was tested, in which 11 participants received four blocks of only one sequence on Day 1, followed by one block of that same sequence on Day 2. This additional group was included to test for

	Day 1	**Day 2**	
Massed condition	A A A A B B B B	B A	(*consolidation group*; n = 12)
	A A A A B B B B	C	(*transfer group;* n = 11)
Alternating condition	A B A B A B A B	B A	(*consolidation group*; n = 12)
	A B A B A B A B	C	(*transfer group*; n = 12)
Random condition	$\boxed{\text{AB}}$ x 8 blocks	$\boxed{\text{AB}}$ $\boxed{\text{AB}}$	(*consolidation group*; n = 12)
	$\boxed{\text{AB}}$ x 8 blocks	C	(*transfer group*; n = 11)
Control group	A (or B) x 4	A (or B)	(n = 11)

Figure 1. Experimental design: A, B, and C represent three different thirteen key-press sequences. A and B were used during training and C only at transfer. A represents the first sequence learned and B the second sequence learned; the actual sequences were counter-balanced across participants.

consolidation of one sequence without any interference. The order of sequence presentation was counterbalanced and on each testing day, participants were first familiarized with the electronic keyboard and the computer-generated stimuli.

Participants were told that they would be learning different motor sequences, but they were not explicitly taught the sequences. They were asked to follow along with the stimuli as accurately as possible, by pressing the key that corresponded to the location of the red illuminated rectangular bar. In order to minimize anticipatory responses and maximize response synchronization, participants were also instructed to synchronize their response with the visual stimulus by waiting until the red bar illuminated. As such, participants were not instructed to respond "as fast as possible" as is typically the case in classical SRT studies (Nissen & Bullemer, 1987).

Behavioural Measures

Learning was assessed by measuring changes in accuracy and response synchronization. Accuracy was scored individually, by calculating the percentage of correct key presses made for each sequence type (i.e., A, B, or C) within each trial and block. Response synchronization was calculated for correct key presses only; it characterized each participant's response time (ms) relative to the stimulus onset, averaged across trials and blocks of practice, for each sequence type. Anticipatory responses were included in the measure because previous studies have shown that anticipation increases with learning (Penhune & Doyon, 2002; Savion-Lemieux & Penhune, 2005). If response synchronization was a classic reaction time (RT) measure, anticipatory responses would be excluded as RT measures the time it takes the participant to make a response after the onset of the stimulus.

As in previous experiments in our laboratory, accuracy represented a component of the task which requires the association of the visual stimulus with the motor response; whereas, response synchronization represented a more procedural component that requires fine-grained sensorimotor integration and timing. Dependent measures were individually averaged across trials for each sequence type within each block of practice on the MFST.

Of note, participants in the random condition completed 6 trials of A and 6 trials of B within each block of practice. In order to analyze an equivalent number of A and B trials within each block (i.e. 12 trials) across all groups, the 6 trials of one sequence from one block were averaged with the 6 trials of the same sequence from the following block (e.g., 6 trials of A, Block 1 + 6 trials of A, block 2/12).

Results

Independent samples t-tests indicated no significant differences for average performance for sequences A and B collapsed across blocks on Day 1 ($p > .211$) for either behavioural measure, indicating that the sequences were of equal difficulty. Moreover, there were no significant differences between the sexes for average performance for sequences A and B on Day 1, for either behavioural measure ($p > .113$), when randomly selecting an equal number of males and females; therefore, behavioural data were collapsed across this dimension.

Analyses were conducted by day. For Day 1, the data were analyzed with repeated measures analyses of variance (ANOVAs; Greenhouse-Geiser correction), with Group as the between-subject factor and Block as the within-subject factor. Differences across the four blocks of A and across the four blocks of B were evaluated separately.

Using repeated measures ANOVAs (Greenhouse-Geiser correction), with Group as the between-subject factor and Block as the within-subject factor, we also assessed for consolidation of sequences B and A. For sequence B, we compared performance on the last block of B on Day 1 to the first block of B on Day 2 (free of across-day interference). For sequence A, we compared performance on the last block of A on Day 1 to the first block of A on Day 2 (in the context of within- and across-day interference). Using the same type of analyses for transfer, we compared performance on the last block of B on Day 1 to the first block of C on Day 2, when the sequence was novel and free of across-day interference. Additionally, a one-way ANOVA was used to compare the percent change for each measure for both consolidation and transfer. This score was calculated by subtracting performance on Day 1 from performance on Day 2, and dividing the total by performance on Day 1 (i.e., for consolidation of B: first block of B on Day 2 – last block of B on Day 1/last block of B on Day 1; for consolidation of A: first block of A on Day 2 – last block of A on Day 1/last block of A on Day 1; for transfer: first block of C on Day 2 – last block of B on Day 1/last block of B on Day 1). Significant main effects and interactions were analyzed using pairwise comparisons, with Bonferroni adjustment for multiple comparisons. The α level was set at 0.05 for all statistical tests. Effect sizes were reported for all significant main effects and interactions, using partial eta square (η^2).

Day 1

When comparing sequence A between the Massed, Alternating, and Random groups across the four blocks of practice on Day 1, for percent correct (Fig. 2), there was a significant main effect of Block $F(2, 4) = 5.03$, $p = .008$ ($\eta^2 = .070$), such that block 1 was significantly less accurate than block 2, $p = .006$. There was also a significant main

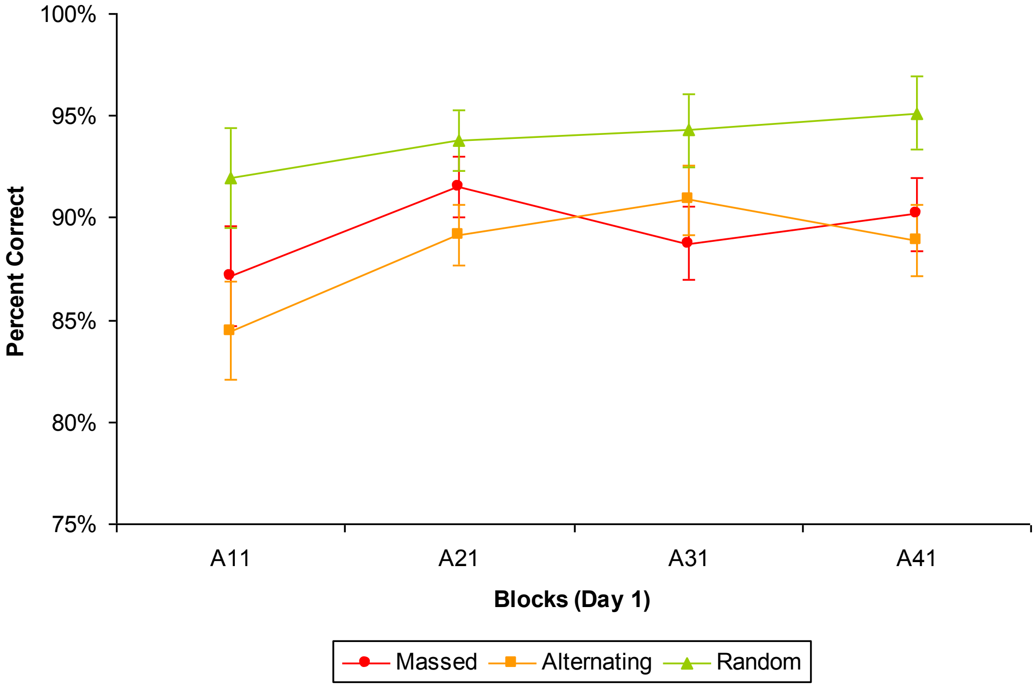

Figure 2. Acquisition of sequence A: Average accuracy data for the Massed, Alternating, and Random conditions across four blocks of acquisition on Day 1.

effect of Group $F(2, 67) = 3.78$, $p = .028$ ($\eta^2 = .101$), such that the Random group was significantly more accurate than the Alternating group $p = .034$; the Alternating and Massed groups did not differ. There was no significant Block X Group interaction $p = .471$. For response synchronization (Fig. 3), there was a significant Block X Group interaction $F(3.8, 126.99) = 4.34$, $p = .003$ ($\eta^2 = .116$). In line with our hypothesis, the Massed group showed significant improvements across all blocks of practice ($p < .005$), the Alternating group showed some significant improvements (specifically when comparing block 1 to blocks 2, 3, and 4; $p < .058$), but the Random group showed no significant improvements.

When comparing sequence B between the Massed, Alternating, and Random groups across the four blocks of practice on Day 1, a similar pattern of results emerged. For percent correct (Fig. 4), there was a significant main effect of Group $F(2, 67) = 4.52$, $p = .014$ ($\eta^2 = .018$), such that the Random group was significantly more accurate than the Alternating group $p = .013$, and the Alternating group and the Massed group did not differ. No significant main effect of Block or Block X Group interaction was found ($p > .137$). For response synchronization (Fig. 5), there was a significant Block X Group interaction $F(4.89, 163.67) = 3.06$, $p = .012$ ($\eta^2 = .084$). Post hoc analyses revealed that the Massed and Alternating groups showed significant improvements when comparing block 1 to all other blocks ($p < .031$) and when comparing block 2 to block 4 ($p = .001$); whereas the Random group showed no significant improvements across blocks on this measure.

Rate of change (Day 1)

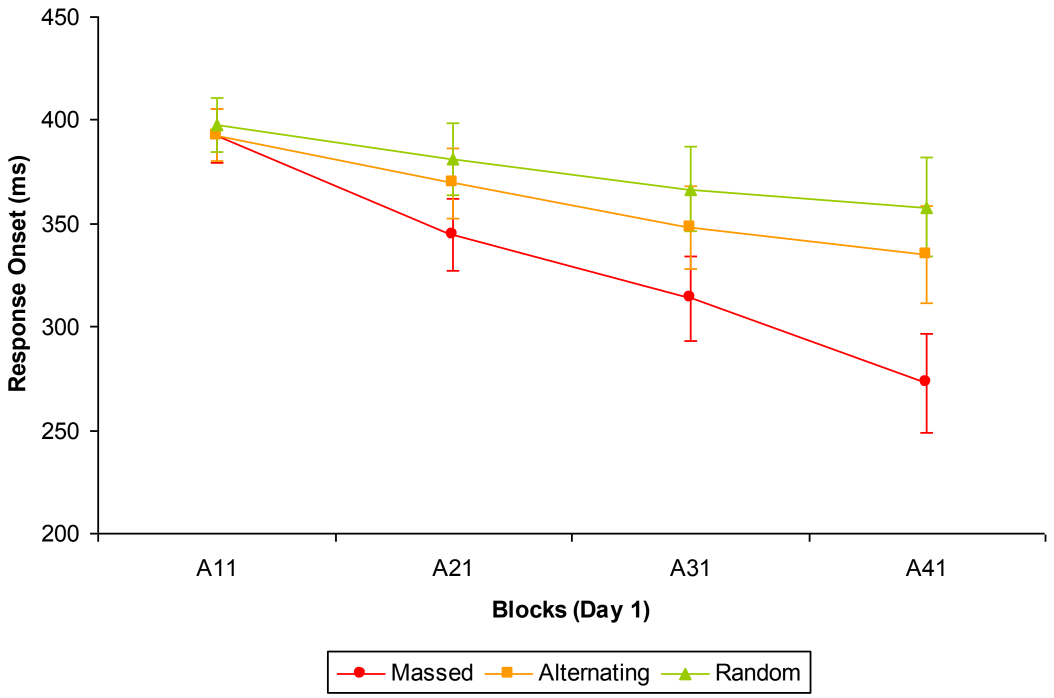

Figure 3. Acquisition of sequence A: Average response synchronization data for the Massed, Alternating, and Random conditions across four blocks of acquisition on Day 1.

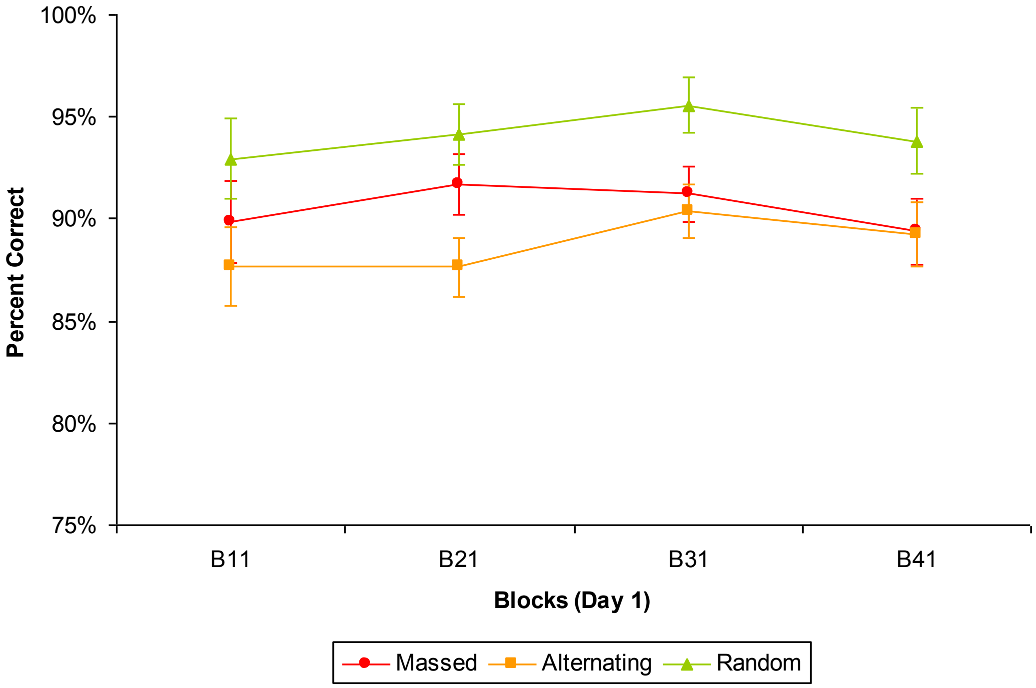

Figure 4. Acquisition of sequence B: Average accuracy data for the Massed, Alternating, and Random conditions across four blocks of acquisition on Day 1.

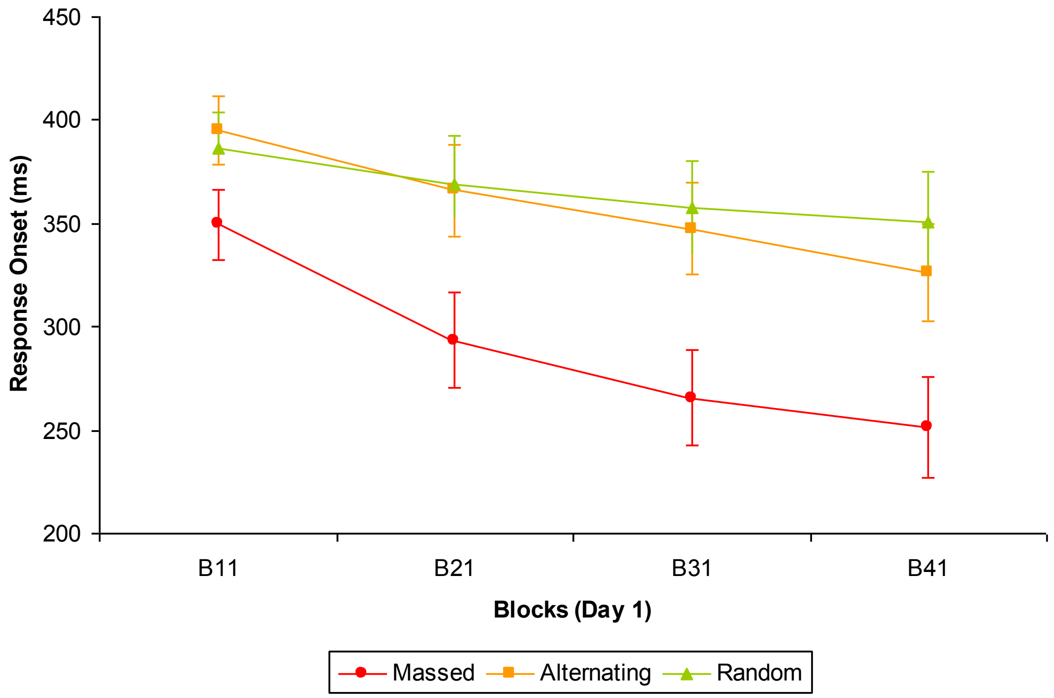

Figure 5. Acquisition of sequence B: Average response synchronization data for the Massed, Alternating, and Random conditions across four blocks of acquisition on Day 1.

An additional set of analyses was performed to quantify and compare the absolute rate of change between the first and last blocks of practice on Day 1, relative to the first block of practice on Day 1, for each sequence type and for each behavioural measure. To do this, the slope for each measure and sequence type was calculated and normalized to the first block of practice of the same sequence type. We used a one-way ANOVA, with Group (Massed, alternating, Random) as the between-subject factor and Bonferroni adjustment for multiple comparisons.

When comparing rate of change for sequence A, for percent correct, there was no significant difference in rate of change between the Massed, Alternating, and Random groups $p = .781$. For response synchronization, there was a significant main effect of Group $F(2, 69) = 5.318$, $p = .007$, such that the Massed group showed the greatest rate of change compared to the other two groups ($p < .078$); the Alternating and Random groups did not differ from each other in their rate of change.

When comparing rate of change for sequence B, for percent correct, there was no significant difference in rate of change between the Massed, Alternating, and Random groups $p = .672$. For response synchronization, there was a significant main effect of Group $F(2, 69) = 5.231$, $p = .008$, such that the Massed group showed a greater rate of change compared to the Random group $p = .006$; the other groups did not significantly differ from each other.

We also compared the rate of change between sequences A and B, for each behavioural measure, using a 3 (Group) x 2 (Sequence Type) repeated measures ANOVA. Results indicated that for percent correct, there was a marginally significant main effect of Sequence Type $F\ (1, 67) = 2.885$, $p = .094$ ($\eta^2 = .041$), such that there was a greater rate of change for sequence A compared to sequence B. No other significant results were noted. For response synchronization, there were no significant main effects and no interaction.

Finally, given the differential pattern of results found for accuracy and response synchronization on Day 1, we also compared the two measures to each other using a 3 (Group) x 2 (Measure) repeated measures ANOVA (Greenhouse-Geiser correction) for each sequence type. Findings showed that for sequence A, there was a significant Group X Measure interaction F (2, 67) = 5.091, $p = .009$ ($\eta^2 = .132$). Post hoc comparisons showed that all groups demonstrated significant differences in the rate of change between the two behavioural measures $p < .001$ (with greater changes on the response synchronization measure). For sequence B, the same pattern of results emerged such that there was a significant Group X Measure interaction F (2, 67) = 5.144, $p = .008$ ($\eta^2 = .133$), with all groups showing significant differences in the rate of change between the two behavioural measures $p < .02$ (with greater changes on the response synchronization measure).

Consolidation

When comparing performance on the last block of B on Day 1 to performance on the first block of B on Day 2, between the Massed, Alternating, Random, and Control groups, we found a similar pattern of results for both measures. For percent correct (Fig. 6), there was a significant main effect of Block $F(1, 43) = 15.9$, $p < .001$ ($\eta^2 = .270$), indicating overall significant improvements across days regardless of group. A significant main effect of Block $F(1, 43) = 7.66$, $p = .008$ ($\eta^2 = .151$) was also found for response synchronization (Fig. 7), with overall significant improvements across days. No other

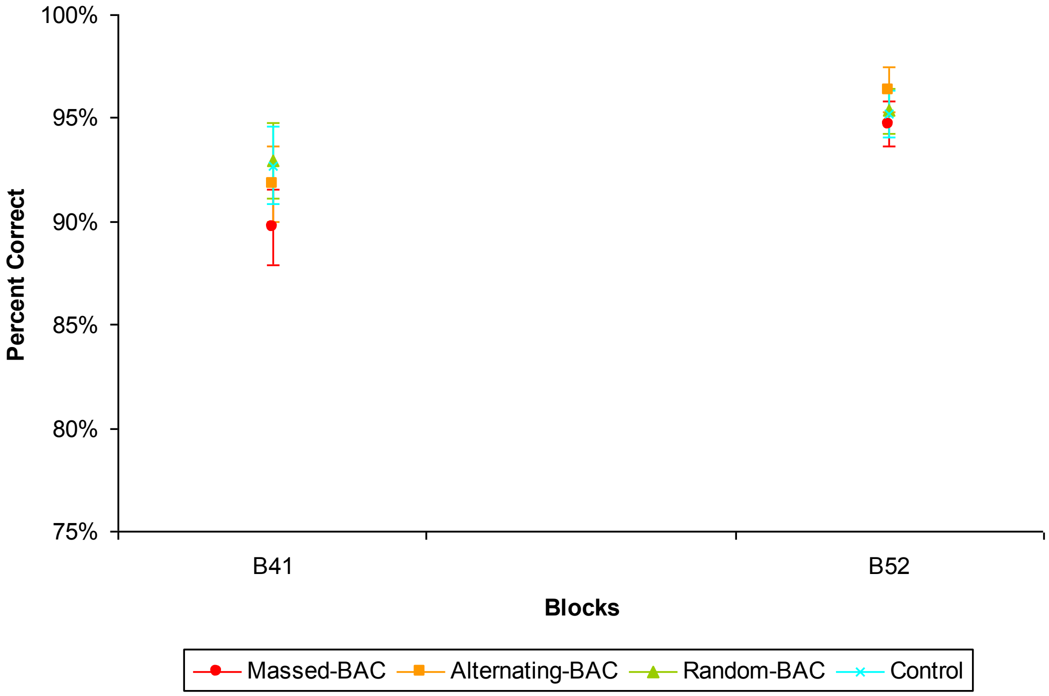

Figure 6. Consolidation without Day 2 interference: Average accuracy data for the Massed, Alternating, Random, and Control conditions across the last block of B on Day 1 and the first of B on Day 2.

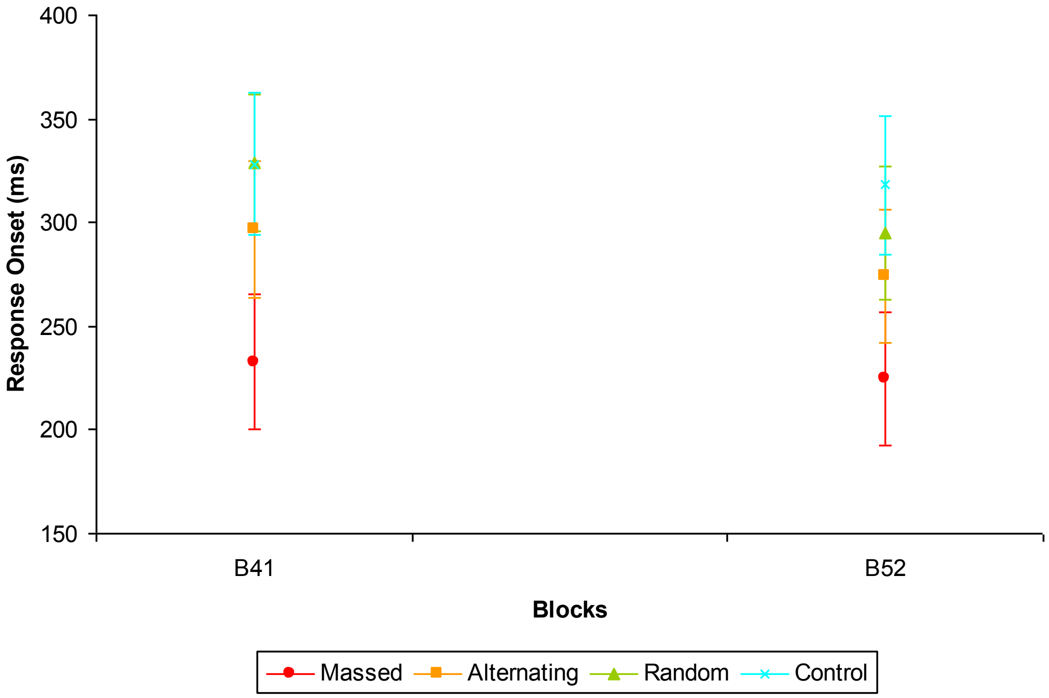

Figure 7. Consolidation without Day 2 interference: Average response synchronization data for the Massed, Alternating, Random, and Control conditions across the last block of B on Day 1 and the first of B on Day 2.

significant main effect of Group or interactions were found for either measure ($p > .175$), suggesting overall consolidation of sequence B, free of between-day interference, regardless of practice pattern.

We also contrasted performance on sequence A on Day 2 to performance on the last block of practice on sequence A on Day 1, in order to look at consolidation of A in the context of interference from practice on sequence B, both within and across days. Overall, there was a significant main effect of Block for both percent correct (Fig. 8) $F(1, 43) = 8.24$, $p = .006$ ($\eta^2 = .161$) and response synchronization (Fig. 9) $F(1, 43) = 10.56$, $p = .002$ ($\eta^2 = .197$), with post hoc analyses indicating general improvements on Day 2. No other significant main effects or interactions were found for both measures ($p > .29$), suggesting overall consolidation of sequence A, in the context of within- and between-day interference, regardless of practice pattern.

An additional set of analyses was performed to evaluate the percent change for each measure on consolidation of sequences B and A on Day 2. No significant results were found between sequence types for either behavioural measure.

Transfer

We compared performance on the last block of B on Day 1 to the first block of C on Day 2, free of across-day interference, for the Massed, Alternating, and Random groups. For percent correct (Fig. 10), there was a marginally significant main effect of Block $F(1, 31) = 3.12$, $p = .087$ ($\eta^2 = .091$), such that C was more accurate than B, indicating a certain degree of transfer. For response synchronization (Fig. 11), there was a significant main effect of Block $F(1, 31) = 8.13$, $p = .008$ ($\eta^2 = .208$), this time showing better performance for B compared to C indicating a loss in performance and/or

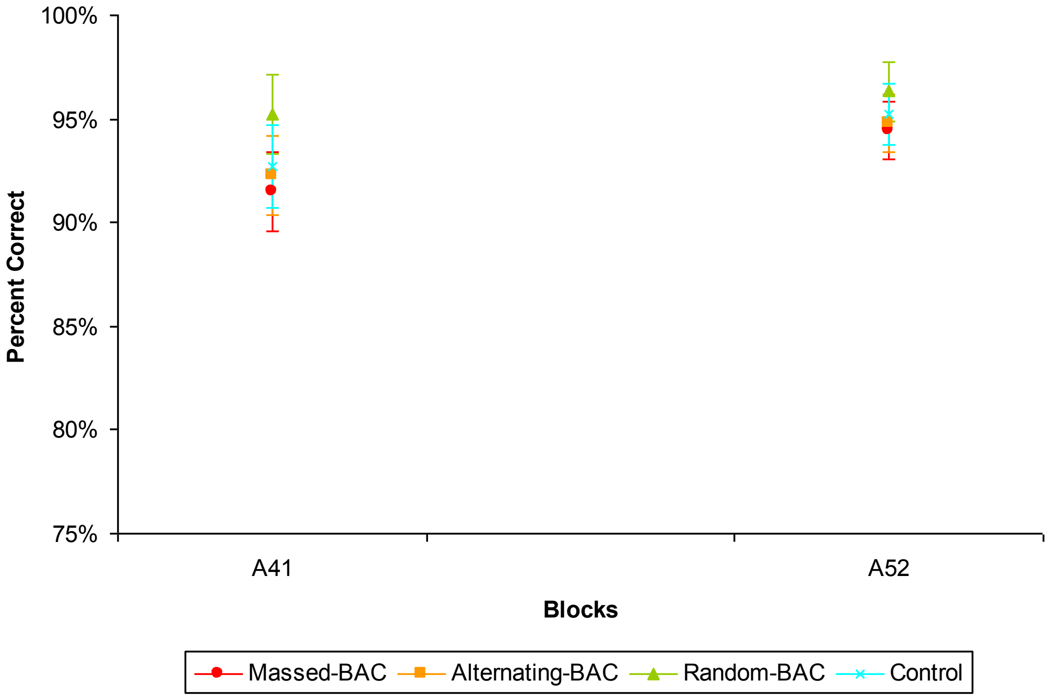

Figure 8. Consolidation with interference: Average accuracy data for the Massed, Alternating, Random, and Control conditions across the last block of A on Day 1 and the first of A on Day 2.

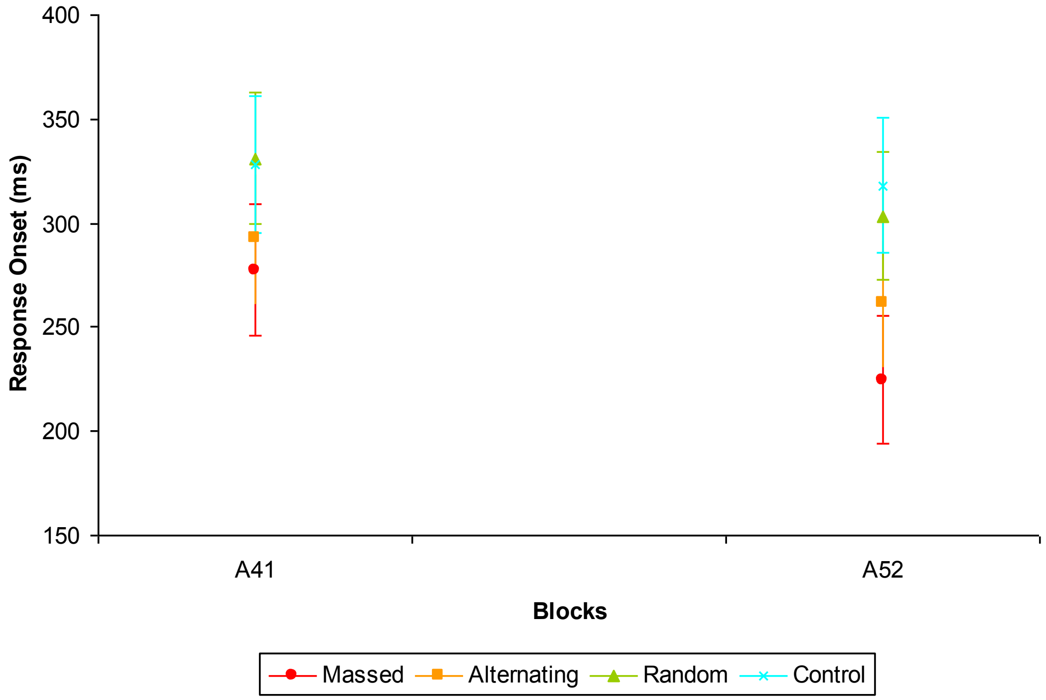

Figure 9. Consolidation with interference: Average response synchronization data for the Massed, Alternating, Random, and Control conditions across the last block of A on Day 1 and the first of A on Day 2.

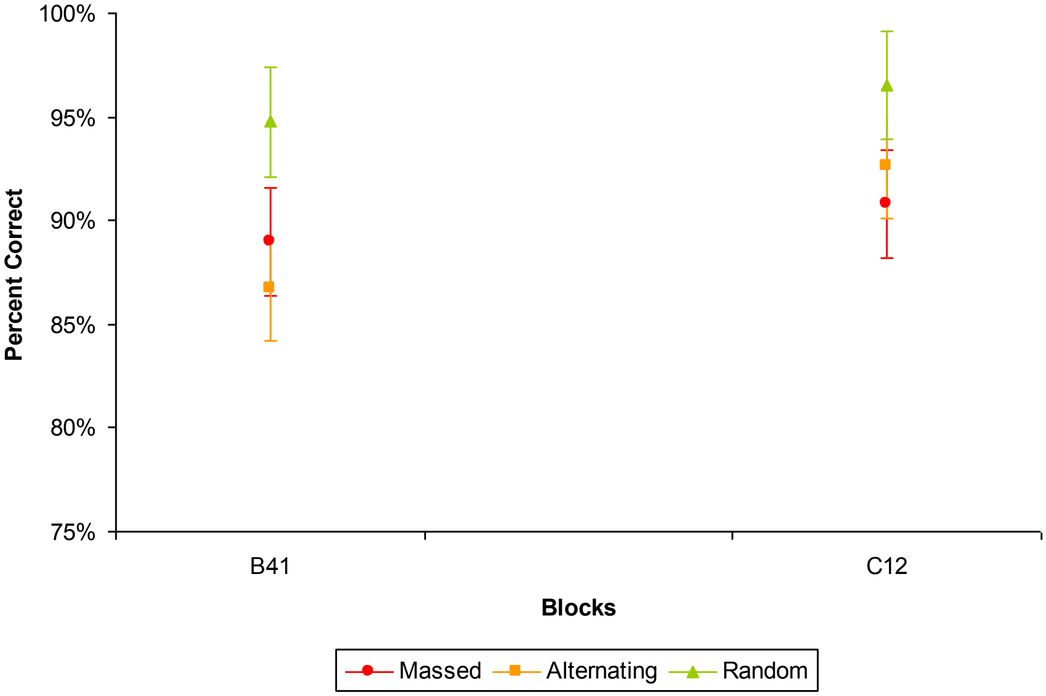

Figure 10. Transfer: Average accuracy data for the Massed, Alternating, and Random conditions between the last block of B on Day 1 to the first block of C on Day 2.

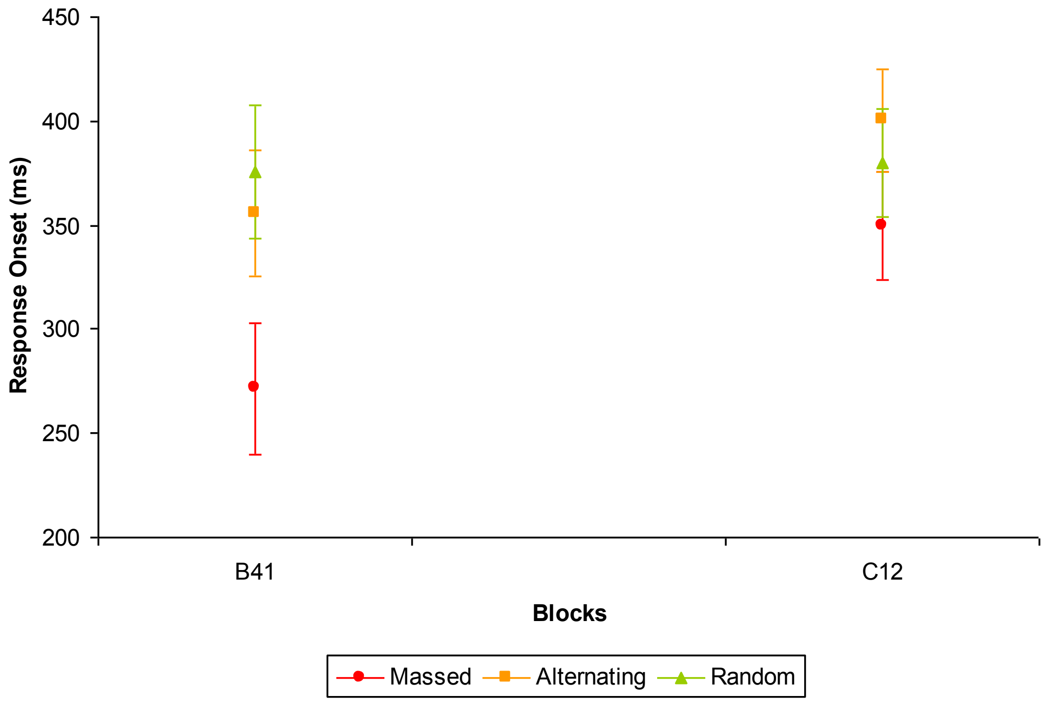

Figure 11. Transfer: Average response synchronization data for the Massed, Alternating, and Random conditions between the last block of B on Day 1 to the first block of C on Day 2.

interference likely leading to negative transfer. No other significant main effects or interactions were found ($p > .084$; Fig. 11).

An additional set of analyses was performed to evaluate the percent change of transfer from sequence B to sequence C for each measure. No significant differences were found between groups for either behavioural measure ($p > .297$).

Discussion

The current study was motivated by early research findings from the contextual interference literature, which demonstrated that high levels of contextual interference typically lead to poor within-day learning, but better across-day retention and transfer. Thus, in this experiment we looked at the effect of three practice patterns (Massed, Alternating, and Random) on the learning (within day), consolidation (across days), and transfer of visual-motor sequences. Overall, we found that on Day 1, for response synchronization, the Massed group showed the greatest improvements in performance across the blocks of practice whereas the Random group showed the least improvements. For response accuracy, surprisingly, the Random group performed better than the Massed and Alternating groups. In other words, massed practice led to enhanced sensorimotor integration and timing (as measured by response synchronization), whereas random practice led to better stimulus-response association (as measured by response accuracy). On Day 2, all groups showed consolidation of the sequences as evidenced by significant improvements in both accuracy and response synchronization between the last block of practice on Day 1 and the first block of practice on Day 2. Further, all groups showed transfer of learning to a novel sequence for response accuracy, but not response synchronization. Taken together, the overall pattern of results provides only partial support for the contextual interference hypothesis, with enhanced performance for the Massed group on Day 1 for response synchronization, but not accuracy. Further, the Random group did not show better performance at consolidation or transfer. Our findings are consistent with differential encoding of specific domains of motor performance and we therefore suggest rethinking the contextual interference hypothesis to take into account different measures of learning. Moreover, given that all groups showed consolidation, we postulate that the learning that occurs in the context of interference can show consolidation, which is not entirely consistent with previous studies showing interference when a second sequence is learned immediately following the first (Brashers Krug et al., 1996; Walker et al., 2003).

An interesting and novel finding that has not been previously reported in the contextual interference literature is the dissociation we found between the behavioural measures used to assess learning and transfer. In many laboratory studies looking at contextual interference from a motor skill perspective, participants are required to move/respond as rapidly as possible (e.g. Garcia, Moreno, Reina, Menayo, & Fuentes, 2008; Seidler, 2004; Shea & Morgan, 1979). Thus, the dependent measure is often "response time". In the present study, we broke down fine motor learning into two different components: accuracy, a component of the task that requires the association of the visual stimulus with the motor response, and response synchronization, a component that requires fine-grained sensorimotor integration and timing. Interestingly, we showed that practice pattern had a differential effect on the learning of these two measures, as we found that massed practice led to enhanced sensorimotor integration and timing, whereas random practice led to better stimulus-response association. We also showed transfer of learning to a novel sequence for response accuracy but not response synchronization, regardless of practice pattern. Taken together, these results support the idea that different components of a motor skill are learned and transferred in different ways (Ghilardi et al., 2009; Hikosaka et al., 1999; Savion-Lemieux & Penhune, 2005).

Based on our findings, we propose that learning the stimulus-response association, or explicit ordering of the task, is a fast process that benefits from structuring initial practice in a random fashion, because it requires the participant to acquire the stimulus-response association in multiple contexts by flexibly switching between the two sequences. This process likely requires greater generalization of the stimulus-response association, as well as more effortful processing and attention. Moreover, once the association has been learned, it seems to be resistant to interference and transferrable to a novel sequence. This is consistent with the elaboration or reconstruction hypotheses of contextual interference, but also applies to acquisition. On the other hand, learning of the sensorimotor integration and timing, or dynamic elements of the task, is a slower process that benefits from structuring initial practice in a blocked fashion, possibly because practice in a single context allows for error-correction and fine-tuning of the response. Interestingly, this component of the task seems to be more resistant to transfer, because without a constant context, the fine timing of the response is difficult to acquire. One model that provides support for this dissociation is that of Hikosaka (1999, 2002). The authors propose that motor sequence skills are handled as two types of sequences when represented within the brain: one spatial and one motor. The spatial sequence, or explicit ordering of the task, requires a high level of attention, is learned quickly, can be identified by rapid improvements in accuracy, and is encoded in the loops between the rostral basal ganglia (BG), prefrontal and parietal cortices, and the lateral cerebellum (CB). The motor sequence, or dynamic elements of the task, requires little attention, is learned more slowly, can be identified through improvements in synchronization, and is encoded between the loops in the caudal BG, motor cortex, and medial CB. Hikosaka's model can further be interpreted in light of the "elaboration" and "action plan reconstruction" hypotheses (Lee & Magill, 1985, respectively; Shea & Zimny, 1983), from the contextual interference literature. As Brady (2008) writes in his review, both hypotheses share a common characteristic, as they suggest that scheduling practice in a random fashion fosters cognitive processing that enhances encoding and thus transfer of the effects. Combining these views with Hikosaka et al.'s model (1999, 2002), we would predict that a random practice pattern is advantageous when initially learning the stimulus-response component of the MFST because it is the one that requires greater cognitive control and attention. Moreover, when this component is learned in the context of multiple sequences, it is more readily transferrable to a novel sequence. In contrast, massed practice benefits learning of the sensorimotor integration and timing components of the MFST because these are the aspects that are under less cognitive control. These components appear to be slower to learn, and more difficult to maintain and transfer, requiring ongoing practice and limited interference. For example, both a novice and skilled pianist may be able to play the correct notes of one of Bach's preludes, but in order to be synchronous and in time requires ongoing practice.

The classic design for testing the contextual interference effect focuses on the effects of practice pattern on tests of retention and transfer on the second day, as these phases best reflect the "permanence and adaptability" of sequence learning (Ste-Marie, Clark, Findlay, & Latimer, 2004). Because of this, many experiments only compare retention and transfer across training condition, but do not compare them to final performance at acquisition. Thus, while studies often claim that random practice results in better Day 2 performance, this performance is not usually compared to performance at the end of acquisition. Therefore, in the present experiment, we were interested in comparing retention and transfer to the acquisition phase. This is also advantageous, because we can compare and discuss our retention results in the context of the motor consolidation literature. Consolidation has been defined and measured in several ways (Krakauer & Shadmehr, 2006; Robertson et al., 2004): improvements in performance after a period of rest or a night of sleep, with no additional practice; resistance from interference by learning of a second sequence or task; the ability to transfer learning to another sequence or task. Interestingly, we found no group differences for consolidation of either sequence B (free of across-day interference from practice on any sequence) or sequence A (in the context of within- and across-day interference from practice on sequence B). Thus, practice pattern did not have any effect on consolidation. This demonstrates that learning that occurs in the context of interference can show consolidation, which is not entirely consistent with previous studies showing a graded interference effect for consolidation (Brashers Krug et al., 1996; Walker et al., 2003). Similar findings have been reported by Criscimagna-Hemminger and Shadmehr (2008), who proposed that with either enough practice, or passage of time, motor memory becomes stable and less resistant to interference. Similarly, it has been shown that even in the early learning phase, if practice is adequate, long-lasting functional and neural changes occur that result in a stable, long-term memory of the motor skill (Baddeley &

Longman, 1978; Hauptmann & Karni, 2002; Ofen-Noy, Dudai, & Karni, 2003; Savion-Lemieux & Penhune, 2005; C. Shea, Lai, Black, & Park, 2000). Thus it appears that in the present experiment the amount (48 trials of each sequence) and the distribution of practice over two days, regardless of the practice pattern, was sufficient to lead to general within-day and across-day improvements.

In summary, the results of the present experiment present a new way of understanding the effect of practice pattern on the acquisition, consolidation, and transfer of visual-motor sequences. Overall, our results challenge the contextual interference hypothesis. We therefore suggest that the contextual interference effect be reconsidered at the behavioural measures level, such that each measure represents a component of sequence learning that can be differentially influenced by practice pattern. Based on the dissociation of our results for accuracy and response synchronization, we postulate that learning the stimulus-response association is a fast and transferrable process that benefits from learning in multiple contexts. On the other hand, learning of the sensorimotor integration and timing aspects of the task is a slow process that is more resistant to transfer and that is promoted by learning in a single context that allows fine-tuning of the response. Thus, when a pianist is faced with learning Rachmaninoff's four piano concertos, learning the association between the musical notes and which keys to hit could be accomplished while learning all four concertos simultaneously (given that the stimulus-response association is a fast and transferrable process); however, learning the sensorimotor integration and timing aspects of the concertos may require practicing one concerto at a time to allow fine-tuning of each piece. Finally, given that all groups showed consolidation, we postulate that learning that occurs in the context of interference can show consolidation.

Chapter 3

The effect of early musical training on adult performance: evidence for a sensitive period in motor learning

ABSTRACT

The effect of early musical training on adult performance: evidence for a sensitive period in motor learning

Developmental changes in the human brain coincide with and underlie changes in a wide range of motor and cognitive abilities. Neuroimaging studies have shown that musical training can result in structural and functional plasticity in the brains of musicians, and that this plasticity is greater for those who begin training early in life. However, previous studies have not controlled for differences between early- and late-trained musicians in the total number of years of musical training and experience. In the present experiment, we tested musicians who began training before and after the age of seven on learning of a timed motor sequence task. The groups were matched for years of musical experience, years of formal training and hours of current practice. Results showed that early-trained musicians performed better than late-trained musicians, and that this performance advantage persisted after five days of practice. Performance differences were greatest for a measure of response synchronization, suggesting that early training has its greatest effect on neural systems involved in sensorimotor integration and timing. These findings support the idea that there may be a sensitive period in childhood where enriched motor training through musical practice results in long-lasting benefits for performance later in life. These results are also consistent with the results of studies showing structural changes in motor-related regions of the brain in trained musicians that are specifically related to training early in life.

Introduction

Mozart began piano training at the age of three, Beethoven before the age of eight. Many music programs for children emphasize beginning training as early as possible in order to develop musical skill. However, very little is known about the real effects of early musical training on adult performance. Behavioural studies comparing early-trained (ET) and late-trained (LT) musicians have shown that early training is essential for the development of absolute or “perfect” pitch (Baharloo, Johnston, Service, Gitschier, & Freimer, 1998; Costa-Giomi, Gilmour, Siddell, & Lefebvre, 2001; Miyazaki & Rakowski, 2002). More recently, brain-imaging studies have shown structural and functional changes in the brain associated with musical training that are greater for those who began training early in life (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Gaser & Schlaug, 2003; Koeneke, Lutz, Wustenberg, & Jancke, 2004; Schlaug, Jancke, Huang, Staiger, & Steinmetz, 1995; Schneider et al., 2002). These findings suggest that there may be a critical or sensitive period for musical training, similar to that observed for language acquisition. However, previous studies have not controlled for differences between ET and LT musicians in the total number of years of musical training and experience. By definition, a musician who begins training early has more years of experience that one who begins later when both are the same age. Therefore, it is possible that the previously observed differences in performance and brain structure can be accounted for simply by the duration of musical training. Therefore, the present experiment examined the effect of musical training on performance of a rhythmic tapping task in ET and LT musicians who were matched for years of musical experience.

Evidence for the effect of musical training on later perceptual skill comes from studies of musicians with absolute or perfect pitch. Baharloo et al. (1998) tested a large sample of 691 musicians. They found that of the 92 musicians in this sample who exhibited perfect pitch, 78% began training before the age of six. Similar results have been obtained by other groups (Costa-Giomi et al., 2001; Miyazaki & Rakowski, 2002) and it has been suggested that there may be a genetic component to the development of this skill (Baharloo et al., 1998).

Maturational changes in the human brain coincide with and underlie changes in a wide range of cognitive and motor abilities (Giedd et al., 1999; Paus, Zijdenbos, Worsley, & Collins, 1999). Recent studies have shown that early musical training can result in both structural and functional plasticity in auditory and motor regions of the brain (Elbert et al., 1995; Gaser & Schlaug, 2003; Koeneke et al., 2004). Elbert (1995) found that expert string players showed a larger cortical representation of the digits of the left hand. Further, he showed a strong correlation between the size of the digit representation and the age of start of musical training; with those who began earlier showing larger representations. Schlaug et al. (1995) reported a larger anterior corpus callosum in musicians compared with non-musicians, with musicians who began training before the age of seven showing a greater difference than those who began after the age of seven. In a recent study (Bengtsson et al., 2005) showed evidence for greater myelination in the right cortico-spinal tract of professionals, and that this difference was specifically related to the number of hours practiced in childhood (< 11 years). Taken together, these findings suggest that there may be a critical or sensitive period in development for the motor component of musical training.

The concept of “critical” and “sensitive” periods in development is drawn from work showing that certain behaviours and their neural substrates do not develop normally if appropriate stimulation is not received during a restricted time period in development (Knudsen, 2004). During a sensitive period, neural systems are particularly responsive to relevant stimuli, and are more susceptible to change when stimulated. Critical periods are sensitive periods that have relatively abrupt onsets and offsets. The classic example of a critical period comes from the work of Hubel and Weisel who showed that if cats are deprived of vision to one eye during the first months after birth, they do not develop normal binocular vision, even when vision is restored to the deprived eye (Hubel & Wiesel, 1965). At the neural level, the pattern of cellular connectivity is altered and cannot be changed after the critical period has elapsed (Wiesel & Hubel, 1965). In contrast to a critical period, where a function cannot be acquired outside the specific developmental window, a sensitive period denotes a period of development where the ability to acquire a specific skill is enhanced compared to other developmental periods. An example of a sensitive period comes from experiments in owls, where spatial representation can be changed by altered sensory input early in life, but normal representation can be relearned later in life (Brainard & Knudsen, 1998).

Evidence for critical or sensitive periods in humans is drawn largely from the domain of language acquisition. Single case studies of individuals chronically deprived of linguistic stimulation in early childhood have shown that these individuals fail to develop normal language even after intensive exposure (Curtiss, 1977). Further, studies of children with complete removal of the language-dominant left hemisphere revealed that as long as the removal occurred early, language could develop relatively normally.

These findings led Lenneberg (1967) to propose that there is a critical period for neural plasticity underlying language functions that extends from early infancy to puberty. This hypothesis has been adapted to the study of second-language acquisition to suggest that exposure to the second language during the sensitive period results in greater fluency than exposure after that time. This hypothesis has been supported by the results of a number of studies showing that second-language proficiency is greater in individuals who were exposed to the second language before age 11-13 (Johnson & Newport, 1989; Weber-Fox & Neville, 2001).

Surprisingly, there are no experimental studies looking at the effect of early motor training on adult performance, despite conventional wisdom and anecdotal evidence suggesting that early training is a prerequisite for excellence in many domains of skilled motor performance. Some suggestive evidence for the importance of motor experience early in life comes from recent studies of children confined to orphanages and later adopted into families in the UK and US. During their time in the orphanages, these children were highly restricted in terms of motor experience. Investigations of these children’s motor abilities following adoption have shown subtle deficits in motor skills such as standing balance and fine motor coordination (Tober & Pollak, 2005). These results indicate that motor deprivation during a putative sensitive period for motor learning can result in long-lasting impairments. Based on this, we can hypothesize that enriched motor experience, such as musical training, during this sensitive period could result in lasting neural changes and improved motor performance later in life.

In the present experiment, we tested musicians who began training before and after the age of seven on a timed motor sequence task (TMST), which has been used in several previous behavioural and neuroimaging studies (Penhune & Doyon, 2002, 2005; Savion-Lemieux & Penhune, 2005). This task requires participants to reproduce a temporally complex rhythmic motor sequence by tapping in synchrony with a series of visual stimuli (Figure 1). The use of this task is advantageous for two reasons. First, the tapped sequences are non-metrical, making them relatively difficult even for musicians, and requiring them to generalize from the more common metrical rhythms encountered in musical training. Second, the task requires synchronization of the motor response with a visual stimulus, again requiring generalization from the usual auditory-motor synchronization required in musical training.

As described above, none of the previous studies examining behavioral and neural differences between ET and LT musicians have controlled for differences between the groups in the total number of years of musical training and experience (Elbert et al., 1995; Gaser & Schlaug, 2003; Koeneke et al., 2004; Schlaug et al., 1995; Schneider et al., 2002). In a preliminary study using the same task (Watanabe et al., 2007) we compared ET and LT musicians matched for age, but not years of experience, and found the predicted enhanced performance for ET musicians. However, we also found a significant correlation between years of experience and performance; indicating that those who had played longer performed better. This suggested that the most important predictor of performance was not age at the start of training, but simple years of experience. Therefore, for the present experiment we moved to a matched sample where subjects in the two groups were matched for years of musical experience, such that later starters had the same number of years of musical experience as those who started earlier. We also controlled years of formal musical training and hours of current practice.

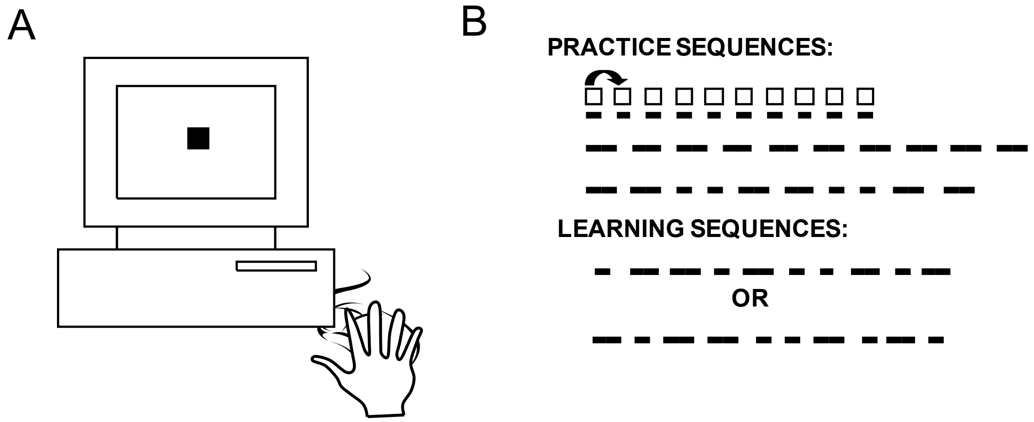

Figure 1. **(A)** Experimental setup. Stimulus sequences were made up of ten white squares, which appeared at the center of the computer screen. Participants responded by tapping on a single key of the computer mouse. **(B)** Stimulus sequences in the practice and learning conditions. Each square in the sequences appeared for either a short (250 ms) or long duration (750 ms), represented by the short or long line lengths. The ISI was constant (500 ms). Practice sequences consisted of four trials of three sequences: all short, all long, and a simple mixture. For the learning condition, sequences were made up of five long and five short elements. Participants were tested on only one of the two possible learning sequences.

Methods

Participants

Participants were thirty young, healthy, right-handed practicing musicians between 17.8 and 36.8 years of age (17 women and 13 men, *M* = 24.9 years, *SD* = 5.3) and ten non-musicians between 19.3 and 33.4 years of age (5 men and 5 women, *M* = 26.2 years, SD = 5.1) tested for a previous study using the same protocol (Savion-Lemieux and Penhune, 2005). All participants were recruited from the undergraduate student population of Concordia University. Musicians were recruited from the Department of Music and from the Montreal-area population. All participants were right-handed as assessed by a handedness questionnaire adapted from Crovitz and Zener (1962). None of the participants had a history of neurological disorders.

For the purposes of this study, a practicing musician was operationally defined as an individual who was currently practicing music and had at least four years of musical experience (range: 7.5-26.0 years). Musical experience was defined as the ability to play a musical instrument or sing, acquired through formal and practical training. The participants were predominantly piano and string players. Two of the musicians identified voice as their current primary musical focus, but both had extensive instrumental training and experience (15 years of guitar; 12 years of piano) and both currently practiced these instruments, although not to the same degree as voice. Similarly, a number of other musicians in the sample had played several instruments over their careers and some continued to play a secondary instrument throughout their careers.

Musicians were divided into two groups: early trained musicians (ET; n=15, 9 women and 6 men) who began training before the age of seven and late-trained musicians

(LT; n=14, 8 women and 6 men) who began training after the age of seven. The age at which musicians began training, the number of years of experience, the amount of formal training and the number of hours per week currently practiced were assessed using a modified version of the Global Index of Musical Training and Experience (Penhune et al., 1999; see supplementary material). Musicians in the two groups were individually matched for years of musical experience and formal training. Years of experience were defined as the total number of years of musical training. Years of formal training were defined as the total number of years spent in formal training (e.g., lessons). Both groups of musicians were compared to a group of non-musician controls who had been tested for a previous experiment using the same protocol (Savion-Lemieux & Penhune, 2005). These individuals were selected to have less than three years of musical training or experience and were not currently practicing music. All subjects were right-handed with no history of neurological or psychiatric disorder. The experimental protocol was approved by the Concordia University Human Research Ethics Committee, Montreal, Canada. Participants gave informed consent and were compensated for their time.

Stimuli

The TMST used in this experiment required participants to reproduce a temporally complex rhythmic motor sequence by tapping in synchrony with a series of visual stimuli using a single key on a computer mouse (Figure 1). The stimuli were ten-element visual sequences consisting of a series of white squares (3 cm^2) presented sequentially in the centre of the dark grey background of a computer screen (21-inch Sony Multiscan G500 monitor, 100Hz). Two different sequences designed to be of equal difficulty were used in this study. Each participant was tested on only one of the two possible sequences, which were counterbalanced across participants. Each sequence was composed of five long (750ms) and five short (250 ms) elements, with a constant inter-stimulus interval (500 ms). The sequences were constructed to have no more than two repeating elements as well as seven transitions from short to long elements. This results in sequences that are temporally regular, but do not conform to a standard musical rhythm. The elements of each sequence can be grouped into a series of intervals of three and five beats (3:5 ratio) based on the beat unit of 250 ms underlying both the stimuli and the inter-stimulus intervals. As these intervals do not represent a simple integer ratio (i.e., division of the intervals yielding an integer value), the sequences represent non-metrical rhythms (Essens, 1986; Essens and Povel, 1985). The presentation of each sequence was cued by a small white square (1 cm^2) that appeared in the middle of the screen. Each block of practice on the TMST contained 12 presentations of the same sequence and lasted 132 s.

Participants performed the TMST using a desktop computer that recorded all generated responses (Intel Pentium III 800-MHz computer, Windows 2000 Professional). Customized Media Control Functions (MCF) software (Digivox, Montreal, Canada) controlled the presentation of the visual stimuli as well as automatically recorded participants' key-press and release durations, which were subsequently used to calculate two indices of learning: accuracy of reproduction and percent asynchrony of responses with target stimuli (described in detail below).

Procedure

At the beginning of each testing session, before performing the TMST, participants completed a baseline practice task. This task consisted of three simple ten-element sequences that were made up of either all long, all short or a simple mixture (Figure 1). Participants were instructed to press and hold the mouse key down at the onset of each stimulus in the sequence, and to release it each time the stimulus disappeared. All participants used the index finger of the right hand. The experimenter provided feedback to ensure that the participant understood and learned the motor skill required for the study.

Once the baseline task was completed on Day 1, participants were explicitly trained to reproduce one of two TMST sequences to a criterion of three consecutive correct repetitions. After the initial training, no further feedback was provided to the individual. Participants then performed three blocks of their assigned TMST sequence. Participants were seated 57 cm away from the computer monitor and short breaks were provided between blocks of practice to prevent fatigue and optimize performance. Upon completion of the last block of trials, participants were asked whether they used any strategy to learn the TMST and instructed not to practice their assigned sequence in between test sessions. On each of the four consecutive days (Day 2 – Day 5), participants returned to the laboratory to perform the baseline task, review their assigned TMST by reproducing one to two trials of the sequence, and complete three blocks of trials.

Behavioural measures

The learning of motor skill tasks, such as the serial reaction time task (SRT), is typically assessed by reductions in reaction time to individual elements of the motor sequence. That is, faster responses correspond to improved performance. However, performance is measured on the TMST by requiring participants to synchronize their responses as precisely as possible with the presented stimuli. Therefore, learning of the

TMST was assessed by examining changes in two different variables: accuracy of responses and synchrony of responses with target stimuli. These measures examined learning of two different aspects of the task. Accuracy reflects learning of the more explicit component of the task – encoding of the correct order of short and long durations in the sequence. However, it still requires the participant to make a relatively accurate motor response – within 2SD of his/her baseline. Response asynchrony reflects the ability to precisely time key-press and key-release responses relative to the visual stimuli.

Performance of the learned sequences was scored individually by using each participant's average short and long responses from the practice sequences for each day of training (Penhune and Doyon, 2002). The first step in scoring was to calculate the average and SD for each participant's long and short responses on the simple practice sequences (Fig 1). Responses on the simple practice sequences that were greater than 2SD from the mean were excluded. The average was then recalculated, and the recalculated average ± 2SD was used as the upper and lower limit for accurate response on the learned sequences. This means that as subjects became more accurate and less variable with practice, the criteria for scoring their performance became more stringent. The percent of correctly reproduced elements was calculated for each trial and the measure of asynchrony was calculated on correct responses only. This was done so that measures of accuracy and asynchrony were not contaminated by gross errors. Percent response asynchrony (PASY) measured the percent difference between onset and offset of stimuli and the onset and offset of participant's key-press responses.

Data analysis

All behavioural measures were averaged across blocks of trials and days of practice. The data were assessed using repeated-measures analysis of variance (ANOVA) with Greenhouse-Geiser correction, with Group as the between-subjects factor and Block or Day as within-subjects factors. Percent correct and PASY measures were analyzed separately. Significant differences across days for the two groups were analyzed using tests of simple main effects with Bonferroni correction for multiple comparisons.

Results

Analysis of demographic data (Table 1) showed that the ET and LT musician groups were well matched, with no significant differences in the total number of years of musical experience, the number of years of formal training, or the number of hours per week they currently practiced. As predicted, the groups were significantly different in terms of the age of start of musical training and in current age. No significant correlations were found between age and any of the behavioural measures of performance. Repeated measures ANOVAs revealed no significant differences in either percent correct or percent response asynchrony between the two different sequences used in the learning trials, and no significant differences between the sexes. Therefore, behavioural data were collapsed across these dimensions. Data for the two vocalists was examined separately, and it was found that these musicians' performance did not differ significantly from the mean of their groups on any behavioral variable.

For percent correct (Figure 2, panel A), a repeated measures ANOVA showed no significant main effect of group, but a significant main effect of day, ($F_{(4,\ 108)} = 18.8$, p <.001), indicating improved performance across groups for the five days of training.

Table 1. Measures of musical training and experience

Group	Age	Age of onset	Years of experience	Formal training	Current: hours/wk
ET: Early Starters (<7yr)	22.1 (±3.4)	5.9 (±0.9)	14.8 (±4.3)	7.7 (±4.2)	11.8 (±9.0)
LT: Late starters (>7yr)	27.5 (±5.6)	11.4 (±2.7)	13.7 (±4.0)	6.3 (±3.7)	13.4 (±12.4)
T-test	*p* <.01	*p* <.001	*n.s.*	*n.s.*	*n.s.*
Non-musicians	26.2				

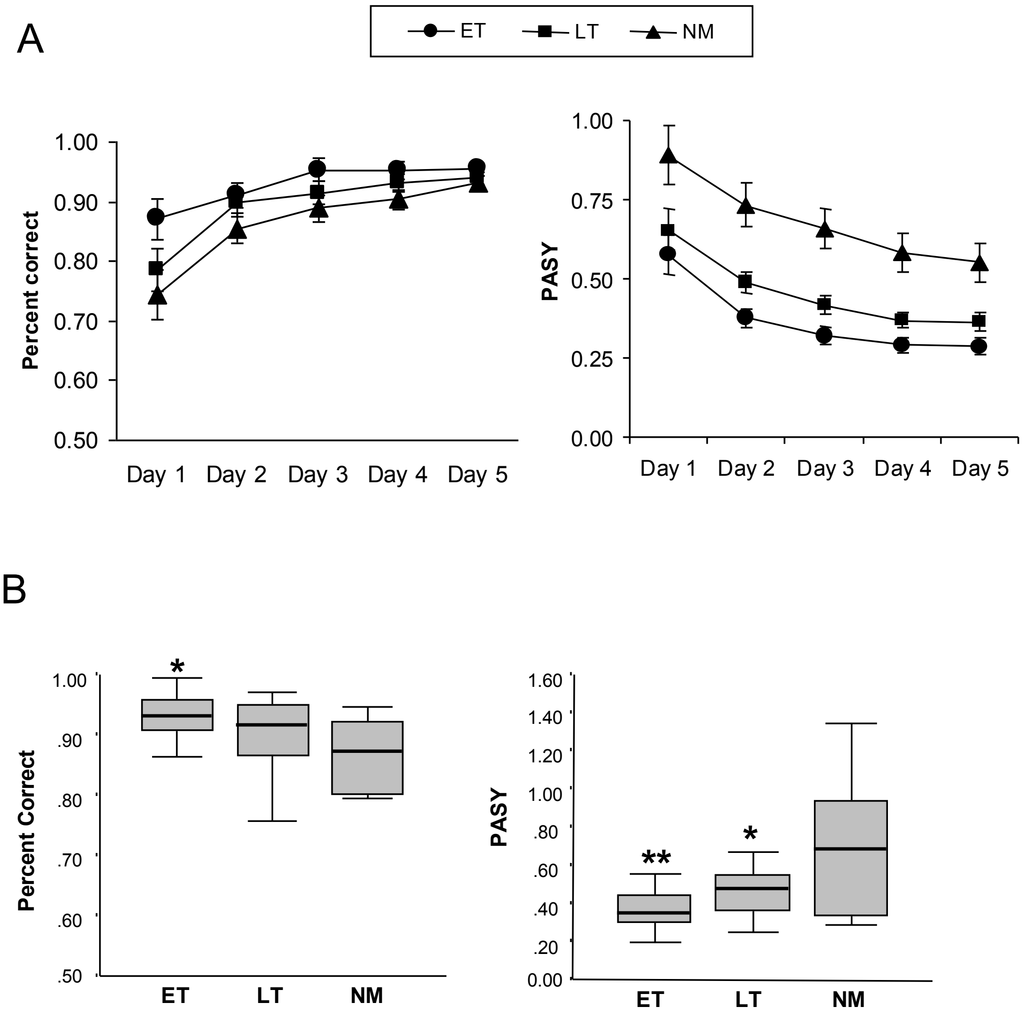

Figure 2. **(A)** Average percent correct and percent response asynchrony (PASY) data for ET, LT, and NM (non-musicians) groups across 5 days of learning. For percent correct, ET musicians performed better than LT musicians only on Day 1; and only ET musicians performed better than NM overall. For PASY, ET musicians performed better than LT musicians overall and specifically on Days 2-5. Both ET and LT musicians performed better than NM for this measure. **(B)** Box and whisker plots for ET, LT, and NM groups. For PASY, ET musicians performed better than both LT and NM groups. Although the ET and LT groups differ on average, of note is the considerable overlap in individual performance.

Post-hoc planned comparisons between groups across days of learning revealed a marginally significant difference between groups only on Day 1 ($p<.09$). Although there was no significant interaction, planned comparisons examining changes in performance across days for the two groups showed that LT musicians showed significant improvement between Day 1 and Day 2 ($p<.01$); whereas ET musicians showed only marginally significant gains between Day 1 and 3 ($p<.09$) and Day 1 and 4 ($p<.07$). In a separate analysis, both groups were compared with non-musicians (Figure 2, panel B). In this comparison, only ET musicians showed overall better performance (ANOVA $_{\text{DAY 1-5}}$: $F_{(2, 36)} = 3.2$, $p < .05$; Planned comparison, ET vs. NM, $p<.05$).

For percent response asynchrony, a significant main effect of group was found ($F_{(1, 27)} = 3.95$, $p = 0.056$), such that ET musicians performed better than LT musicians across the five days of learning (Figure 2, panel A). Post-hoc tests of simple main effect showed that ET musicians performed better than LT musicians on Days 2-4 ($p<.05$) and remained marginally significantly different on Day 5 ($p<.07$). In addition a main effect of day was observed, such that both groups improved across days of learning ($F_{(4, 108)} = 45.9$, $p < .001$). No significant Day x Group interaction was observed; however, post hoc pair-wise comparisons indicated that both groups show significant improvement between Day 1 and 2 (ET=$p<.001$; LT=$p<.008$), and between Days 2 and 3 (ET=$p<.03$; LT=$p<.004$), but that only LT musicians continued to show improvements between Days 3 and 4 (LT=$p<.005$). Neither group showed improvement between Days 4 and 5. In a separate analysis, when the two groups were compared with non-musicians (Figure 2, panel B) both ET and LT musicians showed overall better performance ($F_{(2, 36)} = 7.4$, $p < .01$; ET vs. NM, $p<.01$, LT vs. NM, $p<.05$).

Discussion

The results of this experiment show that ET musicians showed better performance on a novel rhythmic tapping task than LT musicians with similar levels of training and experience. For the more global measure, ET musicians performed better LT musicians only on Day 1, and both groups improved across days of practice. In contrast, for the measure of response synchronization, both groups started out at the same level and showed similar improvements with practice. However, from Day 2 onward, ET musicians showed better performance than LT musicians and this persisted after five days of practice. These findings support the idea that there may be a sensitive period in childhood where enriched motor training through musical practice results in long-lasting benefits for performance later in life. Performance differences were greatest for the measure of response synchronization, suggesting that early training has its greatest effect on neural systems involved in sensorimotor integration and timing. This is consistent with evidence for age-specific developmental changes in motor performance, and age-specific changes in brain regions important for motor control. It is also consistent with the results of studies showing structural changes in motor-related regions of the brain in trained musicians. Importantly, because the task required synchronization with a visual stimulus, these results show that the effects of early training can be generalized to novel motor tasks. Finally, while the ET and LT musicians differed on average, there was considerable overlap in performance between the two groups. This indicates that early training is not the only factor affecting adult performance. Other potential factors that might contribute to the enhanced performance of ET musicians are: individual differences in early ability, motivation, and family support for musical training.

The results of this experiment suggest that there may be a sensitive period in brain development where musical training can have long-term effects on motor performance that can be generalized to novel motor tasks. Maturational changes in the human brain are greatest in childhood, but continue into early adulthood. Following birth, the number of synapses and therefore the volume of grey matter continues to increase for between 3 and 15 months, depending on the region of the brain (Huttenlocher & Dabholkar, 1997). Once this peak is reached, the number of synapses decreases through the process of pruning, which is thought to underlie experience-dependent specialization. In contrast, the amount of white matter increases throughout development. Therefore, although the total size of the brain does not change substantially after the age of five, the amount of white matter increases until sometime around age 20 (Casey, Giedd, & Thomas, 2000). Over the last ten years, a number of studies using structural MRI techniques have examined developmental changes in the volume and proportion of grey and white matter in the brain. The results of these studies have shown that increases in white matter volume are age- and region-specific, with sensory and motor regions showing increases earlier, and frontal and temporal-parietal association areas later (Casey et al., 2000; Sowell et al., 2004). Increasing white matter volume measured by MRI is thought to correspond to increasing number of neuronal axons, greater diameter of axons, or greater thickness of the myelin sheath that surrounds them. A number of studies have shown increases in the white matter concentration of the cortico-spinal track and corpus callosum between childhood and late adolescence (Barnea-Goraly et al., 2005; Paus et al., 1999). It has been hypothesized that these increases may underlie decreases in nerve conduction time that are observed with development and might be related to behavioural phenomena such as decreasing reaction times and increasing motor speed associated with the improvement of fine motor skills across early childhood. A recent study (Bengtsson et al., 2005) examined white matter structure in professional pianists and non-musicians and showed evidence for greater myelination in the right cortico-spinal tract of musicians, and that this difference was specifically related to the number of hours practiced in childhood (< 11 years).

These changes in brain development during childhood are paralleled by changes in motor performance. Children show increasing speed in simple reaction time and repetitive finger tapping (Garvey et al., 2003). Motor evoked potentials show decreasing conduction times and increasing inhibition between the hemispheres (ages 10-13). At the same time, mirror movements, which are relatively common in children up to the age of 6-7, decrease. It appears likely that motor development depends on the maturation of multiple central and peripheral control mechanisms. A recent study of sequential finger pointing in 6-11 year-old children showed a discontinuity in performance around the age of 6-7 (Badan, Hauert, & Mounoud, 2000). Their data show that at that age, when the task is easy, children can utilize strategies that are more typical of older children, but that when the task is hard, they perform more similarly to younger children.

Taken together with the results of the current study, the above evidence suggests that enriched motor learning experienced during the period where neural and behavioural systems are immature appears to induce lasting enhancement in performance. As described in the Introduction, during a sensitive period neural systems are particularly sensitive to relevant stimuli, and are more susceptible to change when stimulated. In a recent review of the neural mechanisms underlying sensitive periods, Knudsen described evidence of synaptic changes at the cellular level that indicate that a sensitive period can be opened by experience (2004). Further, he suggests that intensive experience that occurs early in a sensitive period has a unique advantage, because sculpting of circuits by experience early in a sensitive period will shape the way those circuits respond to additional experience later in the sensitive period and beyond. For example, early plasticity in motor implementation and sensorimotor integration may lay down highly tuned circuits that can later be further optimized by learning mechanisms that remain plastic throughout life. This is consistent with the results of our study which show that ET musicians continued to improve on the measure of response synchronization, and to out-perform the LT musicians across five days of practice. Further support for enhanced plasticity comes from a recent study of tactile discrimination in professional pianists (Ragert, Schmidt, Altenmuller, & Dinse, 2004). This study showed that not only did pianists have lower sensory discrimination thresholds compared to non-pianists, but that with additional training, pianists were able to improve those thresholds to a greater degree than non-pianists.

In the present study, ET musicians showed specific enhancement of their ability to learn to synchronize their motor responses to a rhythmic visual sequence. Current theories of motor control maintain that learning and sensorimotor integration are based on error-correction and predictive control mechanisms that have been linked to the cerebellum. Both neurophysiological studies in animals and neuroimaging studies in humans have demonstrated cerebellar involvement in tasks requiring motor learning (Doyon et al., 2003; Karni et al., 1995; Kleim et al., 2002; Toni, Krams, Turner, & Passingham, 1998); timing (Ivry, Spencer, Zelaznik, & Diedrichsen, 2003; Schubotz, Friederici, & von Cramon, 2000) and sensorimotor integration (Bower, 1995; Gao, Parsons, Bower, Xiong, & Fox, 1996). Further, structural changes in the cerebellum have been shown to occur with learning of a novel task (Kleim et al., 2004). Neuroimaging studies from our lab, using the same task, have shown engagement of the cerebellum during learning (Penhune & Doyon, 2003, 2005). It is possible that in ET musicians, intensive early experience with tasks requiring motor learning, timing and sensorimotor integration results in preferential enhancement of cerebellar circuits. Evidence for cerebellar plasticity in musicians comes from a structural MRI study showing enlargement of the cerebellum that was correlated with lifetime practice in male keyboard players (Hutchinson et al., 2002). Cerebellum, along with the hippocampus, maintains a high degree of plasticity throughout life. Early training may simply enhance the cerebellum's ability to integrate the sensory and motor information required for learning.

The results of this study show convincing group differences in performance for ET and LT musicians. This conclusion is strengthened by the fact that the groups were matched for years of experience, formal training and current practice. However, there were also clear individual differences in performance, and not all ET musicians performed better than LT musicians. Therefore, it is likely that there are other factors that we did not control that contribute to the observed differences between the groups. The most important of these is early motor ability. Early ability may be potentially related to two factors: 1) genetically determined differences in central and peripheral motor control, or general cognitive abilities such as sustained attention; and 2) individual differences in motivation or environment. Evidence from studies of musicians with absolute pitch show that there may be a genetic contribution to this ability (Baharloo et al., 1998; Zatorre, 2003), although it cannot be developed without training. Similarly, a genetic predisposition for earlier development of motor skills or sustained attention abilities could underlie ET musicians' tendency to start training earlier and to obtain greater benefit from practice. Importantly, motivation can strongly affect learning and plasticity, as demonstrated by experiments in which auditory learning is enhanced by reward or survival saliency (Beitel, Schreiner, Cheung, Wang, & Merzenich, 2003; Knudsen, 2004). Therefore, children with greater intrinsic motivation or with greater family motivation may begin earlier and learn better. Finally, environmental factors such as access to musical training and family support for persistence in musical training could also play important roles. In the future, studies examining matched groups of early- and late- starting children undergoing the same type of musical training will shed light on the contributions of these factors.

Chapter 4

Developmental contributions to motor sequence learning

ABSTRACT

Developmental contributions to motor sequence learning

Little is known about how children acquire new motor sequences. In particular, it is not clear if the same learning progression observed in adults is also present in childhood nor whether motor skills are acquired in a similar fashion across development. In the present study we used the multi-finger sequencing task (MFST), a variant of the serial reaction time (SRT) task, to study motor sequence learning, across two consecutive days, in three cross sectional samples of children aged 6, 8, and 10 years, and a control sample of adults. In the MFST, participants reproduced 10-element sequences of key presses on an electronic keyboard, using four fingers of the right hand. Each block of practice included ten intermixed trials of a Repeated (REP) sequence and four trials of Random (RAN) sequences. Performance was assessed by examining changes in accuracy, a more explicit component of the task that requires the association of the visual stimulus with the motor response, and response synchronization, a more procedural component that requires fine-grained sensorimotor integration and timing. Additionally, participants completed Recognition and Recall tests, to further assess explicit knowledge of the repeated sequence. Overall, results showed a developmental progression in motor sequence learning within and across days of practice. Interestingly, the two behavioural measures showed different developmental trajectories. For accuracy, differences were greatest for the two youngest groups early in learning, and these groups also showed the greatest rate of improvement. However, by the end of Day 2, only the six year-olds still lagged behind all other groups. For response synchronization, all child groups differed from adults early in learning, but both child and adult groups showed similar rates of improvement across

blocks of practice. By the end of Day 2, 10 year-olds reached adult levels of performance, whereas 6 and 8 year-olds did not. Taken together, the dissociation observed with our two behavioural measures of sequence learning is consistent with the hypothesis that accuracy or finger-stimulus association may rely on cortical pathways that show the greatest maturation between ages 6 and 10; whereas motor timing and sensorimotor integration may rely on subcortical pathways that continue to develop into young adulthood. Despite developmental differences across blocks of practice on both behavioural measures, there were no significant group differences for either the Recognition or Recall tests. We suggest that explicit knowledge of the MFST is not directly linked to task performance, thus challenging the implicit-explicit distinction in pediatric SRT studies assessing the developmental invariance model.

Introduction

Motor skills are ubiquitous in everyday life. While certain skills, such as walking, are largely innate, most, such as writing and playing the piano, are acquired through practice. In the past decade, numerous studies have investigated the behavioural and neural underpinnings of motor skill learning in adults (For review, see: Doyon & Benali, 2005; Hikosaka et al., 2002; Krakauer & Shadmehr, 2006; Robertson et al., 2004); however, very little is known about how children acquire new motor skills. Recent evidence from pediatric structural neuroimaging research shows ongoing changes in brain systems important for motor learning (Barnea-Goraly et al., 2005; Gogtay et al., 2004; Mackie et al., 2007; Paus et al., 1999; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999; Sowell et al., 2004; Wilke, Krageloh-Mann, & Holland, 2007). Thus, maturational changes in the brain coincide with and likely underlie changes in motor abilities across development. Findings from our laboratory indicate that there may be a sensitive period for motor learning, during which the effects of practice in early childhood may lead to a greater degree of plasticity (Watanabe et al., 2007). In light of these results and given the paucity of research on motor skill learning in children, the overall goal of the present study was to examine developmental contributions to motor sequence learning, across multiple days of practice, in three cross-sectional samples of school-aged children, aged 6, 8, and 10, and a control sample of adults. Another objective was to take an exploratory approach to assessing the existence of a possible sensitive period for motor learning. A variant of the serial reaction time (SRT) paradigm was used to assess learning of both implicit and explicit components of the task (Nissen & Bullemer, 1987). This allowed us to evaluate the developmental invariance model which postulates that while implicit learning develops early and is relatively invariant across childhood, explicit learning shows greater changes over time (Reber, 1993).

Numerous studies on motor sequence learning in adults have consistently identified three stages of learning, corresponding to distinct points in the pattern of incremental changes during acquisition of a new task (Doyon & Benali, 2005; Hikosaka et al., 2002; Karni et al., 1998; Korman, Raz, Flash, & Karni, 2003a; Krakauer & Shadmehr, 2006). The first stage occurs within the initial session, where rapid improvements in performance are observed over relatively few trials. The second, intermediate stage, referred to as consolidation, occurs between the first and second practice sessions. Consolidation has been defined in two ways: first, as significant "off-line" gains in performance following a period of rest with no additional practice; and second, freedom from interference by learning of a second sequence (For review see Krakauer & Shadmehr, 2006). This stage has been argued to be sleep-dependent (Stefan Fischer et al., 2002; Krakauer & Shadmehr, 2006; Robertson et al., 2004; Walker et al., 2003). The third stage occurs throughout the remaining sessions (days or weeks) where slower and more gradual gains eventually lead to plateau in performance (Doyon & Benali, 2005; Hikosaka et al., 2002; Karni et al., 1998; Korman et al., 2003b; Savion-Lemieux & Penhune, 2005). It has been hypothesized that distribution of practice over time is essential for a maximum benefit of practice to be gained, as the time delay allows for plastic changes in the neural representation of the sequence (Korman et al., 2003a; Savion-Lemieux & Penhune, 2005). Support for the presence of separable stages of motor learning comes from functional imaging studies in adults showing that different cortical and subcortical regions are preferentially activated at different stages of learning

(Doyon & Benali, 2005; Hikosaka et al., 1999). For instance, it has been proposed that while the cerebellum, rostral striatum, as well as motor, prefrontal, and parietal cortical regions are primarily active during early learning, the caudal striatum, as well as motor and parietal cortical areas are involved in consolidation and the later stage of learning (Doyon & Benali, 2005).

Despite the explosion of research on motor sequence learning in adults, very little is known about how children acquire new motor sequences. In particular, it is not clear if the same stages of learning observed in adults are present in childhood, nor whether the pattern of learning is the same across development. A large number of developmental studies have focused on the acquisition of basic motor skills, such as pointing (Badan et al., 2000; Ferrel, Bard, & Fleury, 2001), reaching (Kuhtz-Buschbeck, Stolze, Johnk, Boczek-Funcke, & Illert, 1998; Takahashi et al., 2003) and aiming (Contreras-Vidal, Bo, Boudreau, & Clark, 2005; Smits-Engelsman, Sugden, & Duysens, 2006). Overall, these findings indicate that with age basic motor skills are performed with better dexterity, less variability, as well as increased speed and accuracy. However, fewer studies have looked at more fine motor skills, such as finger sequencing (Badan et al., 2000; De Guise & Lassonde, 2001; Dorfberger, Adi-Japha, & Karni, 2007; Ferrel et al., 2001; Meulemans, Van der Linden, & Perruchet, 1998; Thomas et al., 2004; Thomas & Nelson, 2001). Moreover, the majority of these studies have investigated motor learning within a single training session. Overall, findings indicate that with practice there are significant within-day improvements in performance, as evidenced by increases in accuracy and decreases in reaction time. However, there is an absence of reliable developmental differences (Meulemans et al., 1998). Furthermore, to our knowledge, only one study has looked at motor sequence learning in children across multiple consecutive days (Dorfberger et al., 2007). Their results revealed similar learning gains for adults and children aged 9, 12, and 17 when trained on a single sequence but differential off-line gains for the youngest groups. In sum, less is known about the developmental progression of motor sequence learning in childhood. Therefore, the main goal of this study was to assess motor sequence learning, within and across two consecutive days of practice, in younger children aged 6, 8, and 10 years.

Although the changes in children's ability to learn and perform motor skills across development are obvious, the specific changes in underlying brain structure are only beginning to be understood. Evidence from pediatric neuroimaging studies indicates that the brain continues to develop into middle childhood and adolescence, and that these maturational changes coincide with the development of motor abilities (Barnea-Goraly et al., 2005; Gogtay et al., 2004; Mackie et al., 2007; Paus et al., 1999; Sowell et al., 1999; Sowell et al., 2004; Wilke et al., 2007). In particular, these studies show that global grey matter volume increases up until the age of approximately 6-10 and then decreases thereafter (Gogtay et al., 2004; Sowell et al., 2004; Wilke et al., 2007). The decrease in grey matter is paralleled by global increases in white matter. Studies have shown increases in the white matter concentration of the cortico-spinal system between childhood and late adolescence (Barnea-Goraly et al., 2005; Paus et al., 1999; Wilke et al., 2007). It has been hypothesized that these increases may underlie decreases in nerve conduction time that are observed with development. Furthermore, a recent functional neuroimaging study, comparing children's and adults' performance on a motor sequence-learning task, results indicated that while subcortical regions were mainly recruited in children, adults predominantly recruited cortical regions (Thomas et al., 2004). It was hypothesized that these age-related findings underlie age differences in motor response execution. Taken together, plastic modulations in the brain related to development parallel developmental changes in motor abilities throughout childhood.

A central theme in the developmental literature on motor sequence learning revolves around Reber's developmental invariance theory (1993) which suggests that implicit learning develops early and is relatively invariant across childhood, as it is subserved by more evolutionarily primitive, subcortical structures that reach maturity earlier in development (i.e. basal ganglia); whereas explicit learning shows greater changes over time, as it involves more cortical structures which continue to develop across childhood. Although, as described above, recent pediatric neuroimaging studies have shown developmental changes throughout the brain well into adolescence, the understanding of the dissociation between implicit and explicit learning across childhood is still a hot topic of debate amongst developmental cognitive scientists. The SRT task, first introduced by Nissen and Bullemer (1987), is one of the most commonly used paradigms to study implicit and explicit sequence learning. In the SRT task, a stimulus appears in one of several locations and participants are required to respond as quickly and accurately as possible by pressing a button, which corresponds to the spatial location of the stimulus. A fixed, repeating sequence, and random sequences are presented in either a blocked or intermixed fashion. Implicit learning is measured by enhancements in performance on the fixed repeating sequence when compared to the random sequence; explicit learning is typically assessed by a recognition and recall test, measuring the participants' awareness of the fixed sequence. Developmental studies using the SRT paradigm have found mixed results regarding age-related differences in implicit and explicit learning. While one study has found evidence for the developmental invariance model (Meulemans et al., 1998), other studies have showed age-related differences in explicit rather than implicit learning (Thomas & Nelson, 2001) and have proposed that both systems develop in parallel across childhood (Thomas et al., 2004). Interestingly, it has been proposed that performance on the SRT is independent of the explicit knowledge of the repeating sequence (Seger, 1997). Thus, it could be argued that the method of contrasting explicit recall and implicit sequence learning may not fully measure all aspects of implicit and explicit learning. In the present experiment, we suggest that implicit and explicit learning on the SRT task can be assessed at both the task and the measures level. As such, in our view, accuracy assesses a more explicit component of the task that requires association of the visual stimulus with the motor response, whereas response synchronization assesses a more implicit or procedural component, that requires fine-grained sensorimotor integration and timing.

In other domains of skill acquisition, such as gross motor development and language learning, there is evidence suggesting that there may be sensitive periods for optimal learning of specific skills. Knudsen defines the notion of sensitive period as “a broad term that applies whenever the effects of experience on the brain are unusually strong during a limited period in development… during which certain capacities are readily shaped or altered by experience” (Knudsen, 2004, p.1412). Evidence for sensitive periods in humans is mostly drawn from the field of language acquisition where results suggest that second-language proficiency is greater in individuals who were exposed to the second language before puberty (Johnson & Newport, 1989; Weber-Fox & Neville, 2001). In the motor domain, the issue of sensitive periods is rarely discussed. Results from a study on orphan children who were highly limited in terms of their motor experiences in early childhood, found subtle impairments in their gross and fine motor skills, suggesting that motor deprivation during a sensitive period can lead to long-lasting motor deficits (Tober & Pollak, 2005). Furthermore, behavioural and neuroimaging studies with trained adult musicians have shown that experience-driven plasticity can interact with maturational plasticity to produce differential changes in brain structure in individuals with early-musical training (Schlaug, 2001). A recent behavioural study from our laboratory (Watanabe et al., 2007) has found that musicians who began their training before the age of 7 performed significantly better on a timed motor sequence task, compared to those who began their training after the age of 7. Taken together, these results suggest that there may be a sensitive period in childhood for optimal learning of motor skills. Thus, in the present experiment we took an exploratory approach to evaluating the existence of a possible sensitive period for motor learning.

In the current study, we used the multi-finger sequencing task (MFST), a variant of the SRT task, to study motor sequence learning, across two consecutive days, in three cross sectional samples of children aged 6, 8, and 10 years, and a control sample of adults. In the MFST, participants had to “catch an animal”, appearing in one of four locations on a computer screen, by pressing the corresponding key on an electronic keyboard using one of four fingers of the right hand. This task is thought to be more naturalistic and similar to learning a tune on the piano. Performance was assessed by exploring changes in accuracy, a more explicit component of the task that requires the association of the visual stimulus with the motor response, and response synchronization, a more procedural component that requires fine-grained sensorimotor integration and timing. Additionally, at the end of the second session, participants' completed recognition and recall tests, to further assess explicit knowledge of the repeated sequence. Overall, we hypothesized that there would be a developmental progression in motor sequence learning both within and across sessions of practice. Moreover, if there is a sensitive period in motor learning, we expected the greatest incremental behavioural changes to occur between the two youngest groups. Finally, if the invariance theory is supported, we predicted that children and adults would show similar performance on the more implicit measures, whereas they would show developmental differences on the more explicit measures.

Method

Participants

The final sample consisted of 53 right-handed and neurologically healthy participants (28 males and 25 females). Three cross-sectional groups of children, aged 6 (n = 13; *M* = 6 years, 5 months; range = 6 years, 0 to 9 months), 8 (n = 12; *M* = 8 years, 7 months; range = 8 years, 3 to 8 months), and 10 years (n = 13; *M* = 10 years, 3 months; range 10 years, 2 to 9 months) were recruited. A fourth comparison group of university undergraduates (n = 15; *M* = 24 years, 5 months; range = 20 to 34 years) was recruited. All groups scored in the Average to Above Average range on the Vocabulary and Digit Span subtests of the Wechsler Intelligence Scale for Children – 4th edition (WISC-IV; Psychological Corporation, 2003; Child participants) or Wechsler Intelligence Scale for Adults – 3rd edition (WAIS-III: Psychological Corporation, 1997; Adult participants), indicating that they were well matched based on these cognitive measures.

Given that a recent study in our laboratory found behavioural differences in motor skill performance between adult musicians and non-musicians, adult participants in the present study were selected to have less than three years of musical training and experience, as assessed using a modified version of the Global Index of Musical Training and Experience questionnaire (Watanabe et al., 2007). For Child participants, musical training and experience was assessed using a child version of the questionnaire, but information was not used to exclude participants. Participants with a known history of Learning Disabilities (n = 3) or a confidence index above 60 on the Continuous Performance Test – II (CPT-II; MHS, 2004; indicating that performance better matched an Attention Deficit Hyperactivity Disorder profile than a non-clinical profile; n = 6), were excluded from the final sample, based on previous developmental studies showing that these disorders are associated with motor learning impairments (Kooistra, Crawford, Dewey, Cantell, & Kaplan, 2005; O'Driscoll et al., 2005; Pitcher, Piek, & Hay, 2003). Additionally, seven participants were excluded due to experimental error or data collected from only one session.

The experimental protocol was approved by the Concordia University Human Research Ethics Committee and the Lower Canada College Board of Governors, Montreal, Québec. A parent provided written informed consent, and the Child gave verbal assent on each testing session. Adult participants provided written informed consent.

Multi-Finger Sequence Task and Stimuli

The MFST is a variant of the task used by Thomas and Nelson (2001) which was based on Nissen and Bullimer’s (1987) classical SRT task. In the MFST, participants reproduced 10-element sequences of key presses on a MIDI-compatible electronic keyboard (M-Audio O_2, 25 keys), using four fingers of the right hand (i.e., index, middle, ring, and pinkie; Fig 1). Participants were cued to press one of the four marked keys by a visual stimulus presented in the middle of a computer screen (19-inch LCD Samsung). The visual display consisted of four horizontally oriented coloured frames (5 cm^2), which remained on the screen for the entire duration of each trial. The visual cue for each finger movement was a cartoon animal (4.5 cm^2) that appeared sequentially in one of the frames. The cue for Familiarization trials was “Bubbles the Fish” and for Learning trials was “Rolly the Hamster.” The cue duration was 600 ms, with a 400 ms inter-stimulus interval, for a total inter-tap interval of 1000 ms.

Participants were told that they would be playing a computer game where they have to “catch Rolly the Hamster” by pressing the key that corresponded to its location. In order to minimize anticipatory responses and maximize response synchronization, participants were instructed to synchronize their response with the visual stimulus by waiting until the animal appeared in the frame before catching it. Adult and Child participants completed the same task and received the same instructions.

Each trial of the MFST consisted of a 10-element sequence and each block of practice included 14 trials, of which 10 were a Repeated (REP) sequence and 4 were Random (RAN) sequences. The REP and RAN sequences were designed to be of equal difficulty. For instance, the same key was never pressed twice in succession, the same transition between two fingers (e.g., index to pinkie) never occurred twice consecutively, at least one transition between the fingers occurred within each block, and the number of finger transitions was counterbalanced across blocks. Performance on the RAN

Figure 1. Experimental setup.

sequences was used to compare learning of the REP sequence, in order to examine "sequence-specific" learning in relation to a more global or general learning of the task. The blocks were quasi-randomly designed, such that the REP and RAN sequences were differently intermittently spaced within each block of practice. The blocks followed similar rules of presentation, such that they never started or ended with a RAN sequence and two RAN sequences never appeared consecutively. There was a 1300 ms delay between trials and each block of practice lasted 2 min and 48 s. At the end of each block, a brief animation (i.e. "Rolly the Hamster" dancing) was displayed on the screen, as a reward to help the children maintain attention. Breaks were provided between blocks to prevent fatigue and optimize performance.

Prior to practice on the MFST, there was a Familiarization phase which consisted of two simple and predictable sequences (i.e., sequence A: index, middle, ring, pinkie; sequence B: pinkie, ring, middle, index). Each trial consisted of a 4-element sequence and each familiarization block included 15 trials, of which participants observed the first 3 and completed 12. At the end of each block, a brief animation (i.e. "Bubbles the Fish" swimming) was displayed on the screen. Overall, Adult and 10-year-old participants completed 4 familiarization blocks (two of each order). Some children in the two youngest groups required additional familiarization blocks (three of each order), in order to ensure that they were able to coordinate all four fingers of their right hand and follow the target stimulus by looking at the computer screen while moving their fingers.

At the end of the MFST on Day 2, participants completed a Recognition and Recall test. In the Recognition test, participants were shown three MFST sequences and were asked to identify which of the three sequences corresponded to the REP sequence.

In the Recall test, participants were asked to reproduce the REP sequence on the keyboard, with no visual stimulus to guide them.

A Toshiba laptop (Windows XP) recorded all generated responses from the midi-compatible electronic keyboard. In-house custom software written in C++ was used to create and control the presentation of the visual stimuli and automatically recorded the onset and offset of participants' key presses, which were subsequently used to calculate the indices of learning.

Procedure

Child participants were recruited at a local private elementary school. Prior to testing, a letter and consent form were sent to all parents of grades 1, 3, and 5 students. Parents who signed the consent form were contacted by a research assistant to complete a brief telephone interview. If the child met research criteria, they were tested at the school on two consecutive days, approximately 24 hours apart. Adults were recruited by word of mouth at Concordia University and were tested in the laboratory.

On Day 1, participants completed the Familiarization phase, 3 blocks of practice on the MFST, the Vocabulary and Digit Span subtests of the WISC-IV or WAIS-III (refs), as well as a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971). On Day 2, participants again completed the Familiarization phase, followed by 2 blocks of the MFST, as well as the Recall and Recognition tests. Finally, participants completed the CPT-II (MHS, 2004), an attention test used clinically to identify response patterns (in children and adults) that match an Attention Deficit Hyperactivity profile. At the end, Children received a prize and Adults were compensated for their time.

Behavioural measures

To score the MFST data, a 1000 ms response window was created to identify the key press responses that corresponded to each visual stimulus (Fig 2). The window included 100 ms before the stimulus onset, to allow for anticipatory responses, and ended 300 ms after the stimulus offset, to allow for delayed responses. Only the first key pressed within each window was scored.

Learning was assessed by investigating changes in accuracy and response synchronization. Accuracy was scored individually, by calculating the percentage of correct key presses made for each trial, averaged across the two sequence types (REP and RAN) within each block of practice. Response synchronization was calculated for correct key presses only; it characterized each participant's response time (ms) relative to the stimulus onset, averaged across trials and blocks of practice, for each sequence type. In this experiment, accuracy represented a more explicit component of the task, which requires the association of the visual stimulus with the motor response. Response synchronization represented a more procedural component that requires fine-grained sensorimotor integration and timing. Dependent measures were individually averaged across trials for each sequence type (REP and RAN) within each block of practice on the MFST. For the Recognition test, the number of participants who correctly identified the REP sequence was calculated for each group. For the Recall test, the mean percentage of correct key presses was calculated for each group; only the first ten key presses were scored and analyzed.

Results

Independent samples t-tests indicated no significant differences between the sexes on Day 1 mean performance, when averaging REP trials across all blocks of practice, for

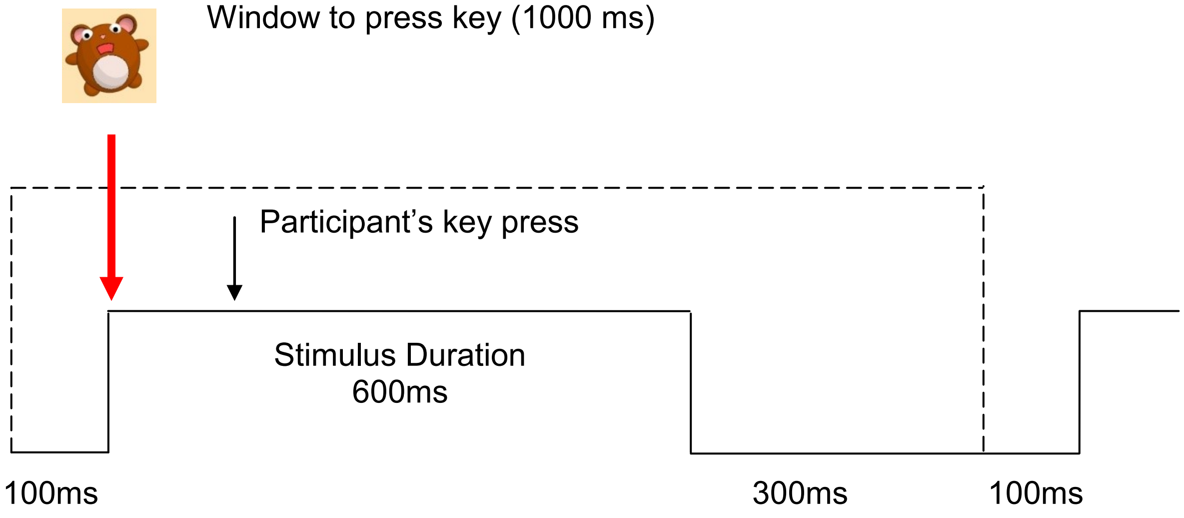

Figure 2. Scoring method for accuracy and response synchronization of key presses.

either behavioural measures ($p \geq .165$). Similarly, when comparing children with and without piano training, no significant differences were found on either behavioural measure ($p \geq .576$), indicating that piano training in the Child groups did not influence performance on the MFST. Therefore, behavioural data were collapsed across these dimensions.

Two types of analyses were conducted with the data. The first type assessed "sequence-specific" learning, by comparing performance on the REP and RAN sequences. In order to analyze an equivalent number of REP and RAN trials within each block of practice, all 4 RAN trials were averaged and compared with the average of the first, fourth, seventh, and last REP trials in each block. The data were analyzed with repeated measures analyses of variance (ANOVAs; Greenhouse-Geiser correction), with Group as the between-subject factor and Sequence Type and Block as the within-subject factors. The second type of analysis evaluated a more global or general learning of the task, by comparing performance on the REP trials only. All 10 REP trials were averaged for each block of practice. The data were analyzed with repeated measures analysis of variance (ANOVAs; Greenhouse-Geiser correction), with Group as the between-subject factor and Block as the within-subject factors. For both types of analyses, differences across the three blocks of practice on Day 1 (early-learning), across the last block of practice on Day 1 and the first block of practice on Day 2 (consolidation), and across the two blocks of practice on Day 2 (late-learning), were evaluated. Significant main effects and interactions were analyzed using pairwise comparisons, with Bonferroni adjustment for multiple comparisons. The α level was set at 0.05 for all statistical tests.

REP vs. RAN: Day 1

When comparing percent correct, on the REP and RAN sequences, between the groups across the three blocks of practice on Day 1 (Fig 3), there was a significant main effect of Sequence Type F (1, 49) = 10.833, $p = .002$ indicating that the REP sequence was performed more accurately than the RAN sequences (M REP = 79.1%, M RAN = 76.3%). A significant main effect of Block F (1.7, 83.32) = 33.032, $p < .001$ was also found, such that overall Block 1 was significantly less accurate than Blocks 2 & 3 ($p < .001$). As predicted, there was a significant main effect of Group F (3, 49) = 51.69, $p < .001$. Post hoc planned comparisons revealed that the Adult and 10-year-old groups did not significantly differ ($p = .318$), whereas the two youngest groups were significantly different from each other and from the Adults and 10-year-olds ($p < .001$). There was also a significant Block X Group interaction F (5.1, 83.32) = 5.462, $p < .001$. Post hoc comparisons revealed that on all blocks, groups were significantly different from each other ($p < .016$), except the Adults and 10-year-olds ($p > .064$), suggesting that their level of accuracy was similar from the beginning. When looking at performance across blocks within each group, post hoc analyses revealed that Adults showed no significant improvements across blocks ($p > 1.00$), whereas 10 year-olds showed significant improvements between Blocks 1 and 2 ($p = .05$), and 8-year-olds and 6-year-olds showed significant improvements when comparing Block 1 to the other two blocks ($p < .001$). This pattern of results indicates that, on this measure, Adults were performing at ceiling whereas the Child groups showed within-day learning. Finally, no significant Sequence Type X Block, Sequence X Group, and Sequence Type X Block X Group interactions were found ($p \geq .058$) for percent correct.

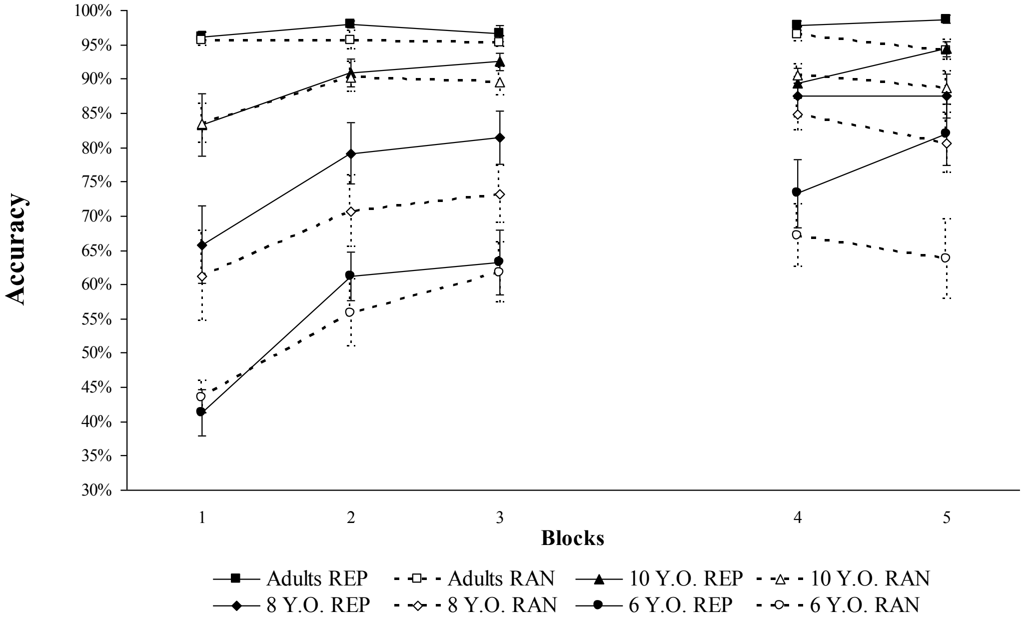

Figure 3. Average accuracy data for all groups across five blocks of practice for matched REP (four trials per block) and RAN sequences (four trials per block).

For response synchronization (Fig 4), a similar pattern of results was observed. There was a significant main effect of Sequence Type F (1, 49) = 70.487, $p < .001$ indicating that key press responses were more synchronous on the REP sequence than the RAN sequences (*M* REP = 514.763 ms, *M* RAN = 550.517 ms). There was also a significant main effect of Block F (1.81, 88.75) = 51.017, $p < .001$, such that there were significant improvements in response synchronization across the three blocks of practice ($p \leq .001$). As expected, there was a significant main effect of Group F (3, 49) = 15.312, $p < .001$. Post hoc planned comparisons revealed that Adults performed significantly more synchronously than all child groups ($p > .005$). Moreover, 10-year-olds' responses were significantly more synchronized than 6-year-olds' responses ($p = .041$). There was also a significant Sequence Type X Block interaction F (1.88, 92.31) = 4.916, $p = .011$, with post hoc analyses indicating that overall key presses were significantly faster on the REP sequence on all blocks ($p \leq .002$), suggesting an early emergence of "sequence-specific" learning. Lastly, there was a significant Block X Group interaction F (5.43, 88.75) = 2.735, $p = .021$, such that overall Adults were significantly faster than Children on all blocks ($p \leq .006$). Interestingly, by Block 3, Adults and 10-year-olds showed no significant differences in performance ($p = .132$), indicating that by the end of Day 1, 10-year-olds reached Adult level of performance. When looking at performance across blocks within each group, only the Child groups showed improvements in performance ($p \leq .06$), indicating that the Adults were performing at ceiling whereas the Child groups showed within-day learning. No significant Sequence Type X Group and Sequence Type X Block X Group interactions were found ($p \geq .110$).

REP vs. RAN: Consolidation

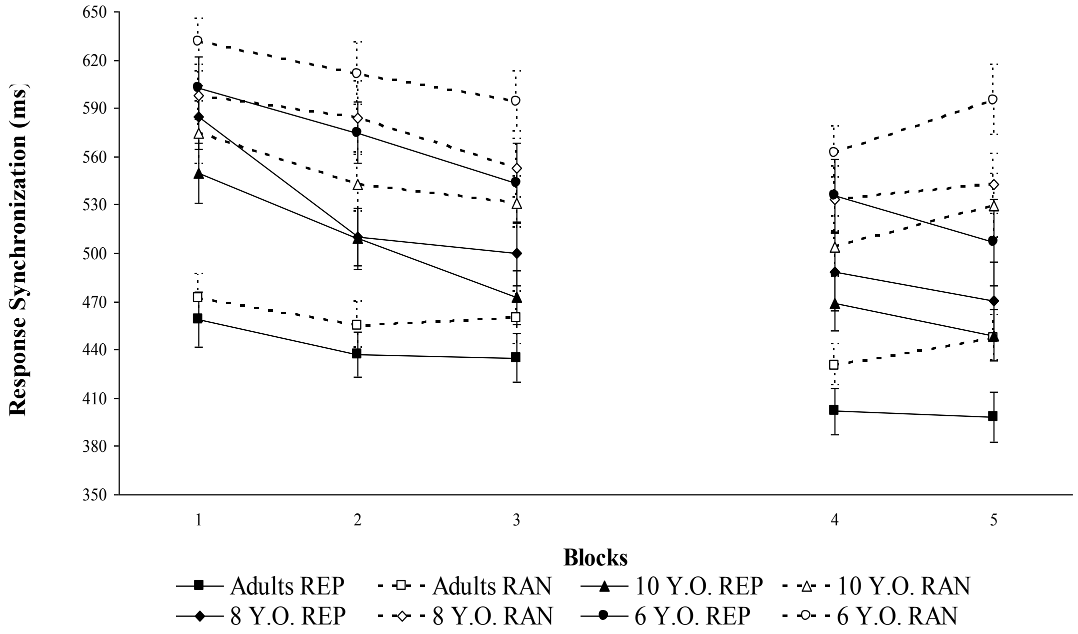

Figure 4. Average response synchronization data for all groups across five blocks of practice for matched REP (four trials per block) and RAN sequences (four trials per block).

When comparing group performance, on the REP and RAN sequences, across the last block of practice on Day 1 and the first block on Day 2 for percent correct (Fig 3), a significant main effect of Sequence Type F (1, 49) = 8.991, $p = .004$ was found, such that the REP sequence was performed more accurately than the RAN sequences (M REP = 85.2%, M RAN = 82.3%). There was also a significant main effect of Block F (1, 49) = 12.39, $p = .001$, indicating overall consolidation. As predicted, there was a significant main effect of Group F (3, 49) = 31.309, $p < .001$. Post hoc planned comparisons revealed that 6-year-olds made significantly more errors than all groups ($p < .001$), and 8-year-olds, but not 10-year-olds, were significantly less accurate than Adults ($p < .001$, $p = .426$, respectively). Lastly, there was a significant Block X Group interaction F (3, 49) = 4.129, $p = .011$. Post hoc planned comparisons revealed that only 8-year-olds and 6-year-olds showed significant improvements in performance between the two blocks ($p \leq .002$). No significant Sequence Type X Block, Sequence Type X Group, and Sequence Type X Block X Group interactions were observed ($p \geq .137$).

For response synchronization (Fig 4), overall performance on the REP sequence was more synchronous than on the RAN sequences F (1, 49) = 66.089, $p < .001$ (M REP = 480.713 ms, M RAN = 520.997 ms). Furthermore, there were significant improvements in response synchronization across the two blocks of practice F (1, 49) = 22.769, $p < .001$, indicating overall consolidation. Lastly, there was a significant main effect of Group F (3, 49) = 11.028, $p < .001$, where planned comparisons showed that Adults were significantly more synchronous than all Child groups ($p \leq .05$). Moreover, 10-year-olds significantly differed from 6-year-olds ($p = .051$). No significant interactions were noted ($p \geq .346$).

REP vs. RAN: Day 2

When comparing group accuracy, on the REP and RAN sequences, across the two blocks of practice on Day 2 (Fig 3), there was a significant main effect of Sequence Type F (1, 49) = 32.667, *p* < .001, such that overall the REP sequence was performed more accurately than the RAN ones (*M* REP = 88.8%, *M* RAN = 83.3%). There was also a significant Sequence Type X Block interaction F (1, 49) = 13.703, *p* = .001. Post hoc analyses comparing performance on each sequence type across the two blocks indicated significant improvements on the REP sequence (*p* = .002), but marginally significant decrements on the RAN sequences (*p* = .059). As expected, there was a significant main effect of Group F (3, 49) = 18.357, p < .001, such that 6-year-olds were significantly less accurate than all groups (p ≤ .004) and 8-year-olds were significantly less accurate than Adults (*p* = .013). Finally, there was a significant Sequence Type X Group interaction F (3, 49) = 5.519, *p* = .002, such that only the 6-year-old and 8-year-old groups showed sequence-specific learning (*p* ≤ .023). No other significant interactions were found.

For response synchronization (Fig 4), there was a significant main effect of Sequence Type F (1, 49) = 111.082, *p* < .001, such that the REP sequence was more synchronously performed than the RAN sequences (*M* REP = 464.952 ms, *M* RAN = 518.088 ms). Moreover, there was a significant Sequence Type X Block interaction F (1, 49) = 24.6, p < .001. Post hoc analyses revealed significant improvements on the REP sequence, but significant decrements in performance on the RAN sequences (*p* < .001). No other interactions were observed (*p* > .231). There was also a significant main effect of Group F (3, 49) = 10.552, *p* < .001, such that Adults were significantly more synchronous than all Child groups (*p* ≤ .036), but the Child groups did not differ from each other ($p \geq .093$). No other significant interactions were found.

REP: Day 1

Having established that sequence-specific learning occurred for the task, we took advantage of the added power of additional trials by comparing performance across groups for the REP sequences only. The results of these analyses largely confirmed the results comparing performance on the REP and RAN sequences, such that overall, there was a developmental progression in motor sequence learning within and across blocks of practice, and there was a differential pattern of results for percent correct and response synchronization.

For percent correct, across the three blocks of practice on Day 1 (Fig 5), there was a significant main effect of Block F (2, 92.58) = 43.336, $p < .001$, such that overall there were significant improvements in performance across all blocks ($p \leq .046$). Furthermore, there was a significant main effect of Group F (3, 49) = 42.963, $p < .001$. Post hoc analyses revealed that only the Adult and 10-year-old groups did not significantly differ ($p = .181$), indicating that by Day 1, 10-year-olds reached Adult level of performance on this measure. Finally, there was a significant Block X Group interaction F (6, 92.58) = 7.221, $p < .001$, such that only 8-year-olds and 6-year-olds showed significant improvements across blocks of practice ($p \leq .058$).

For response synchronization (Fig 6), there was a significant main effect of Block F (1.81, 88.67) = 56.173, $p < .001$, such that overall there were significant improvements in performance across all blocks ($p \leq .009$). Moreover, there was a significant main effect of Group F (3, 49) = 11.562, $p < .001$, such that Adults were significantly faster than all Child groups ($p \leq .011$). Lastly, there was a significant Block

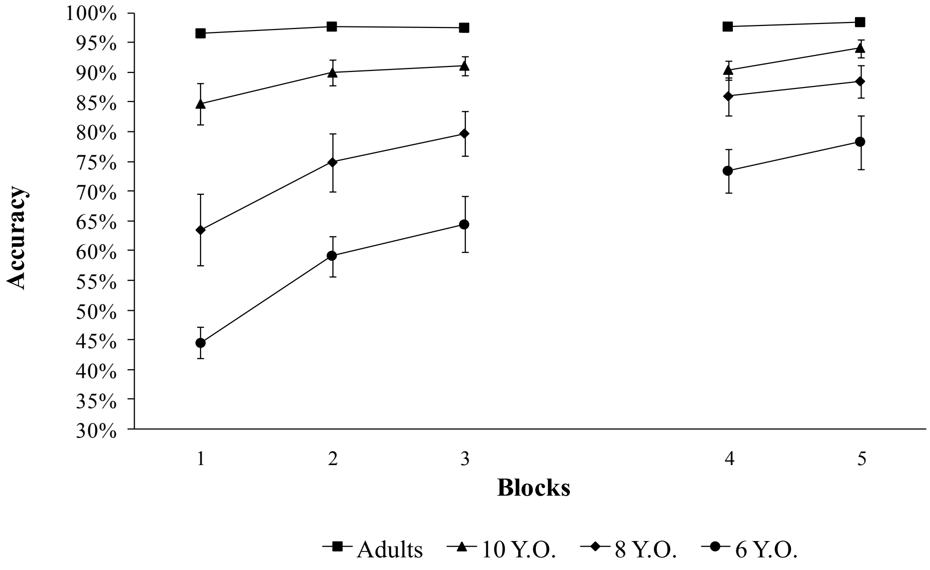

Figure 5. Average accuracy data for all groups across five blocks of practice for all REP trials (14 trials per block).

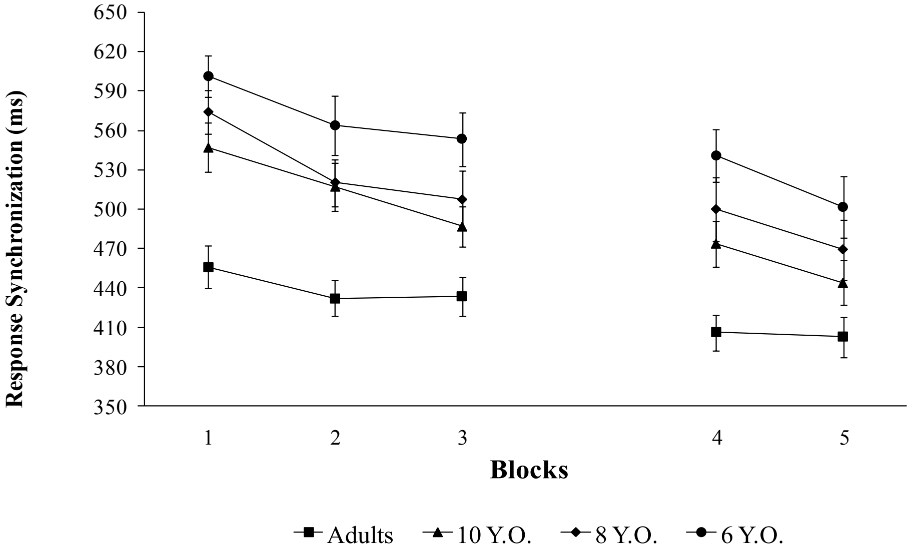

Figure 6. Average response synchronization data for all groups across five blocks of practice for all REP trials (14 trials per block).

X Group interaction F (5.43, 88.67) = 2.689, $p = .023$. Post hoc analyses revealed that Adults reached ceiling in performance by Block 2, 10-year-olds showed significant improvements across all blocks ($p \leq .007$), and 8-year-olds and 6-year-olds showed significant improvements between Block 1 and Blocks 2 and 3 ($p \leq .001$), but not between Blocks 2 and 3 ($p \geq .440$).

REP: Consolidation

When comparing percent correct between the groups across the last block of practice on Day 1 and the first block on Day 2 (Fig 5), results indicated overall consolidation F (1, 49) = 15.445, $p < .001$. There was also a significant main effect of Group F (3, 49) = 24.135, $p < .001$, such that 6-year-olds made significantly more errors than all groups ($p \leq .003$), and 8-year-olds made significantly more errors than Adults ($p = .001$). Finally, there was a significant Block X Group interaction F (3, 49) = 6.647, $p = .001$, with post hoc comparisons indicating that only 8-year-olds and 6-year-olds showed significant improvements across the two blocks ($p \leq .002$), suggesting that Adults and 10-year-olds reached ceiling in performance on this measure.

For response synchronization (Fig 6), a similar pattern of results emerged, such that overall there were significant improvements across the two blocks of practice F (1, 49) = 8.126, $p = .006$. A significant main effect of Group F (3, 49) = 9.473, $p < .001$, revealed that Adults were significantly faster than the two youngest Child groups ($p \leq .009$), and 10-year-olds were marginally faster than the 6-year-olds ($p = .068$) but not the 8-year-olds ($p = 1.00$), indicating that by Day 2, 8-year-olds reached 10-year-olds' level of performance. No significant Block X Group interaction was observed ($p = .275$).

REP: Day 2

When comparing percent correct between the groups across the two blocks of practice on Day 2 (Fig 5), there was a significant main effect of Block F (1, 49) = 13.431, *p* = .001, indicating improvements in performance across blocks. Moreover, there was a significant main effect of Group F (3, 49) = 15.78, *p* < .001, such that 6-year-olds were significantly less accurate than all other groups (*p* ≤ .014), and 8-year-olds were significantly less accurate than Adults (*p* = .014) but not 10-year-olds (*p* = .945), indicating that by Day 2, 8-year-olds reached 10-year-olds' level of performance. No significant Block X Group interaction was observed (*p* = .275).

For response synchronization (Fig 6), there was a significant main effect of Block F (1, 49) = 42.495, *p* < .001, revealing significant improvements across the two blocks of practice. Moreover, there was a significant main effect of Group F (3, 49) = 7.156, *p* < .001, such that only the Adults were significantly faster than the two youngest Child groups (*p* < .024). Lastly, there was a significant Block X Group interaction F (3, 49) = 4.444, *p* = .008, with post hoc analyses indicating that all Child groups showed continued improvements across the two blocks of practice (*p* < .001).

Comparison of the rate of change between accuracy and response synchronization

Given the differential pattern of results found for accuracy and response synchronization, an additional analysis was performed to quantify and compare the absolute rate of change between the first and last blocks of practice, relative to the first block of practice, for both behavioural measures (Fig 7). To do this, the slope for each measure was calculated and normalized to the first block of practice. This allowed us to compare the two measures to each other using a repeated measures ANOVA (Greenhouse-Geiser correction), with Group as the between-subject factor and Measure

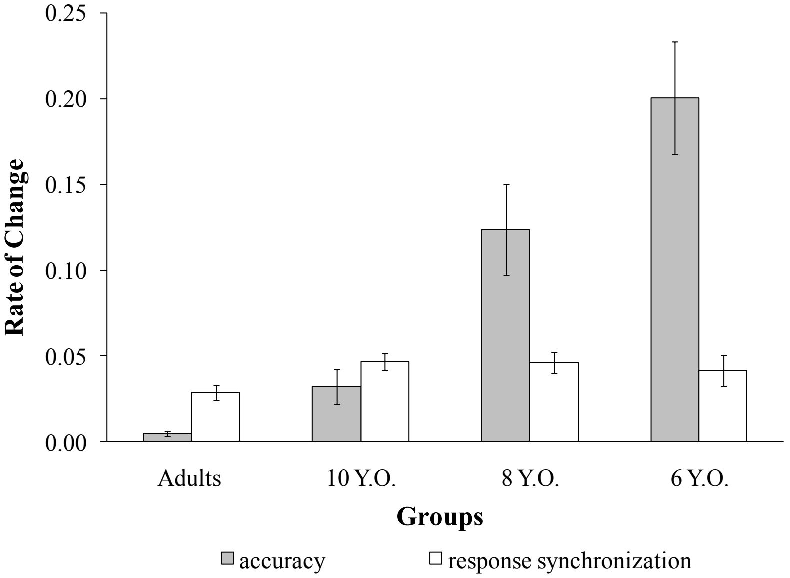

Figure 7. Comparison of rate of change between the first and last blocks of practice, relative to the first block of practice, for accuracy and response synchronization for all groups.

as the within-subject factors. Significant main effects and interactions were analyzed using pairwise comparisons, with Bonferroni adjustment for multiple comparisons. Results indicated that there was a significant Measure X Group interaction F (3, 49) = 14.394, $p < .001$. Post hoc comparisons looking at group differences for each measure revealed that for percent correct, the rate of change was similar for Adults and 10-year-olds, and these two groups differed from the two youngest groups ($p < .027$) who did not differ from each other ($p > .05$). When comparing both measures for each group, we found that there were no significant differences in the rate of change for percent correct and response synchronization, for the two oldest groups, likely driven by a ceiling effect. However, we found that the two youngest groups showed significant differences in the rate of change for the two measures, such that the rate of change was greater for percent correct than response synchronization ($p < .05$).

Recognition and Recall Tests

In order to compare the number of participants who correctly identified the REP sequence on the Recognition test, a Chi-square analysis was employed. For the Recall test, a one-way ANOVA was used to compare the mean percentage of correct key presses between the groups. Surprisingly, despite consistent significant group differences across blocks of practice for both percent correct and response synchronization, there were no significant group differences for either the Recognition (Fig 8) or Recall tests (Fig 9; $p > .05$).

Correlations with Neuropsychological Measures

To assess the association between an overall measure of performance on the MFST (using an average of all REP trials, across the five blocks of practice, for percent

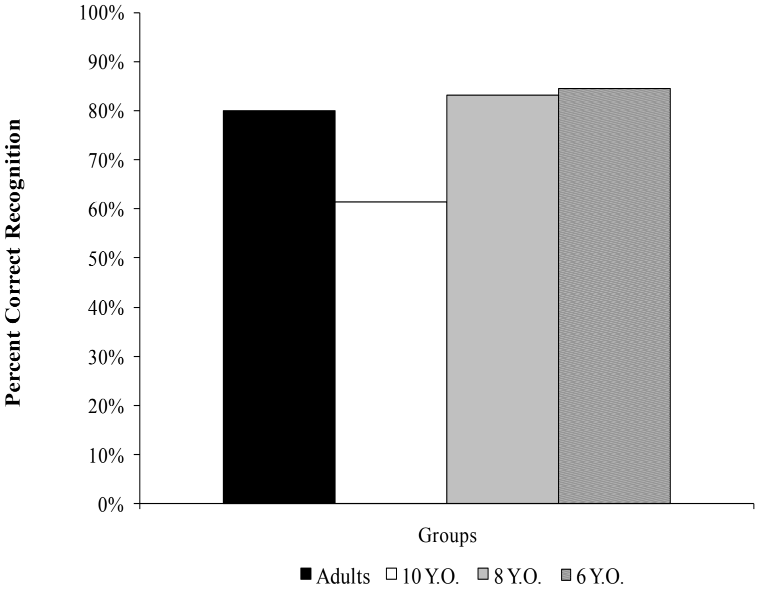

Figure 8. Recognition data for 6-year-olds, 8-year-olds, 10-year-olds, and Adults. Recognition data are the percent of participants who correctly identified the REP sequence from a three alternative forced choice.

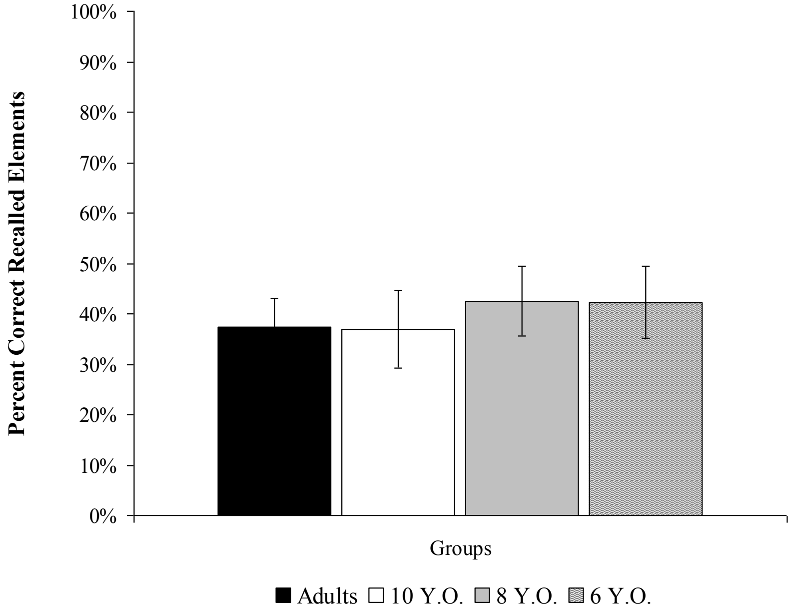

Figure 9. Recall data for 6-year-olds, 8-year-olds, 10-year-olds, and Adults. Recall data show the average percent of correctly produced key-presses from the first 10 responses on the explicit recall test.

correct) and neuropsychological measures administered, two-tailed Pearson correlations were performed by group. Overall, no significant correlations were found between overall performance on the MFST and the Vocabulary and Digit Span subtests of the Wechsler Intelligence Scales ($p > .05$). Additionally, no significant correlations were found between overall performance on the MFST and absolute span (as calculated based on the maximum number of correctly recalled numbers on the Digit Forward subtest of the Wechsler Intelligence Scales) and d' (a sensitivity index of CPT performance, computed on the basis of the ability to discriminate between target and false alarm stimuli; $p > .05$).

Discussion

The main goal of the current experiment was to examine developmental differences in motor sequence learning, across two days of practice, in three cross-sectional samples of children, aged 6, 8, and 10 years, and a control sample of adults. Overall, our results showed a developmental progression in motor sequence learning within and across days of practice. Interestingly, the two behavioural measures, accuracy and response synchronization, showed different developmental trajectories. For percent correct, which measures explicit stimulus-response association, differences were greatest for the two youngest groups early in learning, and these groups also showed the greatest rate of improvement across all blocks of practice. By the end of Day 2, only the six year-olds still lagged behind all other groups. For response synchronization, which measures implicit sensorimotor integration and timing, all child groups differed from adults early in learning, but both child and adult groups showed similar rates of improvement across blocks of practice. By the end of Day 2, 10 year-olds reached adult levels of performance, whereas 6 and 8 year-olds did not. We postulate that this differential pattern of results is consistent with the idea that brain systems required for stimulus response association develop earlier than those involved in fine-grained sensorimotor integration and timing. Despite developmental differences across blocks of practice on both behavioural measures, there were no significant group differences for either the Recognition or Recall tests. We suggest that explicit knowledge of the MFST is not directly linked to task performance, thus challenging the implicit-explicit distinction in pediatric SRT studies assessing the developmental invariance model (Meulemans et al., 1998; Thomas et al., 2004; Thomas & Nelson, 2001).

The first goal of this study was to assess developmental differences in motor sequence learning within and across days of practice. In contrast to the abundant literature on the progression of motor sequence learning in adults, to our knowledge, only one child study to date has looked at motor sequence learning within the context of multiple days of practice (Dorfberger et al., 2007). In that study, the authors compared performance on a finger-to-thumb opposition sequence task in 9, 12, and 17-year-olds, within an initial training session as well as following 24-hours, 48-hours, and 6-weeks post-training intervals. Overall, results indicated that all age groups showed significant within- and across-session improvements in performance. The rate of learning did not differ among the groups and was similar to that reported for adults. Moreover, gains were observed in both speed and accuracy. In the present study, we used a somewhat similar design but our groups were comprised of younger children. We specifically chose to examine cross-sectional samples of school-aged children, between the ages of 6 and 10 years, as this age range parallels the most significant changes in brain regions related to motor learning (Barnea-Goraly et al., 2005; Gogtay et al., 2004; Mackie et al., 2007; Paus et al., 1999; Sowell et al., 1999; Sowell et al., 2004; Wilke et al., 2007). Thus, we hypothesized that there would be a developmental progression in sequence learning both within and across days of practice. In line with our hypothesis, overall we found that the degree and rate of learning was greatest for the two youngest groups. Accordingly, distribution of practice, over two days appeared to benefit most 6 and 8-year-olds, who showed both significant within-day gains and consolidation (as evidenced by "off-line" improvements between the last block of practice on Day 1 and the first block on Day 2). Surprisingly, 10-year-olds performed more similarly to Adults than to the other child groups, suggesting an incremental change in motor performance and control likely related to more mature motor pathways.

Contrary to Dorfberger et al. (2007), we found a differential pattern of results for the two behavioural measures of learning. For accuracy, 10-year-olds reached Adults' level of performance by the end of Day 1, demonstrating early ceiling on this measure. The two youngest groups showed improvements within Day 1 and across Days 1 and 2, but 8-year-olds reached 10-year-olds' level of performance by Day 2, whereas 6-year-olds continued to show significant gains in accuracy on Day 2. For response synchronization, all groups continued to show significant improvements in performance within and across Days 1 and 2. Moreover, additional analyses comparing the rate of change between the two behavioural measures confirmed that learning on the more global measure (i.e. percent correct) showed relatively rapid changes, particularly for the two youngest groups, whereas learning on the more procedural measure (i.e. response synchronization) showed slower changes that did not differ across groups. Thus, we hypothesize that the greater rate of change observed for the accuracy measure, particularly for the 6 and 8 year-olds, likely reflects rapid learning of the explicit stimulus-response association. In other words, we postulate that accuracy, a more global component of the task, represents a measure of finger-stimulus mapping, and/or finger individuation and is more sensitive to rapid changes in younger children. In contrast, we hypothesize that synchronization is a more difficult parameter of motor control to learn and maintain, as it requires ongoing practice and relies heavily on sensorimotor integration and timing. Previous studies have proposed that different parameters of a motor sequence are likely to be acquired in separate but interacting systems (Hikosaka et al., 1999; Hikosaka et al., 2002; Savion-Lemieux & Penhune, 2005).

In the present study, the developmental differences found for the two parameters of sequence learning are consistent with age-related changes in motor ability and the extended maturational timeline of motor pathways in the brain. Findings from recent structural neuroimaging studies have demonstrated age and region-specific changes in grey and white matter densities, with primary sensory and motor regions developing earlier, and frontal and temporal-parietal association areas later (Gogtay et al., 2004; Paus et al., 2001; Paus et al., 1999; Sowell et al., 2004; Wilke et al., 2007). In particular, these studies show that global grey matter volume increases up until the age of approximately 6-10 and then decreases thereafter (Gogtay et al., 2004; Sowell et al., 2004; Wilke et al., 2007). This decrease in grey matter is mirrored by and is partially the result of concurrent global increases in white matter. More specifically, studies have shown increases in the white matter concentration of the cortico-spinal system between childhood and late adolescence (Barnea-Goraly et al., 2005; Paus et al., 1999; Wilke et al., 2007). It has been hypothesized that these increases may underlie decreases in nerve conduction time that are observed with development, and might be related to behavioural phenomena such as decreasing reaction times and increasing motor control associated with the improvement of fine motor skills across early childhood (Garvey et al., 2003). In addition to changes in cortical motor pathways, structural imaging studies have also shown changes in the white-matter pathways of the striatum and in the total volume of the cerebellum that continue into late adolescence (Barnea-Goraly et al., 2005; Mackie et al., 2007; Sowell et al., 1999). Taken together, the dissociation observed between our two behavioural measures of sequence learning is consistent with the hypothesis that accuracy or finger-stimulus association may rely predominantly on cortical maturation that occurs between ages 6 and 10; whereas motor timing and sensorimotor integration may rely on the maturation of white matter pathways that continue to develop into young adulthood.

Notably, our study involved coordination of four fingers of the right hand, similar to playing a sequence on the piano. An interesting observation made while testing the younger participants is that when asked to move one finger in response to the visual stimulus, at times, they appeared to produce simultaneous motion in neighbouring fingers. The younger child groups also required more familiarization trials before beginning the task, in order to learn the association between their fingers and the stimulus locations. Previous studies have shown that involuntary movements and poor performance of hand movements are normal features in young children (Denckla, 1973; Garvey et al., 2003; Wolff, Gunnoe, & Cohen, 1993). For example, a recent study that examined the cortical correlates of neuromotor development in healthy children has shown that as children got older (i.e. 10 years old), their finger speeds got faster and they exhibited fewer mirror movements (Garvey et al., 2003), indicating better motor control. It was suggested that this developmental change in motor control parallels the maturational changes observed in the motor cortex and the cortico-spinal tract. Surprisingly, to our knowledge, there are numerous studies on fine motor control abilities in adults, such as determining the nature of interdependency between fingers during force production tasks (Hager-Ross & Schieber, 2000; Lang & Schieber, 2004; Reilly & Hammond, 2000, 2006; Slobounov, Chiang, Johnston, & Ray, 2002), but relatively little is known about developmental changes in these fine motor control abilities in children. Thus, future studies could explore this phenomenon in children in order to better understand the relationship between motor performance and motor control across development.

In the current study, we chose to employ the same task for all groups, in order to compare group differences across a common paradigm. Given that we observed continued improvements on the response synchronization measure; that there were no significant correlations between our neuropsychological measures and performance on the task; and that no group differences were found on the Recognition and Recall tests, we can conclude that the task was appropriate for all ages. However, there were ceiling effects for the accuracy measure in Adults and 10-year-olds. Thus, it is not clear if the different rates of learning on both behavioural measures would be more similar if all groups started at the same level of performance. We are currently collecting data for a new study comparing motor sequence learning in children and adults using the same paradigm, but in which the speed of the task will be individually adjusted in order for all participants to begin testing at similar levels of accuracy.

One of the most predominant themes in the developmental literature on motor sequence learning revolves around Reber's developmental invariance model, which postulates that implicit learning is invariant across childhood, given its reliance on ontogenically older brain areas such as the basal ganglia and cerebellum (1993). For instance, Meulemans et al. (1998) assessed implicit learning of the SRT in 6 and 10 year olds, as well as adults and found that children and adults showed similar sequence-specific learning levels (i.e., larger discrepancy in reaction times between performance on the repeating-sequence trials and the random-sequence trials, when comparing the first and last block of practice), thus supporting the idea that implicit learning mechanisms are present early in development. However, these findings have been challenged by more recent functional neuroimaging findings, which demonstrated parallel developments in implicit and explicit learning systems, as evidenced by both age-related and learning-related changes in neural activity (Thomas et al., 2004).

In the present study, we reported global sequence-specific learning effects (as demonstrated by significant main effects of Sequence Type across all points of comparison and for both behavioural measures). Notably, at the end of Day 2, there were significant improvements on the repeating sequence but decrements on the random sequences, providing further evidence for sequence-specific learning. We hypothesize that this dissociation in performance between the repeating and random sequences emerged primarily due to interference or negative transfer effects, as once performance of the predictable repeating sequence became more effortless, it interfered with performance of the unpredictable random sequences. In contrast, when comparing performance on the Recognition and Recall tests, at the end of Day 2, we found no evidence of age-related differences in explicit learning, as all groups performed similarly on these tests. Interestingly, it is not the case that Adults and 10 year olds, who demonstrated ceiling effects on the accuracy measure, showed enhanced explicit knowledge of the repeating sequence, indicating that the sequence was acquired largely implicitly. It appears that performance on this task is independent of the explicit knowledge of the repeating sequence, thus challenging the validity of the implicit-explicit distinction assessed in several SRT pediatric studies (Meulemans et al., 1998; Reber, 1993; Thomas et al., 2004; Thomas & Nelson, 2001). Similar findings were reported by Seger (1997), who showed that performance on two independent forms of implicit learning did not depend on explicit knowledge.

Given the lack of association between implicit learning, as measured by performance on the motor task, and explicit knowledge of the sequence, as measured by the Recall and Recognition tests, we propose a different and novel approach for assessing implicit and explicit learning. In our view, rather than considering overall performance on the task as a form of implicit learning and recall or recognition of the repeating sequence as a form of explicit learning, we propose to evaluate the implicit-explicit distinction at the behavioural measures level. Thus, we suggest that accuracy represents a measure of more explicit stimulus-response association, whereas response synchronization represents a more implicit measure of fine-grained sensorimotor integration and timing.

The last objective of the present study was to take an exploratory approach to evaluating the existence of a possible sensitive period for motor learning, based on previous findings that demonstrated that musical training before the age of seven enhanced adult motor performance (Watanabe et al., 2007). Overall, we found that 10-

year-olds reached ceiling in accuracy by the end of Day 1, whereas the two youngest child groups continued to improve across blocks; however, all child groups benefited from continued practice on the synchronization measure. This differential pattern of results provides partial support for discontinuity in performance between the ages of 8 and 10, with respect to the more explicit measure of learning, but not the more implicit measure. We hypothesize that this pattern of results is consistent with the idea that brain systems required for finger-stimulus association develop earlier (i.e. between the ages of 6 and 10 years) than those involved in fine-grained sensorimotor integration and timing which continue to develop into young adulthood.

In summary, the results of this experiment present a new way of assessing developmental changes in motor sequence learning using a modified SRT paradigm. The MFST offers a more naturalistic approach to study motor sequence learning that is similar to playing the piano or typing. Overall, our results challenge the implicit-explicit distinction in pediatric SRT studies assessing the validity of the developmental invariance model. Based on our differential pattern of results for accuracy and synchronization, we propose that implicit and explicit learning should be considered at the behavioural measures level, such that each measure represents an implicit or explicit component of sequence-learning. The finding that accuracy was poorer for two youngest child groups is consistent with the hypothesis that basic motor control of the fingers may rely predominantly on cortical maturation that occurs earlier in development. In contrast, the finding that response synchronization shows similar, ongoing changes for all groups suggests that motor timing and sensorimotor integration may rely on the maturation of white matter pathways that continue to develop into young adulthood.

Chapter 5

General Discussion

The purpose of the present dissertation was to investigate the effect of a selection of factors on fine motor sequence learning both within and across days of practice. Specifically, three studies were conducted to investigate factors related to how individuals are trained, namely contextual setting of learning (i.e. organization of practice), and factors related to individual characteristics, namely musical training and development. Ultimately, the goal of these studies was to explore ways to optimize motor sequence learning, as sequence learning is a significant part of our daily lives.

The first paper (Savion-Lemieux & Penhune, 2010) investigated the effect of three practice patterns (i.e., massed, alternating, and random) on the learning and transfer of motor sequences. The main goal of this experiment was to assess the "contextual interference" hypothesis, which suggests that when more than one skill is learned in a single session, massed patterns of practice lead to better within-day acquisition, but random patterns of practice lead to better retention and transfer. Overall, results provided only partial support for the contextual interference hypothesis: on day 1, massed practice led to enhanced sensorimotor integration and timing (as measured by response synchronization), whereas random practice led to better stimulus-response association (as measured by accuracy). On day 2, all groups showed consolidation for both measures, as well as transfer for accuracy but not response synchronization. These findings are consistent with differential encoding of specific domains of motor performance. We postulated that learning of the stimulus-response association is a fast process that benefits from random practice because it requires the acquisition of this association in multiple contexts. We further postulated that once the association is learned, it seems resistant to interference and is transferrable to a novel sequence. In contrast, learning of the sensorimotor integration and timing is a slower process that benefits from blocked practice because practice in a single context allows fine-tuning of the response.

The second paper (Watanabe, Savion-Lemieux, & Penhune, 2007) examined the effect of musical training on adult motor performance. In this experiment, we tested musicians who began training before and after the age of seven. This is the first study in the literature where the groups were matched for years of musical experience, years of formal training, and hours of current practice. The main goal of this experiment was to evaluate the existence of a putative sensitive period in motor learning, similar to that observed for language acquisition. Overall, results showed that early-trained musicians performed better than late-trained musicians, and that this performance advantage persisted after five days of practice. Performance differences were greatest for response synchronization, suggesting that early training has its greatest effect on neural systems involved in sensorimotor integration and timing. These findings supported the idea that there may be a sensitive period in childhood where enriched motor training through musical practice results in long-lasting benefits for performance later in life. These results are also consistent with the results of studies showing structural changes in motor-related regions of the brain in trained musicians that are specifically related to training early in life.

The final paper (Savion-Lemieux, Bailey, & Penhune, 2009) looked at the effect of development on motor sequence learning. In this experiment, we tested three cross sectional samples of children aged 6, 8, and 10 years, and a control sample of adults, across two consecutive days. The main goal of this experiment was to take a developmental approach to studying motor sequence learning. Furthermore, we hypothesized that if there were a sensitive period for motor learning, we would predict that children's ability to learn motor skills might change across development. Overall, findings showed a developmental progression in motor sequence learning within and across days of practice. Interestingly, the two behavioural measures showed different developmental trajectories. For accuracy, 6 and 8 year-olds performed more poorly early in learning but showed the greatest rate of improvement with practice. By the end of Day 2, only the 6 year-olds still lagged behind all other groups. For response synchronization, all child groups differed from adults early in learning, but both child and adult groups showed similar rates of improvement across blocks of practice. By the end of Day 2, 10 year-olds reached adult levels of performance, whereas 6 and 8 year-olds did not. This pattern of results suggests that accuracy or finger-stimulus association may rely on cortical pathways that show the greatest maturation between ages 6 and 10; whereas motor timing and sensorimotor integration may rely on subcortical pathways that continue to develop into young adulthood.

Together, the findings from the three papers presented in this dissertation shed light on the behavioural underpinnings of fine motor sequence learning. Importantly, this body of research offers insight into the progression of motor sequence learning both within and across days of practice. Surprisingly, very few studies to date have taken an across-day approach to the study of motor sequence learning. Moreover, results from all three experiments suggest that motor sequences are not represented as unitary components, but rather learned and encoded in different forms. This multi-faceted representation provides important implications for motor training in various domains. Finally, there is some preliminary evidence to suggest the existence of a putative sensitive period in motor learning, similar to that observed in language acquisition.

Contributions

While many studies have looked at motor learning at different stages, fewer have taken an across-day approach to examine how motor learning changes across time in the same group of participants. Overall, findings from all three papers in this dissertation support the progression of sequence learning across time, characterized by rapid within-session improvements and slower incremental improvements across days of practice. Importantly, we have shown that both adults and children show consolidation, defined as significant improvements in or maintenance of performance between the last block of practice on the initial practice session and the first block on the second session, after a period of rest of 24 hours with no additional practice. Interestingly, we (Savion-Lemieux and Penhune, 2005) and others (Baddely & Longman, 1978; (Doyon et al., 2009; Hauptmann & Karni, 2002; Ofen-Noy et al., 2003; Shea et al., 2000; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002) have shown that even minimal amounts of practice spread over time are sufficient to induce consolidation of a motor sequence. Together, these results indicate that distribution of practice, or passage of time, is essential for a maximum benefit of practice to be gained, as the time delay allows for consolidation of learning. In a recent study, Steele and Penhune (2010) presented evidence for the role of the primary motor cortex (M1) in motor sequence consolidation. Greater activity in this region during the first block of learning on day 1 predicted greater improvements between days 1 and 2. Evidence for the role of M1 in consolidation also comes from repetitive transcranial magnetic stimulation studies that have shown that stimulation of M1 soon after the initial session of practice disrupted motor sequence consolidation (Baraduc, Lang, Rothwell, & Wolpert, 2004; Hotermans, Peigneux, de Noordhout, Moonen, & Maquet, 2008; Muellbacher et al., 2002), whereas direct stimulation of M1 facilitated sequence consolidation (Reis et al., 2009). Consolidation-related processes have been linked to sleep-dependent mechanisms (e.g., Landsness et al., 2009). For instance, Sejnowski and Destexhe (2000) have shown that spindle oscillations during the early stages of slow-wave sleep are important for opening molecular gates required for synaptic plasticity (Fogel & Jacob, 2001; cited in Walker et al., 2002). Sleep spindles have also been shown to be involved in the offline consolidation of a new sequence of finger movements known to be sleep dependent (e.g., Morin et al., 2008). Taken together, it appears that optimal learning requires distribution of practice over days, and that consolidation, mediated by factors such as sleep, may reflect the most dramatic step of an ongoing process, mediated by motor cortical plasticity. Thus, the proverb “practice makes perfect” implies that repetition over time, even if minimal, yields optimal results.

While distribution of practice over time promoted fine motor sequence learning globally, a robust dissociation was found, in all three papers, between the two behavioural measures used to assess learning. In our papers, we broke down fine motor sequence learning into two different components: accuracy, a more explicit component of the task that requires the association of the visual stimulus with the motor response, and synchronization, a more procedural component that requires fine-grained sensorimotor integration and timing. Overall, our results show that these two components are learned and consolidated differently. On one hand, learning of the stimulus-response association, or finger-stimulus mapping, appeared to be a fast process, as significant improvements on the accuracy measure were often rapid and occurred within the first blocks of practice on day 1. This more explicit process seemed to require more effortful processing and attention initially; however, once the stimulus-response association was acquired, it seemed to be resistant to interference and transferrable to a novel sequence. On the other hand, learning of the sensorimotor integration and timing elements of the task appeared to be a slower and more difficult process to learn, as significant improvements on this measure persisted across days of practice. This more procedural process seemed to be under less cognitive control, be more susceptible to interference, and rely heavily on ongoing practice. Furthermore, given the differences observed on the synchronization measure between the musician groups in study 2 and the child groups in study 3, we hypothesized that synchronization may rely on brain systems that develop later.

Interestingly, the dissociation we found is in line with a model put forward by Hikosaka and colleagues (2002). In their model, the authors propose that motor sequence skills are handled as two types of sequences: one spatial and one motor. The spatial sequence requires a high level of attention, is learned quickly, can be identified by rapid improvements in accuracy, and is encoded in loops between the rostral basal ganglia, prefrontal and parietal cortices, and the lateral cerebellum. Alternatively, the motor sequence requires little attention, is learned more slowly, can be identified through improvements in speed, and is encoded between the loops in the caudal basal ganglia, motor cortex, and medial cerebellum. Similarly, Steele and Penhune (2010) found evidence for two different sets of brain networks that optimize each component of learning. According to their findings, the left primary motor cortex and right cerebellar region were positively correlated with improvements in synchronization, whereas enhancements in accuracy were correlated with increases in specific hippocampus, Brodmann, and putamen regions. Taken together, there is growing evidence to suggest that motor sequences are acquired in separate but interacting systems that are characterized by unique behavioural and neural signatures. Furthermore, our results suggest that different factors differentially influence each component of learning. This multi-faceted view provides a new window into our understanding of motor sequence learning and offers important implications for teaching sequencing skills in disciplines such as sports and musical training, as well as in physical rehabilitation.

Perhaps the most novel contribution of this dissertation pertains to the notion of a putative sensitive period in motor learning. A sensitive period is defined as “a broad term that applies whenever the effects of experience on the brain are unusually strong during a limited period in development…during which certain capacities are readily shaped or altered by experience” (Knudsen, 2004, p. 1412). In other words, a sensitive period denotes a time window when sensory experience has a greater influence on behavioural and cortical development. Alternatively, a critical period refers to a more rigid developmental window, readily influenced by genes, in which a function cannot be acquired outside it. A classic example of a critical period comes from the work of Hubel and Wiesel (1965) who demonstrated that if cats are deprived of vision to one eye during a short period after birth, they do not develop normal binocular vision, even when vision is restored to the deprived eye. They have shown that the deprivation of vision to one eye during the “critical period” after birth permanently altered the neural circuitry of the cats. Similarly, in humans, studies of congenitally deaf children who received cochlear implants after a critical window (around age 3-4) never developed normal cortical responses to auditory stimuli (see Kral & Eggermont, 2007; Sharma, Nash, & Dorman, 2009 for reviews). Until recently, most of the evidence for sensitive periods in humans was drawn from the domain of language acquisition. Classic early examples of a sensitive period came from single case studies of individuals who were chronically deprived of linguistic stimulation in early childhood and who failed to develop normal language, even after intensive exposure (Curtiss, 1977). With respect to second-language acquisition, it has been shown that individuals who are exposed to a second language before age 11-13 develop greater proficiency than those who are exposed later in life (Johnson & Newport, 1989; Weber-Fox & Neville, 2001). Our results from studies 2 and 3, combined with results from various neuroimaging studies in musical training, provide new evidence that there may be a sensitive period in childhood where enriched motor training, through musical practice, results in long-lasting benefits for motor performance later in life. First, neuroimaging studies have shown that musicians who begin training early in childhood show greater structural and functional plasticity in auditory and motor regions of the brain compared to those who start later (e.g., Elbert et al., 1995; Schlaug et al., 1995). For example, Schlaug and colleagues (1995) reported that musicians had a larger anterior corpus callosum than non-musicians did, and that those who began training before age seven showed a greater difference than those who began after age seven. More recently, professional pianists were shown to have greater density of white matter in motor pathways, and that density was relative to the number of hours they had practiced before age eleven (Bengtsson, 2005). Second, in study 2, we found that musicians who began training before age seven showed better synchronization than musicians who began training after age seven (after accounting for number of years of training and experience). Finally, in study 3, we found a developmental progression in motor sequence learning, such that 6-year-olds consistently performed more poorly than 8- and 10- year-olds, particularly on the measure of response synchronization. Together, these sets of findings suggest that enriched musical experience early in childhood, when neural systems are immature, can induce long-lasting changes in adult motor performance, particularly for sensorimotor integration and timing We hypothesize that early plasticity in sensorimotor integration may lay down highly tuned circuits that can later be further optimized by learning mechanisms that remain plastic throughout life. Thus, early training may enhance the cerebellum's ability to integrate the sensory and motor information required for learning. The notion of a sensitive period in the motor domain offers exciting applications for music training. It can certainly help explain the ingenuity behind musical masters such as Mozart and Yo-Yo Ma. Importantly, longitudinal designs, looking at ability and brain development would need to be conducted to further examine the possibility of a sensitive period in motor performance. For example, longitudinal studies of children beginning training before and after the putative sensitive period would need to be conducted. Importantly, behavioural tasks with norms for different ages will need to be developed to assess whether potential performance changes in children who begin training early differ from expected maturational changes. Moreover, longitudinal studies could also extend to other types of motor training, such as sports, to see if the sensitive period hypothesis extends to motor domains other than music.

Future directions

Though results from this dissertation are a step in the right direction, future research is required to clarify the complex interactions between the variables involved in the process of motor sequence learning. One limitation of this dissertation is that the analyses employed focused on group differences while overlooking individual differences. While individual differences in sequence learning were sometimes noted when testing participants (e.g., not all early-trained musicians performed better than late-trained musicians did), these differences were obscured by the repeated measures analyses employed. An interesting line of research for future studies would be to look at individual differences in the rate of learning between individuals by plotting individual performance curves. Such an analysis would allow for a better understanding of individual variability and its meaning. Moreover, individual differences could be used as predictors for later learning as well as predictors for structural and/or functional neural differences.

We specifically selected patterns of practice, musical training, and development as the factors of focus, but it is imperative to note that numerous other factors may have contributed to our results. For instance, genetic, personality, and environmental factors may have played a pivotal role in the differences found in study 2 between the early-trained and late-trained musicians. Perhaps early-trained musicians had a genetic predisposition for earlier development of motor skills which may have intensified their motivation to start training earlier or obtain greater benefit from practice. Moreover, children with greater intrinsic motivation, greater family support, and/or exposure to musical training in the home may be more inclined to start training at an early age. Similarly, cognitive factors may have accounted for some of the developmental differences reported in study 3. Although we did not find significant correlations between an overall measure of motor performance and a small collection of neuropsychological measures (i.e., Vocabulary and Digit Span on the Wechsler Intelligence Scales and a CPT measure), one might speculate, for example, based on the literature on executive function development (e.g., Best, Miller, & Jones, 2009; Brocki & Bohlin, 2004) that perhaps a more comprehensive battery of cognitive measures (e.g., intelligence, executive control, and memory abilities) paired with more sophisticated statistical analyses (e.g., regression and HLM) may help clarify the different developmental trajectories noted in motor learning. In sum, future research taking into account genetic, personality, environmental, and cognitive factors would further to help unravel the underpinnings of motor sequence learning.

While this dissertation focused solely on motor learning, it is important to highlight the contribution of motor control to the study of motor learning. Because it is difficult to study the motor system as a whole (Schmidt & Lee, 2005), motor learning and motor control are often studied in isolation and are treated as independent concepts. However, these two concepts are not mutually exclusive and should be more often studied in relation to each other. For example, in study 3, an interesting observation was made while testing the younger participants; when asked to move one finger in response to the visual stimulus, at times, they appeared to produce simultaneous motion in neighbouring fingers. This observation was accidental and could not be further investigated. We hypothesized that the developmental changes observed in motor control most likely parallel the maturational changes noted in the motor cortex and the cortico-spinal tract. However, surprisingly, to our knowledge, little was known about the developmental changes in fine motor control ability in children. Thus, future studies should investigate the relationship between motor control and motor learning across development. With the advent of motion-capture technology, it would be interesting to couple motor learning paradigms with real-time tracking of finger or limb movements in order to explore the relationship between motor learning and changes in movement kinematics that occur with learning. These types of experimental designs could be extended to studying individuals across the lifespan (to look at the relationship between age, learning, and motor control), as well as clinical populations with motor impairments such as patients with stroke, children with global developmental delays, Attention Deficit Hyperactivity Disorder, or cerebral palsy, and adults with Parkinson’s disease, Huntington’s disease, or damage to the cerebellum or frontal areas.

Taken together, results from this dissertation offer important new information on the effect of practice pattern, musical training, and development on fine motor sequence learning. Overall, we found that optimal learning requires distribution of practice over time, that synchronization is a more difficult parameter to learn and maintain, and that there may be a putative sensitive period for motor learning, similar to that observed for language acquisition. Ultimately, understanding motor learning at the behavioural level helps to elucidate the bidirectional relationship between motor skill learning and brain plasticity, and facilitates the design of neuropsychological studies based on behavioural outcomes. Future investigations should thus focus on elucidating the neural basis of fine motor sequence learning. Finally, unraveling the behavioural and neural underpinnings of motor sequence learning would offer exciting applications in areas such as music, sport, and industry, as well as in clinical practice (e.g., the rehabilitation of skills after injury or stroke).

References

Badan, M., Hauert, C.-A., & Mounoud, P. (2000). Sequential pointing in children and adults. *Journal of Experimental Child Psychology, 75*, 43-69.

Baddeley, A., & Longman, D. (1978). The influence of length and frequency of training session on the rate of learning to type. *Ergonomics, 21*(8), 627-635.

Baharloo, S., Johnston, P., Service, S., Gitschier, J., & Freimer, N. (1998). Absolute pitch: An approach for identification of genetic and nongenetic components. *American Journal of Human Genetics, 62*, 224-231.

Baraduc, P., Lang, N., Rothwell, J. C., & Wolpert, D. M. (2004). Consolidation of Dynamic Motor Learning Is Not Disrupted by rTMS of Primary Motor Cortex. *Current Biology, 14*(3), 252-256.

Barnea-Goraly, N., Menon, V., Eckert, M., Tamm, L., Bammer, R., Karchemskiy et al. (2005). White matter development during childhood and adolescence: A cross-sectional diffusion tensor imaging study. *Cerebral Cortex, 15*, 1848-1854.

Battig, W. (1966). Facilitation and Interference. In E. Bilodeau (Ed.), *Acquisition of skill* (pp. 215-244). New York: Academic Press.

Battig, W. (1972). Intratask interference as a source of facilitation in transfer and retention. In R. Thompson & J. Voss (Eds.), *Topics in learning and performance* (pp. 131-159). New York: Academic Press.

Beitel, R., Schreiner, C., Cheung, S., Wang, X., & Merzenich, M. (2003). Reward-dependent plasticity in the primary auditory cortex of adult monkeys trained to discriminate temporally modulated signals. *Proceedings of the National Academy of Sciences of the USA, 100*(19), 11070-11075.

Bengtsson, S., Nagy, Z., Skare, S., Forsman, L., Forssberg, H., & Ullén, F. (2005). Extensive piano practicing has regionally specific effects on white matter development. *Nature Neuroscience, 8*(9), 1148-1150.

Best, J. R., Miller, P. H., & Jones, L. L. (2009). Executive Functions after Age 5: Changes and Correlates. *Dev Rev, 29*(3), 180-200.

Bower, J. (1995). The cerebellum as a sensory acquisition controller. *Human Brain Mapping, 2*, 255-256.

Brady, F. (2004). Contextual interference: A meta-analytic study. *Perceptual and Motor Skills, 99*, 116-126.

Brady, F. (2008). The contextual interference effect and sport skills. *Perceptual and Motor Skills, 106*(2), 461-472.

Brainard, M., & Knudsen, E. (1998). Sensitive periods for visual calibration of the auditory space map in the barn owl optic tectum. *Journal of Neuroscience, 18*(10), 3929-2942.

Brashers Krug, T., Shadmehr, R., & Bizzi, E. (1996). Consolidation in human motor memory. *Nature, 382*(6588), 252-255.

Brocki, K. C., & Bohlin, G. (2004). Executive functions in children aged 6 to 13: a dimensional and developmental study. *Developmental Neuropsychology, 26*(2), 571-593.

Casey, B., Giedd, J., & Thomas, K. (2000). Structural and functional brain development and its relation to cognitive development. *Biological Psychology, 54*, 241-257.

Contreras-Vidal, J., Bo, J., Boudreau, J., & Clark, J. (2005). Development of visuomotor respresentations for hand movement in young children. *Experimental Brain Research, 162*(2), 155-164.

Costa-Giomi, E., Gilmour, R., Siddell, J., & Lefebvre, E. (2001). Absolute pitch, early musical instruction and spatial abilities. *Annals of the New York Academy of Sciences, 930*, 394-396.

Criscimangna-Hemminger, S., & Shadmehr, R. (2008). Consolidation patterns of human motor memory. *Journal of Neuroscience, 28*(39), 9610-9618.

Cross, E., Schmitt, P., & Grafton, S. (2007). Neural substrates of contextual interference during motor learning support a model of active preparation. *Journal of Cognitive Neuroscience, 19*(11), 1854-1871.

Crovitz, H., & Zener, K. (1962). A test for assessing hand and eye dominance. *American Journal of Psychology, 75*, 271-276.

Curtiss, S. (1977). *Genie: A Psycholinguistic Study of a Modern-day Wild Child*. New York: Academic Press.

De Guise, E., & Lassonde, M. (2001). Callosal contributions to procedural learning in children. *Developmental Neuropsychology, 19*(3), 253-272.

Denckla, M. (1973). Development of speed in repetitive and successive finger-movements in normal children. *Developmental Medicine and Child Neurology, 15*(5), 635-645.

Dorfberger, S., Adi-Japha, E., & Karni, A. (2007). Reduced susceptibility to interference in the consolidation of motor memory before adolescence. *Public Library of Science One, 2*(2), e240.

Doyon, J., & Benali, H. (2005). Reorganization and plasticity in the adult human brain during learning of motor skills. *Current Opinion in Neurobiology, 15*, 161-167.

Doyon, J., Korman, M., Morin, A., Dostie, V., Hadj Tahar, A., Benali, H. et al. (2009). Contribution of night and day sleep vs. simple passage of time to the consolidation of motor sequence and visuomotor adaptation learning. *Exp Brain Res, 195*(1), 15-26.

Doyon, J., Penhune, V., & Ungerleider, L. (2003). Distinct contributions of the cortico-striatal and cortico-cerebellar systems to motor skill learning. *Neuropsychologia, 41*(3), 252-262.

Doyon, J., Song, A., Karni, A., Lalonde, F., Adams, M., & Ungerleider, L. (2002). Experience-dependent changes in cerebellar contributions to motor sequence learning. *Proceedings of the National Academy of Sciences of the USA, 99*(2), 1017-1022.

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.

Ferrel, C., Bard, C., & Fleury, M. (2001). Coordination in childhood: modifications of viuomotor representations in 6- to 11-year-old children. *Experimental Brain Research, 138*(3), 313-321.

Fischer, S., Hallschmid, M., Elsner, A. L., & Born, J. (2002). Sleep forms memory for finger skills. *Proceedings of the National Academy of Sciences of the USA, 99*(18), 11987-11991.

Fischer, S., Nitschke, M., Melchert, U., Erdmann, C., & Born, J. (2005). Motor memory consolidation in sleep shapes more effective neuronal representations. *Journal of Neuroscience, 25*(49), 11248-11255.

Floyer-Lea, A., & Matthews, P. (2005). Distinguishable brain activation networks for short- and long-term motor skill learning. *Journal of Neurophysiology, 94*, 512-518.

Fogel, S., & Jacob, J. S., C (2001). Increased sleep spindle activity following simple motor procedural learning in humans. *Actas de Fisiolgia, 7*, 123.

Gao, J., Parsons, L., Bower, J., Xiong, J., & Fox, P. (1996). Cerebellum implicated in sensory acquisition and discrimination rather than motor control. *Science, 272*, 545-547.

Garcia, J., Moreno, F., Reina, R., Menayo, R., & Fuentes, J. (2008). Analysis of effects of distribution of practice in learning and retention of a continuous and a discrete skill presented on a computer. *Perceptual and Motor Skills, 107*(1), 261-272.

Garvey, M., Ziemann, U., Bartko, J., Denckla, M., Barker, C., & Wassermann, E. (2003). Cortical correlates of neuromotor development in healthy children. *Clinical Neurophysiology, 114*, 1662-1670.

Gaser, C., & Schlaug, G. (2003). Brain structure differences between musicians and non-musicians. *Journal of Neuroscience, 23*(27), 9240-9245.

Ghilardi, M., Moisello, C., Silvestri, G., Ghez, C., & Krakauer, J. (2009). Learning of a sequential motor skill comprises explicit and implicit components that consolidate differently. *Journal of Neurophysiology, 101*(5), 2218-2229.

Giedd, J., Blumenthal, J., Jeffries, N., Castellanos, F., Liu, H., Zijdenbos, A. et al. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neuroscience, 2*, 861-863.

Gogtay, N., Giedd, J., Lusk, L., Hayashi, K., Greenstein, D., Vaituzis, A. et al. (2004). Dynamic mapping of human cortical development during childhood and through early adulthood. *Proceedings of the National Academy of Sciences of the USA, 101*(21), 8174-8179.

Hager-Ross, C., & Schieber, M. (2000). Quantifying the independence of human finger movements: Comparisons of digits, hands and movement frequencies. *Journal of Neuroscience, 20*(22), 8542-8550.

Hauptmann, B., & Karni, A. (2002). From primed to learn: The saturation of repetition priming and the induction of long-term memory. *Cognitive Brain Research, 13*, 313-322.

Hikosaka, O., Nakahara, H., Rand, M., Sakai, K., Lu, X., Nakamura, K. et al. (1999). Parallel neural networks for learning sequential procedures. *Trends in Neurosciences, 22*(10), 464-471.

Hikosaka, O., Nakamura, H., Sakai, K., & Nakahara, H. (2002). Central mechanisms of motor skill learning. *Current Opinion in Neurobiology, 12*(2), 217-222.

Hotermans, C., Peigneux, P., de Noordhout, A. M., Moonen, G., & Maquet, P. (2008). Repetitive transcranial magnetic stimulation over the primary motor cortex disrupts early boost but not delayed gains in performance in motor sequence learning. *European Journal of Neuroscience, 28*(6), 1216-1221.

Hubel, D., & Wiesel, T. (1965). Binocular interaction in striate cortex of kittens reared with artificial squint. *Journal of Neurophysiology, 28*, 1041-1059.

Hutchinson, S., Kobayashi, M., Horkan, C., Pascual-Leone, A., Alexander, M., & Schlaug, G. (2002). Age-related differences in movement representation. *NeuroImage, 17*, 1720-1728.

Huttenlocher, P., & Dabholkar, A. (1997). Regional differences in synaptogenesis in human cerebral cortex. *Journal of Comparative Neurology, 387*, 167-178.

Ivry, R., Spencer, R., Zelaznik, H., & Diedrichsen, J. (2003). The cerebellum and event timing. *Annals of the New York Academy of Sciences, 978*, 302-317.

Johnson, J., & Newport, E. (1989). Critical period effects in second language learning: The influence of maturational state on the acquisition of English as a second language. *Cognitive Psychology, 21*(1), 60-99.

Karni, A. (1996). The acquisition of perceptual and motor skills: A memory system in the adult human cortex. *Brain Research, 5*, 39-48.

Karni, A., Meyer, G., Jezzard, P., Adams, M., Turner, R., & Ungerleider, L. (1995). Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature, 377*, 155-158.

Karni, A., Meyer, G., Rey-Hipolito, C., Jezzard, P., Adams, M., Tuner, R. et al. (1998). The acquisition of skilled motor performance: Fast and slow experience-driven changes in primary motor cortex. *Proceedings of the National Academy of Sciences of the USA, 95*, 861-868.

Keller, G., Li, Y., Weiss, L., & Relyea, G. (2006). Contextual interference effect on acquisition and retention of pistol-shooting skills. *Perceptual and Motor Skills, 103*(1), 241-252.

Kleim, J., Hogg, T., VandenBerg, P., Cooper, N., Bruneau, R., & Remple, M. (2004). Cortical synaptogenesis and motor map reorganziation occur during late, but not early, phase of motor skill learning. *Journal of Neuroscience, 24*(3), 628-633.

Kleim, J. A., Freeman, J. H., Jr., Bruneau, R., Nolan, B. C., Cooper, N. R., Zook, A. et al. (2002). Synapse formation is associated with memory storage in the cerebellum. *Proceedings of the National Academy of Sciences of the USA, 99*(20), 13228-13231.

Knudsen, E. (2004). Sensitive periods in the development of the brain and behavior. *Journal of Cognitive Neuroscience, 16*(8), 1412-1425.

Koeneke, S., Lutz, K., Wustenberg, T., & Jancke, L. (2004). Long-term training affects cerebellar processing in skilled keyboard players. *NeuroReport, 15*(8), 1279-1282.

Kooistra, L., Crawford, S., Dewey, D., Cantell, M., & Kaplan, B. (2005). Motor correlates of ADHD: contribution of reading disability and oppositional defiant disorder. *Journal of Learning Disabilities, 38*(3), 195-206.

Korman, M., Raz, N., Flash, T., & Karni, A. (2003a). Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance. *Proceedings of the National Academy of Sciences of the USA, 100*(21), 12492-12497.

Korman, M., Raz, N., Flash, T., & Karni, A. (2003b). Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance. *Proceedings of the National Academy of Sciences of the USA, 100*, 12492-12497.

Krakauer, J., & Shadmehr, R. (2006). Consolidation of motor memory. *Trends in Neurosciences, 29*(1), 58-64.

Kral, A., & Eggermont, J. (2007). What's to loose and what's to learn: Development under auditory deprivation, cochlear implants and limits of cortical plasticity. *Brain Research Reviews, 56*, 259-269.

Kuhtz-Buschbeck, J., Stolze, H., Johnk, K., Boczek-Funcke, A., & Illert, M. (1998). Development of prehension movements in children: a kinematic study. *Experimental Brain Research, 122*(4), 424-432.

Kurahashi, A., Leming, K., Carnahan, H., & Dubrowski, A. (2008). Effects of expertise, practice and contextual interference on adaptations to visuo-motor misalignment. *Student Health Technology and Information, 132*, 225-229.

Landsness, E. C., Crupi, D., Hulse, B. K., Peterson, M. J., Huber, R., Ansari, H. et al. (2009). Sleep-dependent improvement in visuomotor learning: a causal role for slow waves. *Sleep, 32*(10), 1273-1284.

Lang, C., & Schieber, M. (2004). Human finger independence: Limitations due to passive mechanical coupling versus active neuromuscular control. *Journal of Neurophysiology, 92*, 2802-2810.

Lee, T., & Magill, R. (1985). Can forgetting facilitate skill acquistion? In D. Goodman, R. Wilberg & I. Franks (Eds.), *Differing perspectives in motor learning, memory and control* (pp. 3-22). Amsterdam: North-Holland.

Lenneberg, E. (1967). *Biological Foundations of Language*. New York: Wiley.

Mackie, S., Shaw, P., Lenroot, R., Pierson, R., Greenstein, D., Nugent, T. et al. (2007). Cerebellar development and clinical outcome in attention deficit hyperactivity disorder. *American Journal of Psychiatry, 164*, 647-655.

Magill, R., & Hall, K. (1990). A review of the contextual interference effect in motor skill acquisition. *Human Movement Science, 9*(3-5), 241-289.

Maslovat, D., Chua, R., Lee, T., & Franks, I. (2004). Contextual interference: Single task versus multi-task learning. *Motor Control, 8*(2), 213-233.

Meulemans, T., Van der Linden, M., & Perruchet, P. (1998). Implicit sequence learning in children. *Journal of Experimental Child Psychology, 69*(3), 199-221.

Miyazaki, K., & Rakowski, A. (2002). Recognition of notated melodies by possessors and non-possessors of perfect pitch. *Perception and Psychophysics, 64*, 1337-1345.

Morin, A., Doyon, J., Dostie, V., Barakat, M., Hadj Tahar, A., Korman, M. et al. (2008). Motor sequence learning increases sleep spindles and fast frequencies in post-training sleep. *Sleep, 31*(8), 1149-1156.

Muellbacher, W., Ziemann, U., Wissel, J., Dang, N., Kofler, M., Facchini, S. et al. (2002). Early consolidation in human primary motor cortex. *Nature, 415*(6872), 640-644.

Nissen, M., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology, 19*, 1-32.

O'Driscoll, G., Depatie, L., Holahan, A., Savion-Lemieux, T., Barr, R., Jolicoeur, C. et al. (2005). Executive functions and methylphenidate response in subtypes of attention-deficit/hyperactivity disorder. *Biological Psychiatry, 57*(11), 1452-1460.

Ofen-Noy, N., Dudai, Y., & Karni, A. (2003). Skill learning in mirror reading: How repetition determines acquisition. *Cognitive Brain Research, 17*, 507-521.

Oldfield, R. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9*(1), 97-113.

Paus, T., Collins, D., Evans, A., Leonard, G., Pike, B., & Zijdenbos, A. (2001). Maturation of white matter in the human brain: A review of magnetic resonance studies. *Brain Research Bulletin, 54*(3), 255-266.

Paus, T., Zijdenbos, A., Worsley, K., & Collins, D. (1999). Structural maturation of neural pathways in children and adolescents: In vivo study. *Science, 283*(5409), 1908-1911.

Penhune, V., & Doyon, J. (2002). Dynamic cortical and subcortical networks in learning and delayed recall of timed motor sequences. *Journal of Neuroscience, 22*(4), 1397-1406.

Penhune, V., & Doyon, J. (2003). Dynamic cortical and subcortical networks involved in early learning and consolidation of timed motor sequences. *Cognitive Neuroscience Society Abs, 134*.

Penhune, V., & Doyon, J. (2005). Cerebellum and M1 interaction during early learning of timed motor sequences. *NeuroImage, 26*, 801-812.

Pitcher, T., Piek, J., & Hay, D. (2003). Fine and gross motor ability in males with ADHD. *Developmental Medicine and Child Neurology, 45*(8), 525-535.

Ragert, P., Schmidt, A., Altenmuller, E., & Dinse, H. (2004). Superior tactile performance and learning in professional pianists: Evidence for meta-plasticity in musicians. *European Journal of Neuroscience, 19*, 473-478.

Reber, A. (1993). *Implicit learning and tacit knowledge: An essay on the cognitive unconscious*. New York: Oxford University Press.

Reilly, K., & Hammond, G. (2000). Independence of force production by digits of the human hand. *Neuroscience Letters, 290*, 53-56.

Reilly, K., & Hammond, G. (2006). Intrinsic hand muscles and digit independenceon the preferred and non-preferred hands of humans. *Experimental Brain Research, 173*, 564-571.

Robertson, E., Pascual-Leone, A., & Miall, R. (2004). Current concepts in procedural consolidation. *Nature reviews: Neuroscience, 5*, 1-6.

Russell, D., & Newell, K. (2007). How persistent and general is the contextual interference effect? *Research Quarterly for Excercise and Sport, 78*(4), 318-327.

Savion-Lemieux, T., & Penhune, V. (2005). The effects of practice and delay on motor skill learning and retention. *Experimental Brain Research, 161*, 423-431.

Schlaug, G. (2001). The brain of musicians. A model for functional and structural adaptation. *Annals of the New York Academy of Sciences, 930:*, 281-299.

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

Schmidt, R., & Bjork, R. (1992). New conceptualizations of practice: Common principles in three paradigms suggest new concepts for training. *Psychological Science, 3*(4), 207-217.

Schmidt, R., & Lee, T. (2005). *Motor control and learning: A behavioral emphasis* (4th ed.). Champaign, IL: Human Kinetics.

Schneider, P., Scherg, M., Dosch, H., Specht, H., Gutschalk, A., & Rupp, A. (2002). Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. *Nature Neuroscience, 5*(7), 688-694.

Schubotz, R., Friederici, A., & von Cramon, D. (2000). Time perception and motor timing: a common cortical and subcortical basis revealed by fMRI. *NeuroImage, 11*(1), 1-12.

Seger, C. (1997). Two forms of sequential implicit learning. *Conscious Cognition, 6*(1), 108-131.

Seidler, R. (2004). Multiple motor learning experiences enhance motor adaptability. *Journal of Cognitive Neuroscience, 16*(1), 65-73.

Seidler, R., Purushotham, A., Kim, S.-G., Ugurbil, K., Willingham, D., & Ashe, J. (2005). Neural correlates of encoding and expression in implicit sequence learning. *Experimental Brain Research, 165*, 114-124.

Sekiya, H. (2006). Contextual interference in implicit and explicit motor learning. *Perceptual and Motor Skills, 103*(2), 333-343.

Sharma, A., Nash, A., & Dorman, M. (2009). Cortical development, plasticity and re-organization in children with cochlear implants. *Journal of Communication Disorders, 42*, 272-279.

Shea, C., Lai, Q., Black, C., & Park, J. (2000). Spacing practice sessions across days benefits the learning of motor skills. *Human Movement Science, 19*(5), 737-760.

Shea, C., & Zimny, S. (1988). Knowledge incorporation in motor representation. In O. Meijer & K. Roth (Eds.), *The motor-action controversy* (pp. 289-314). Amsterdam: North-Holland.

Shea, J., & Morgan, R. (1979). Contextual interference on the acquisition, retention and transfer of a motor skill. *Journal of Experimental Psychology: Human Learning and Memory, 5*, 179-187.

Shea, J., & Zimny, S. (1983). Context effects in memory and learning movement information. In R. Magill (Ed.), *Memory and control of action* (pp. 345-366). Amsterdam: North-Holland.

Slobounov, S., Chiang, H., Johnston, J., & Ray, W. (2002). Modulated cortical control of individual fingers in experienced musicians: An EEG study. *Clinical Neurophysiology, 113*, 2013-2024.

Smits-Engelsman, B., Sugden, D., & Duysens, J. (2006). Developmental trends in speed accuracy trade-off in 6-10 year-old children performing rapid reciprocal and discrete aiming movements. *Human Movement Science, 25*(1), 37-49.

Sowell, E., Thompson, P., Holmes, C., Jernigan, T., & Toga, A. (1999). *In vivo* evidence for post-adolescent brain maturation in frontal and striatal regions. *Nature Neuroscience, 2*(10), 859-861.

Sowell, E., Thompson, P., Leonard, C., Welcome, S., Kan, E., & Toga, A. (2004). Longitudinal mapping of cortical thickness and brain growth in normal children. *Journal of Neuroscience, 24*(38), 8223-8231.

Ste-Marie, D., Clark, S., Findlay, L., & Latimer, A. (2004). High levels of contextual interference enhance handwriting skill acquisition. *Journal of Motor Behavior, 36*(1), 115-126.

Steele, C. J., & Penhune, V. B. (2010). Specific increases within global decreases: a functional magnetic resonance imaging investigation of five days of motor sequence learning. *J Neurosci, 30*(24), 8332-8341.

Takahashi, C., Nemet, D., Rose-Gottron, C., Larson, J., Cooper, D., & Reinkensmeyer, D. (2003). Neuromotor noise limits motor performance, but not motor adaptation, in children. *Journal of Neurophysiology, 90*(2), 703-711.

Thomas, K., Hunt, R., Vizueta, N., Sommer, T., Durston, S., Yang, Y. et al. (2004). Evidence of developmental differences in implicit sequence learning: An fMRI study of children and adults. *Journal of Cognitive Neuroscience, 16*(8), 1339-1351.

Thomas, K., & Nelson, C. (2001). Serial reaction time learning in preschool- and school-age children. *Journal of Experimental Child Psychology, 79*, 364-387.

Tober, C. L., & Pollak, S. D. (2005). Motor Development of Post-Institutionalized Children Across Time. *Biennial Meeting of the Society for Research in Child Development, Atlanta, GA,*.

Toni, I., Krams, M., Turner, R., & Passingham, R. (1998). The time course of changes during motor sequence learning: A whole-brain fMRI study. *NeuroImage, 8*, 50-61.

Walker, M., Brakefield, T., Seidman, J., Morgan, A., Hobson, J., & Stickgold, R. (2003). Sleep and the time course of motor skill learning. *Learning and Memory, 10*, 275-284.

Walker, M. P., Brakefield, T., Morgan, A., Hobson, J. A., & Stickgold, R. (2002). Practice with sleep makes perfect: sleep-dependent motor skill learning. *Neuron, 35*(1), 205-211.

Watanabe, D. (2003). The effect of musical experience on the acquisition and retention of a temporal motor sequence task. Unpublished undergraduate thesis, Concordia University, Montreal, Canada.

Watanabe, D., Savion-Lemieux, T., & Penhune, V. (2007). The effect of early musical training on adult motor performance: Evidence for a sensitive period in motor learning. *Experimental Brain Research, 176*, 332-340.

Weber-Fox, C., & Neville, H. (2001). Sensitive periods differentiate processing of open- and closed-class words: An ERP study of bilinguals. *Journal of Speech, Language and Hearing Research, 44*(6), 1338-1353.

Wiesel, T., & Hubel, D. (1965). Extent of recovery from the effects of visual deprivation in kittens. *Journal of Neurophysiology, 28*, 1060-1072.

Wilke, M., Krageloh-Mann, I., & Holland, S. (2007). Global and local development of gray and white matter volume in normal children and adolescents. *Experimental Brain Research, 178*, 296-307.

Willingham, D. (1998). A neuropsychological theory of motor skill learning. *Psychological Review, 105*(3), 558-584.

Wolff, P., Gunnoe, C., & Cohen, C. (1993). Associated movements as a measure of developmental age. *Developmental Medicine and Child Neurology, 25*(4), 417-429.

Zatorre, R. (2003). Absolute pitch: A model for understanding the influence of genes and development on neural and cognitive function. *Nature Neuroscience, 6*(7), 692-695.

Zetou, E., Michalopoulou, M., Giazitzi, K., & Kioumourtzoglou, E. (2007). Contextual interference effects in learning volleyball skills. *Perceptual and Motor Skills, 104*(3, Pt 1), 995-1004.

Appendix A

Master's Manuscript

Exp Brain Res (2005) 161: 423–431
DOI 10.1007/s00221-004-2085-9

RESEARCH ARTICLE

Tal Savion-Lemieux · Virginia B. Penhune

The effects of practice and delay on motor skill learning and retention

Received: 21 February 2004 / Accepted: 26 July 2004 / Published online: 13 November 2004

Abstract The present study assessed the effects of amount of practice and length of delay on the learning and retention of a timed motor sequence task. Participants learned to reproduce ten-element visual sequences by tapping in synchrony with the stimulus. Participants were randomly assigned to a varied-practice condition or a varied-delay condition. In the varied-practice condition, participants received either one, three, or six blocks of practice followed by a fixed 4-week delayed-recall. In the varied-delay condition, participants received three blocks of practice followed by a varied delay of either 3 days, or 2, 4, or 8 weeks. Learning was assessed by changes in accuracy, response variance, and percent response asynchrony. Our results showed that amount of practice per se did not affect learning and retention of the task. Rather, distribution of practice over several days was the most important factor affecting learning and retention. We hypothesize that passage of time is essential for a maximum benefit of practice to be gained, as the time delay may allow for consolidation of learning, possibly reflecting plastic changes in motor cortical representations of the skill. With regards to delay, our findings suggest that explicit and motoric components of a motor sequence are likely to be learned and maintained in separate but interacting systems. First, only the longest delay group showed decrements in percent correct, indicating that longer lengths of delay might hinder retrieval of explicit aspects of the task. Second, all groups showed a decrement in percent response asynchrony, suggesting that synchronization may be a more difficult parameter to maintain because it relies heavily on sensorimotor integration.

Keywords Motor skill · Learning · Retention · Practice · Delayed-recall

Introduction

Throughout life, a vast array of motor skills are learned and retained. While certain skills, such as walking and talking, are largely innate, others, such as playing the saxophone and swinging a baseball bat, are primarily learned. Motor skill learning is the process by which motor skills become effortlessly performed through practice. Once a skill is well learned, it can be retained for months and even years (Hikosaka et al. 2002; Karni and Sagi 1993; Nezafat et al. 2001; Penhune and Doyon 2002; Shadmehr and Brashers-Krug 1997). Numerous behavioral and neuroimaging studies have looked at factors influencing motor skill learning (for review see Schmidt and Lee 1999); however, very few have considered factors affecting long-term retention (Fleishman and Parker 1962; Karni et al. 1995; Shadmehr and Brashers-Krug 1997). Therefore, in the present investigation we examined the effects of different levels of practice and different lengths of delay on the learning and retention of a complex timed motor sequence. The timed motor sequence task (TMST) used in this study requires participants to reproduce a sequence by tapping in synchrony with ten-element visual stimuli using a single key of the computer mouse. Participants practiced the TMST for five consecutive days, followed by a delayed-recall session. In the varied-practice condition, amount of practice but not length of delay was modulated. In the varied-delay condition, length of delay but not amount of practice was modulated. We hypothesized that amount of practice would influence the learning and retention of the TMST. Furthermore, we expected length of delay to affect retention of the TMST.

Three stages of motor skill learning have been identified, corresponding to distinct points in the pattern of incremental changes seen in performance across sessions of practice (for review see Doyon and Ungerleider 2002; Karni et al. 1998; Korman et al. 2003). The first

T. Savion-Lemieux (✉) · V. B. Penhune
Department of Psychology, Laboratory for Motor Learning, Cognitive Learning, and Neural Plasticity, Concordia University,
7141 Sherbrooke St. W., Science Pavilion SP-250,
Montreal, Québec, H4B 1R6, Canada
e-mail: t_savion@alcor.concordia.ca
Tel.: +1-514-8482424 ext. 7567
Fax: +1-514-8482817

stage occurs within the initial session of practice, where rapid improvements in performance are observed (Karni and Sagi 1993; Toni et al. 1998; Van Mier et al. 1997). The second stage, referred to as consolidation, occurs following the initial practice session. At consolidation, significant improvements in performance are observed following a period of rest, of greater than 4 h, with no additional practice (see, for example, Karni and Sagi 1993; Shadmehr and Brashers-Krug 1997). In addition, it has been demonstrated that a night of sleep further improves performance of a recently acquired skill (Maquet et al. 2003; Stickgold et al. 2001; Walker et al. 2003). The third stage of motor skill learning occurs throughout the remaining practice sessions (days or weeks), where slower and more gradual gains lead to a plateau in performance (see, for example, Karni et al. 1995; Korman et al. 2003). Finally, once a skill is well-learned, few declines in performance are noted, even after extended delays with no additional practice (see, for example, Hikosaka et al. 2002; Karni and Sagi 1993; Shadmehr and Brashers-Krug 1997).

Support for separable stages of motor skill learning comes from animal and human studies showing that different cortical and subcortical regions are preferentially involved at different phases of learning (Doyon and Ungerleider 2002; Hikosaka et al. 1999; Karni et al. 1998; Van Mier 2000). For instance, a number of neuroimaging studies of motor sequence learning have shown that the cerebellum is primarily active during the early stage of learning, while the basal ganglia, primary motor cortex (M1), and the supplementary motor area are involved in consolidation and the later stage of learning (Doyon et al. 1996; Grafton et al. 1994; Jenkins et al. 1994; Karni et al. 1995; Toni et al. 1998; Van Mier et al. 1997). Studies of long-term practice have shown plasticity in M1 of both humans and monkeys (Karni et al. 1998; Nudo et al. 1996; Pascual-Leone et al. 1995). A recent positron emission tomography (PET) study from our laboratory (Penhune and Doyon 2002) examined the network of active brain regions during the acquisition and retention of the TMST. We found that the cerebellum was primarily active during the early stage of learning, suggesting that this structure is important in adjusting movement kinematics. The basal ganglia was found to be activated at consolidation, indicating that this structure is likely involved in automatization of movements. Lastly, the motor, primary motor, and parietal cortices were shown to be active at delayed-recall, suggesting that these cortical areas are mainly responsible for storing motor representations of the timed motor sequence. Based on these results, we predicted that motor cortical activity would be modulated by changes in the amount of practice on the task, or in the length of delay before recall. Thus, the aim of the current experiment was to look at behavioral changes related to the amount of practice and length of delay before recall on the learning and retention of the same TMST.

A wide range of behavioral experiments have explored the effects of practice on performance at different stages of motor skill learning. Studies looking at early learning have consistently shown rapid improvements in performance within a single session of training, as evidenced by significant decreases in reaction time and increases in response accuracy. For example, participants exhibited improved performance on a novel maze tracing task after only a 10-min practice session (Van Mier et al. 1997). Furthermore, findings have demonstrated that spacing practice intervals with periods of rest significantly improved performance within the first day of learning, compared to massing practice with no periods of rest (Bourne and Archer 1956; Shea et al. 2000). Participants who received 60-s rest periods after completion of 30-s work trials on a pursuit rotor tracking task performed significantly better than participants who received no rest, or 15-, 30-, or 45-s rest periods (Bourne and Archer 1956). Experiments examining consolidation can also provide support for the effectiveness of spaced practice. The majority of these studies have shown that a period of rest of greater than 4 h, or a night of sleep, results in improvements in performance between the first and second training sessions (Karni and Sagi 1993; Shea et al. 2000; Walker et al. 2002, 2003). Across longer-term learning, spacing practice sessions beyond the first and second days of practice also results in enhanced performance; however, improvements in this later stage of learning are slower and more gradual (Karni and Sagi 1993; Karni et al. 1995; Shea et al. 2000), suggesting that improvements at consolidation may simply reflect the most dramatic step of an ongoing process. After a critical amount of training, however, performance reaches a plateau where performance is close to ceiling and changes are very small (Karni 1996; Karni et al. 1998; Welford 1987). For example, beyond 3 weeks of 10–20 min of daily practice on a simple sequential finger opposition task, little change in accuracy and speed of movement were noted (Karni et al. 1995). Taken together, these results suggest that practice spaced across days of training results in early rapid changes in average performance, followed by later more gradual changes. Interestingly, relatively few current studies have looked at the effect of different amounts of practice on the acquisition and retention of a motor skill across several days of practice (Hauptmann and Karni 2002; Ofen-Noy et al. 2003). Therefore, the first goal of this study was to look at the effects of different amounts of practice on the learning of the TMST.

Another important issue in motor skill learning is the accuracy and durability of the skill after a delay with no practice. Most studies measuring retention of motor skills are focused on consolidation and, therefore, usually look at short-term retention, typically 24-h delayed-recall (Shea and Kohl 1990; Shea et al. 2000). Very few studies have directly examined long-term retention of a motor skill. In 1962, Fleishman and Parker looked at factors influencing retention and re-learning of a motor skill. Participants were trained on a complex hand tracking task over the course of 17 daily sessions. After a period of either 9, 14, or 24 months with no additional practice, participants were retested on the same task. Results showed that the groups were globally comparable at re-test, with no significant losses in performance. More recently, Karni and Sagi (1993) found no forgetting on a visual discrimination task even after 3 years without practice. Behavioral results from our previous PET study found no forgetting of the TMST after a 1-month delay-recall (Penuhne and Doyon 2002). However, in all of these studies, it was not clear whether retention was related to the amount of practice on the task or to the length of delay before recall. Therefore, a second aim of the current study was to examine the effects of different amounts of practice and different lengths of delay on the retention of the TMST.

Materials and methods

Participants

The sample consisted of 58 healthy volunteers (30 males, 28 females). All participants were between the ages of 18 and 35 [mean (M)=23.97, SD=4.30], right handed, assessed using a handedness questionnaire adapted from Crovitz and Zener (1962), and selected to have less than 3 years of musical training or experience, assessed using the Global Index of Musical Training and Experience (Penhune et al. 1999). None of the participants had a history of neurological disorders. Participants were requested to refrain from drinking alcohol prior to each testing session. Seven additional participants were tested, but were excluded from the final sample due to failure to learn the test within 48 trials, not presenting themselves on the final day of testing, or experimental error. The experimental protocol was approved by the Concordia University Human Research Ethics Committee, Montreal, Canada. Participants gave informed consent and were compensated for their time.

Stimuli and task conditions

The TMST (Penhune and Doyon 2002) used in this experiment requires participants to reproduce a complex timed motor sequence by tapping in synchrony with a visual stimulus using a single key of the computer mouse, with the index finger of the right hand. The stimuli were ten-element visual sequences, made-up of a series of white squares (3 cm^2) presented sequentially on a black background, in the center of the computer screen (21-inch Sony Trinitron Multiscan G500 computer monitor, running at 100 Hz).

Two sequences, designed to be of equal difficulty, were employed. Each participant was tested on only one of the two possible sequences, and the sequences were counter-balanced across participants. Each sequence was made-up of five long (750 ms) and five short (250 ms) elements, with a constant interstimulus interval (500 ms) (Fig. 1). The sequences were constructed to have no more than two repeated elements and to have seven transitions from short to long. This results in sequences that are temporarily regular, but do not follow a typical musical rhythm (i.e., syncopated rhythms). The presentation of each sequence was cued by a smaller white square (1 cm^2) that appeared in the middle of the screen. Participants were instructed to press and hold the key down at the onset of each stimulus in the sequence, and to release it when the stimulus disappeared. Each block of practice on the TMST contained 12 presentations of the same sequence and lasted 2 min 12 s.

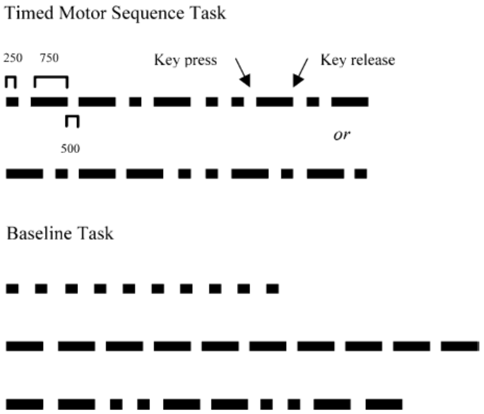

Fig. 1 Structure of the timed motor sequences and the baseline sequences. Sequences in both tasks comprised of white squares that appeared sequentially at the center of the computer monitor. *Top panel* illustrates the two different sequences used in the timed motor sequence task (TMST). *Bottom panel* illustrates the three sequences used in the baseline task. Squares appeared for either long (750 ms) or short (250 ms) durations, with a constant interstimulus interval (500 ms)

At each testing session, prior to performing the TMST, participants completed a baseline task that was used to score performance on the TMST. This task consisted of three simple ten-element sequences that were made-up of either all long, all short, or simple-mixture (Fig. 1). There were four repetitions of each sequence. Custom software (Media Control Functions; Digivox, Montreal, Canada), running on an Intel Pentium III 800-MHz computer (under Windows Millennium), controlled stimulus delivery and automatically recorded participants' key-press and release durations, which were subsequently used to calculate the three indices of learning: accuracy of reproduction, variance of response duration, and percent asynchrony of responses with target stimuli.

Design and procedure

Participants were randomly assigned to one of two conditions: a varied-practice condition (n=28) or a varied-delay condition (n=40) (Fig. 2). Within each condition, participants were divided into groups (with 8 to 10 participants per group). Participants in the varied-practice condition were divided into three groups who

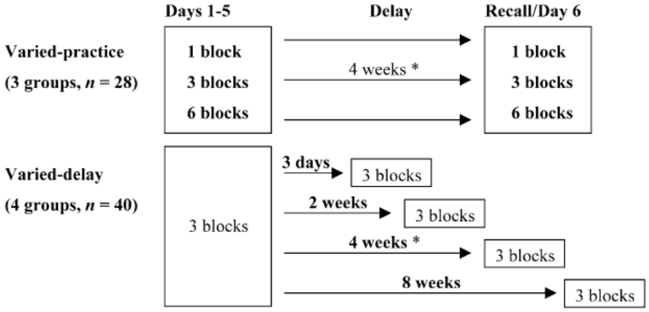

Fig. 2 Experimental design. *Top panel* shows the varied-practice condition where participants received either one, three, or six blocks of practice on the TMST, over five consecutive days (days 1–5), followed by a fixed 4-week delayed-recall session (day 6). *Bottom panel* shows the varied-delay condition where participants received a fixed amount of practice on the TMST, over five consecutive days (days 1–5) followed by a variable delayed-recall (day 6) of either 3 days, or 2, 4, or 8 weeks

received either one block (12 trials), three blocks (36 trials), or six blocks (72 trials) of practice on the TMST on each of five consecutive days, followed by a fixed 4-week delayed-recall. Participants in the varied-delay condition were divided into four groups who received three blocks of practice on the TMST on each of five consecutive days, followed by a variable delayed-recall of either 3 days, or 2, 4, or 8 weeks. The group who received three blocks of practice followed by a 4-week delayed-recall was included in the analyses for both conditions.

Testing occurred on five consecutive sessions (days 1–5), followed by a delayed-recall session (day 6). On all testing days, participants first completed the baseline task used to score the TMST. On day 1, participants were trained to reproduce one of the two timed motor sequences, to a criterion of three consecutive correct repetitions. After this initial training, participants were no longer provided feedback on their performance. On days 1–5, participants completed one to six blocks of practice on the TMST. On each day, participants briefly reviewed the timed motor sequence by reproducing it one or two times prior to beginning practice. After a delay with no practice, participants returned to the laboratory for a final testing session (day 6), and followed the same protocol as per days 2–5.

Participants were always seated 57 cm away from the computer monitor. Breaks were provided between blocks of practice to prevent fatigue and optimize performance. Participants were specifically instructed not to practice the sequences between sessions and were debriefed on the final day of testing to ensure they complied with that instruction.

Behavioral measures

Since timing was a parameter of interest in this study, as participants explicitly learned to synchronize their response with the target stimuli, learning was not measured by decreases in reaction time, as is the case in classic motor skill learning experiments. Instead, learning was assessed by investigating changes in three variables: accuracy, response variance, and percent response asynchrony. Accuracy was scored individually, by using each participant's average short and long responses from the baseline sequences, for each day, ±2 SD as the upper and lower limits for correct response for short and long elements, respectively. The percent of correct long and short elements was calculated for each trial and was averaged across each block. Although percent correct measures accuracy of the motor response, in this experiment, it was also considered to represent a measure of explicit knowledge of the order of the short and long elements in the sequence. In contrast, response variance and percent response asynchrony were considered to measure more specifically motor components of the task. Response variance measured the stability of response, by using the coefficient of variation (SD/M) of correct responses durations. Finally, percent response asynchrony measured the percent difference between onset and offset of stimuli and onset and offset of responses (for additional information on scoring of the sequence, refer to Penhune et al. 1999).

Data analysis

All dependent measures were averaged across blocks and days of practice, for each of the two conditions. The data were analyzed with repeated measure ANOVAs (Greenhouse-Geiser correction), with Group as the between-subject factor and Day or Block as within-subject factors. Differences across days 1–5 of learning, across the last block of practice on day 1 and the first block of practice on day 2 (consolidation), and across the last block of practice on day 5 and the first block of practice on day 6 (delayed-recall) were evaluated for the two conditions separately. In addition, one-way ANOVAs, with Group as the between-subject factor, were conducted to assess performance across blocks of practice on day 1 for the varied-delay condition and on the last block of practice on day 1 for the varied-practice condition (early learning). Significant main effects and interactions were analyzed using pairwise comparisons, with Bonferroni adjustment for multiple comparisons. The α level was set at 0.05 for all statistical tests.

Results

Varied-practice condition

A one-way analysis of variance indicated that mean age did not differ between the three groups, $F_{(2,24)}=0.25$, $P=0.78$. Groups did not differ on trials to criterion for explicit learning of the TMST on day 1, $F_{(2,23)}=0.93$, $P=0.41$, indicating no pretraining differences in learning capacity. Furthermore, there were no significant differences between the sexes, $F_{(1,24)}=2.90$, $P=0.10$, nor between the two timed motor sequences, $F_{(1,24)}=0.20$, $P=0.66$, on trials to criterion. Therefore data were collapsed across these two dimensions.

Days 1–5 of learning

Contrary to our hypothesis, groups did not differ in their performance as measured by percent correct, response variance, or percent response asynchrony when compared across days 1–5 of learning (Fig. 3). These results indicate that amount of practice did not affect learning of the TMST. However, collapsed across groups, significant changes were observed for all three measures across days of learning, percent correct: $F_{(2.33,4.65)}=22.63$, $P=0.00$, coefficient of variation: $F_{(1.91,3.83)}=27.75$, $P=0.00$, percent response asynchrony: $F_{(2.59,5.18)}=52.37$, $P=0.00$. *Post hoc* comparisons showed a similar pattern of results for all measures, with overall significant improvements in performance between days 1–4 ($P<0.05$), but not between days 4–5, suggesting that participants appeared to be reaching a plateau in performance by day 4.

Learning day 1

No significant differences were observed for any dependent variable when comparing the final block of practice for each group on day 1, suggesting that amount of practice, per se, had no effect on early learning of the TMST.

Consolidation

For both percent correct and percent asynchrony values, significant improvements were observed between the last block of practice on day 1 and the first block of practice on day 2, percent correct: $F_{(1,2)}=5.72$, $P=0.025$, percent response asynchrony: $F_{(1,2)}=13.93$, $P=0.00$, indicating that learning of the TMST continued the following day (day 2). For response variance, a Group × Day interaction approached significance, $F_{(2,24)}=3.04$, $P=0.07$, with *post hoc* comparisons revealing marginally significant improvements in performance for the one-block practice group ($P=0.07$) and the three-block practice group ($P=0.06$), but not for the six-block practice group ($P=0.26$).

Recall

Comparisons of percent correct and response variance for the last block of practice on day 5 and the first block of practice on day 6 showed no significant changes for any group, indicating that, overall, the sequences were well retained (Fig. 3). For percent response asynchrony, there was a significant Day × Group interaction, $F_{(2,24)}=5.118$,

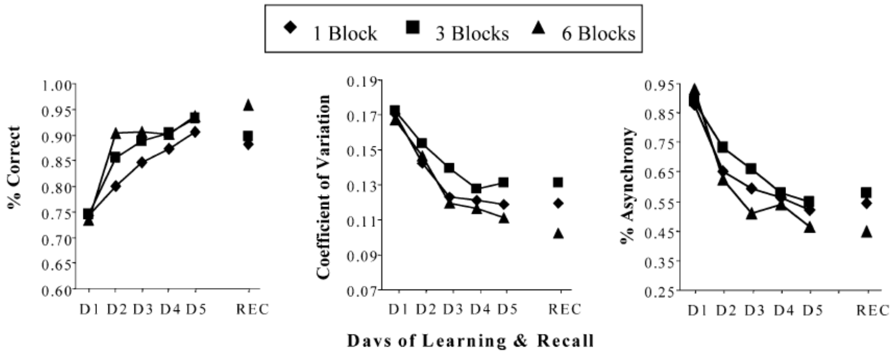

Fig. 3 Changes in performance for the TMST across days of practice (*D1–D5*) and at delayed-recall (*REC*) for the varied-practice groups. *Left graph* shows the change in percentage correct, *middle graph* shows changes in the coefficient of variation, and *right graph* shows changes in percent response asynchrony

P=0.01. *Post hoc* analyses revealed that the only group that showed significant decrements in performance was the three-block practice group (P=0.01).

Varied-delay condition

A one-way analysis of variance showed that average mean age did not differ between the four groups, $F_{(3,36)}$=1.24, P=0.31. Groups did not differ on trials to criterion for explicit learning of the TMST on day 1, $F_{(3,36)}$=1.27, P=0.30, indicating no pretraining differences in learning capacity. Furthermore, there were no significant differences between the sexes, $F_{(1,38)}$=1.91, P=0.18, nor between the two timed motor sequences, $F_{(1,38)}$=0.034, P=0.86, on trials to criterion. Therefore data were collapsed across these two dimensions.

One participant from the three-block practice group was excluded from the analyses when comparing performance across blocks of practice at delayed-recall (experimental error).

Days 1–5 of learning

The groups did not differ in their performance as measured by percent correct, response variance, or percent asynchrony, when compared across days 1–5 of learning, indicating no differences in level of learning before recall (Fig. 4). Across days of practice, all groups showed significant improvements in performance for all three measures, percent correct: $F_{(2.32,6.95)}$=29.22, P=0.00, coefficient of variation: $F_{(2.34,7.02)}$=39.97, P=0.00, percent response asynchrony: $F_{(1.67,5)}$=58.05, P=0.00. *Post hoc* analyses showed a similar pattern of results for all measures, with overall significant improvements in performance between days 1–4 (P<0.05), but not between days 4–5, indicating that participants appeared to be reaching a plateau in performance by day 4.

Learning day 1

As expected, no significant group differences were observed across blocks of practice on day 1 for any dependent variable. All groups showed significant improvement in performance across blocks as measured by percent correct, $F_{(1.91,5.72)}$=4.58, P=0.015, and percent asynchrony, $F_{(1.64,4.91)}$=15.53, P=0.00, but not response variance. For percent correct and percent response asynchrony, *post hoc* analyses yielded significant differences between the first and last block of practice (P<0.05).

Consolidation

There were no significant group differences between the last block of practice on day 1 and the first block of practice on day 2. All groups showed significant improvements in performance for all three measures (P<0.05), indicating that learning of the TMST continued on the second day of learning.

Recall

For percent correct, there was a marginally significant Day × Group interaction, $F_{(3,36)}$=2.48, P=0.08, such that only the 8-week-delay group showed significant decrements in performance between the last block of practice on day 5 and the first block of practice on day 6 (P=0.04) (Fig. 4). These results indicate that longer lengths of delay before recall appear to negatively affect the more explicit components of the TMST. Contrary to our hypothesis, comparisons of response variance and percent response asynchrony revealed no significant group differences. However, there were significant decrements in performance at delayed-recall for percent response asynchrony for all groups, $F_{(1,3)}$=5.31, P=0.03, suggesting that this

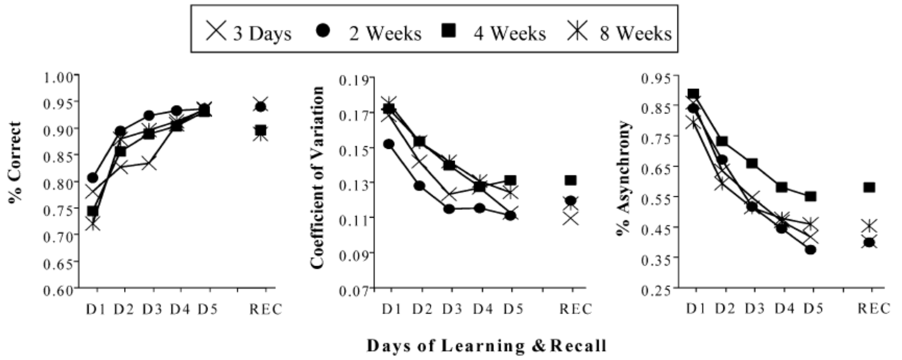

Fig. 4 Changes in performance for the TMST across days of practice (*D1–D5*) and at delayed-recall (*REC*) for the varied-delay groups. *Left graph* shows the change in percentage correct, *middle graph* shows changes in the coefficient of variation, and *right graph* shows changes in percent response asynchrony

measure is sensitive to delay, but not length of delay per se.

Discussion

The present study examined the effects of different levels of practice and different lengths of delay on the learning and retention of the TMST. For the varied-practice condition, our results demonstrated that all groups showed a similar rate of learning across the 5 days of practice as well as a comparable pattern of retention at delayed-recall, indicating that amount of practice per se did not affect learning and retention of the TMST. Our results show that distribution of practice over several days, rather than amount of practice, is the most important factor affecting motor skill learning and retention. Thus, in line with other studies (Hauptmann and Karni 2002; Korman et al. 2003; Ofen-Noy 2003), we suggest that passage of time is essential for a maximum benefit of practice to be gained, as the time delay may allow for consolidation of learning, possibly reflecting plastic changes in motor cortical representations of the skill. In the varied-delay condition, delay differentially affected specific parameters of performance at recall. First, only the longest delay group showed decrements in percent correct between day 5 and recall, suggesting that longer lengths of delay might hinder retrieval of explicit knowledge of the order of the short and long elements of the sequence. Second, all groups showed a decrement in percent response asynchrony between day 5 and recall, indicating that this measure is sensitive to delay, but not to the length of delay. This relative loss in the ability to synchronize may reflect the fact that ongoing practice is required to maintain this aspect of motor control which relies heavily on sensorimotor integration. Taken together, these results suggest that different components of a motor sequence are likely to be learned and maintained in separate but interacting systems.

Effects of practice on motor skill learning and retention

The first goal of this study was to examine the effects of practice on motor skill learning and retention. No group differences were observed across days 1–5, across blocks of practice on day 1, between the last block of practice on day 1 and the first block of practice on day 2 (consolidation), or between the last block of practice on day 5 and recall. Thus, the group that received only one block of practice performed as well as the groups who received either three or six blocks of practice, indicating that amount of practice per se did not account for learning and retention. These results are consistent with previous results that have shown that minimal amounts of practice trials, distributed over several days, are sufficient to trigger performance gains (Hauptmann and Karni 2002; Ofen-Noy et al. 2003).

It may be argued that the reason why no group differences were found, particularly during the early phase of learning, is that all participants were explicitly taught the TMST prior to practicing it, leaving little room for improvement. However, none of the participants in the varied-practice condition started at ceiling, as average performance on day 1 for percent correct for all groups was only M=0.74 (SD=0.15), with very similar averages for all three groups (one-block: M=0.74, SD=0.15; three-blocks: M=0.74, SD=0.13; six-blocks: M=0.73, SD=0.19). Furthermore, participants continued to show improvements in performance across the subsequent days of practice. In fact, analyses for all three measures revealed improvements in performance up until day 4, suggesting that it was only then that task performance had stabilized across all three varied-practice groups. A similar pattern of findings was observed for the varied-delay groups who received a fixed amount of practice.

The fact that we did not find any performance differences between the varied practice groups, but found global improvements across days of practice and good retention at delayed-recall indicates that total amount of practice is not the major factor affecting learning. Rather, we show that distribution of practice over several days may be a more important variable that influences both learning and retention.

In a recent study of across-day learning, Ofen-Noy et al. (2003) found that increasing the amount of practice on a mirror reading task was not the most important factor in enhancing learning. Rather, "passage of time" was found to be essential to learning of the task. Additional support for this idea comes from a study of repetition priming showing that training over multiple sessions, even if minimal, is sufficient to trigger learning (Hauptmann and Karni 2002). These hypotheses are also consistent with previous studies that have shown that spaced practice augments subsequent performance on motor tasks, relative to massed or continuous practice (Baddely and Longman 1978; Shea et al. 2000). For example, Baddeley and Longman (1978) found that learning a typing task was enhanced when training was provided 1 h a day for 60 days as opposed to two sessions of 2 h a day for 15 days. Thus, spacing practice over several sessions might contribute to enhanced learning because it allows for more time to process and encode the information received.

Related to the notion of spaced practice, studies of consolidation have consistently shown that a period of rest or a night of sleep significantly enhances learning on a recently acquired motor skill (Karni et al. 1994; Shea et al. 2000; Walker et al. 2002). For instance, Walker et al. (2002) reported that after a 12-h night of sleep, compared to a 12-h wake period, significant gains in speed and accuracy were found for a sequential finger tapping task. This is in agreement with our findings in both the varied-practice and varied-delay conditions showing gains in performance when comparing the last block of practice on day 1 to the first block of practice on day 2. Interestingly, Sejnowski and Destexhe (2000) have shown that sleep-dependent mechanisms, such as spindle oscillations during the early stages of slow-wave sleep, are important for opening molecular gates required for synaptic plasticity. Sleep spindles have also shown to be enhanced after training on a motor task (Fogel et al. 2001, cited in Walker et al. 2002).

In relation to long-term retention of motor skills, other studies have found similarly good retention for periods from several weeks up to 2 or 3 years (Hikosaka et al. 2002; Karni et al. 1995, 1998; Nezafat et al. 2001). Karni et al. (1995) looked at motor cortical changes occurring during learning of a finger-to-thumb opposition task across several weeks of practice. The authors found an expanded representation of the trained sequence in the motor cortex by the fourth week of training, when asymptotic performance was reached, suggesting that M1 might be important for long-term storage of the motor skill. Moreover, Kleim et al. (2004) have shown that motor map reorganization and synapse formation occur during the late phase of learning (i.e., beyond the first few sessions of practice). From these two sets of findings, it might be hypothesized that once a skill is well-learned and performance reaches asymptote, long-lasting functional and neural changes occur that result in a stable, long-term memory of the motor skill.

In summary, we show that distribution of practice over several days, rather than amount of practice, is the critical factor affecting motor skill learning and retention. From our results and other findings reviewed, it appears that consolidation is an ongoing process with behavioral and neural changes showing the greatest effects between day 1 and day 2 of practice, but continuing until asymptotic performance is reached. Finally, we have shown that once a motor skill is consolidated, it is remembered for long periods of time, likely reflecting motor cortical plasticity that underlies long-term memory of the skill.

Effects of delay on motor skill retention

The final goal of the present investigation was to look at the effects of length of delay on motor skill retention. In the varied-delay condition at recall, only the 8-week-delay group showed significant decrements in percent correct, but all groups showed decrements in percent asynchrony. This pattern of findings indicates that it is likely that different components of a motor skill are learned and retained in different ways. In line with this conclusion, Hikosaka et al. (2002) recently proposed that motor skills are acquired and retained in two independent but parallel forms, speed and accuracy. In this study, both humans and monkeys were trained on a visual-motor sequence task for a period of approximately one week and a half (monkeys were trained for a longer period of time). After a delay of 16 months, participants returned for two additional testing sessions. On day 1, participants learned new sequences. On day 2, participants performed the old sequences and the new sequences. Interestingly, accuracy was higher for the recently acquired sequences compared to the old sequences, but speed of performance was greater for the old sequences than the recent sequences. Comparable findings were found for the animal subjects. Thus, speed of performance was better retained than accuracy. Taken together, these findings suggest that the more explicit components of a motor task, such as accuracy, and the more purely motoric components of the task, such as speed and synchronization, may be processed and maintained differently. Of note, in our experiment, accuracy was considered to represent a measure of more explicit (or global) knowledge of the order of short and long elements in the sequence. Consistent with Hikosaka (2002), our results showed that longer delays produced decrements in performance accuracy. In contrast, whereas Hikosaka found overall speed to be maintained at delayed-recall, our findings showed synchronization to be negatively affected by delay. This may reflect the fact that synchronization is a more difficult parameter of motor control to maintain than overall speed. This relative loss in the ability to synchronize may reflect the fact that ongoing practice is required to maintain this aspect of motor control which relies heavily on sensorimotor integration. For example, a skilled saxophonist may recall numerous pieces, but in order to swing in time with a group of other musicians requires ongoing practice.

Conclusion

The present investigation is among the first to examine the effects of both amount of practice and length of delay on the learning and retention of a TMST. Consistent with other findings described above, our results showed that amount of practice had no significant effect on the learning and retention of a motor skill, and showed that even minimal amounts of practice spread over several days are sufficient to induce long-term memory of that skill. Thus, it appears that learning and consolidation are ongoing processes mediated by factors such as sleep, and that once a skill is consolidated it is well retained, likely reflecting motor cortical plasticity. With regards to delay, our findings indicate that the explicit and motoric components of a motor task may be stored in separate but interacting systems. Future studies examining these different components of motor skill learning and retention would be of interest. Importantly, this study looked at group differences; an area that remains to be explored is individual differences in the behavioral and neuronal basis of motor skill learning and retention.

Acknowledgements We wish to thank those who participated in this study. We also thank John Connolly, Donald Watanabe, and Alison Simioni for assistance in data collection. This work was supported by the Natural Sciences and Engineering Research Council of Canada (V.B.P.), the Fonds de la recherche en santé du Québec (V.B.P.), and the Centre for Research in Human Development (T.S.L.).

References

Baddeley AD, Longman DJA (1978) The influence of length and frequency of training session on the rate of learning to type. Ergonomics 21:627–635

Bourne LE Jr, Archer EJ (1956) Time continuously on target as a function of distribution of practice. J Exp Psychol 51:25–33

Crovitz HF, Zener K (1962) A group-test for assessing hand- and eye-dominance. Am J Psychol 75:271–276

Doyon J, Ungerleider L (2002) Functional anatomy of motor skill learning. In: Squire L, Schacter D (eds) Neuropsychology of memory. Guilford Press, New York, pp 225–238

Doyon J, Owen A, Petrides M, Sziklas V, Evans A (1996) Functional anatomy of visuomotor skill learning in human subjects examined with positron emission tomography. Eur J Neurosci 8:637–648

Fleishman EA, Parker JF Jr (1962) Factors in the retention and relearning of perceptual-motor skill. J Exp Psychol 64:215–226

Fogel S, Jacob J, Smith C (2001) Increased sleep spindle activity following simple motor procedural learning in humans. Congress physiological basis for sleep medicine, Uruguay, Actas de Fisiologia

Grafton S, Woods R, Tyszka M (1994) Functional imaging of procedural motor learning: relating cerebral blood flow with individual subject performance. Hum Brain Map 1:221–234

Hauptmann B, Karni A (2002) From primed to learn: the saturation of repetition priming and the induction of long-term memory. Cogn Brain Res 13:313–322

Hikosaka O, Nakahara H, Rand M, Sakai K, Lu X, Nakamura K, Miyauchi S, Doya K (1999) Parallel neural networks for learning sequential procedures. Trends Neurosci 22:464–471

Hikosaka O, Rand M, Nakamura H, Miyauchi S, Kitaguchi K, Sakai K, Lu X, Shimo Y (2002) Long-term retention of motor skill in macaque monkeys and humans. Exp Brain Res 147:494–504

Jenkins I, Brooks D, Nixon P, Frackowiak R, Passingham R (1994) Motor sequence learning: a study with positron emission tomography. J Neurosci 14:3775–3790

Karni A (1996) The acquisition of perceptual and motor skills: a memory system in the adult human cortex. Cog Brain Res 5:39–48

Karni A, Sagi D (1993) The time course of learning a visual skill. Nature 365:250–252

Karni A, Tanne D, Rubenstien BS, Askenasy JJM (1994) Dependence on REM sleep of overnight improvement of a perceptual skill. Science 265:679–682

Karni A, Meyer G, Jezzard P, Adams M, Turner R, Ungerleider L (1995) Functional MRI evidence for adult motor cortex plasticity during motor skill learning. Nature 377:155–158

Karni A, Meyer G, Rey-Hipolito C, Jezzard P, Adams M, Tuner R, Ungerleider L (1998) The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. Proc Nat Acad Sci U S A 95:861–868

Kleim J, Hogg T, VandenBerg P, Cooper N, Bruneau R, Remple M (2004) Cortical synaptogenesis and motor map reorganziation occur during late, but not early, phase of motor skill learning. J Neurosci 24:628–633

Korman M, Raz N, Flash T, Karni A (2003) Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance. Proc Nat Acad Sci U S A 100:12492–12497

Maquet P, Schwartz S, Passingham R, Frith C (2003) Sleep-related consolidation of a visuomotor skill: brain mechanisms as assessed by functional magnetic resonance imaging. J Neurosci 23:1432–1440

Nezafat R, Shadmehr R, Holcomb H (2001) Long-term adaptation to dynamics of reaching movements: A PET study. Exp Brain Res 140:66–76

Nudo R, Milliken G, Jenkins W, Merzenich M (1996) Use-dependent alterations of movement representations in primary motor cortex of adult squirrel monkeys. J Neurosci 16:785–807

Ofen-Noy N, Dudai Y, Karni A (2003) Skill learning in mirror reading: how repetition determines acquisition. Brain Res Cogn Brain Res 17:507–521

Pascual-Leone A, Dang N, Cohen L, Brasil-Neto J, Cammarota A, Hallett M (1995) Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. J Neurosci 74:1037–1045

Penhune V, Doyon J (2002) Dynamic cortical and subcortical networks in learning and delayed recall of timed motor sequences. J Neurosci 22:1397–1406

Penhune V, Zatorre R, Feindel W (1999) The role of auditory cortex in retention of rhythmic patterns as studied in patients with temporal lobe removals including Heschl's gyrus. Neuropsychologia 37:315–331

Schmidt RA, Lee TD (1999) Motor control and learning: a behavioral emphasis. Human Kinetics, Champaign, IL

Sejnowski TJ, Destexhe A (2000) Why do we sleep? Brain Res 886:208–223

Shadmehr R, Brashers-Krug T (1997) Functional stages in the formation of human long-term motor memory. J Neurosci 17:409–419

Shea CH, Kohl RM (1990) Specificity and variability of practice. Res Q Exerc Sport 61:169–177

Shea CH, Lai Q, Black C, Park JH (2000) Spacing practice sessions across days benefits the learning of motor skills. Hum Mov Sci 19:737–760

Stickgold R, Hobson JA, Fosse R, Fosse M (2001) Sleep, learning, and dreams: off-line memory reprocessing. Science 294:1052–1057

Toni I, Krams M, Turner R, Passingham R (1998) The time course of changes during motor sequence learning: a whole-brain fMRI study. Neuroimage 8:50–61

Van Mier H (2000) Human learning. In: Mazziota J (ed) Human brain mapping: the systems. Academic, New York, pp 605–662

Van Mier H, Ojemann J, Miezin F, Akbudak E, Conturo T, Raichle M, Peterson S (1997) Practice-related changes in motor learning measured by fMRI. Soc Neurosci Abstr 23:1051

Walker MP, Brakefield T, Morgan A, Hobson JA, Stickgold R (2002) Practice with sleep makes perfect: sleep-dependent motor skill learning. Neuron 35:205–211

Walker MP, Brakefield T, Seidman J, Morgan A, Hobson JA, Stickgold R (2003) Sleep and the time course of motor skill learning. Learn Mem 10:275–284

Welford AT (1987) On rates of improvement with practice. J Mot Behav 19:401–415

Appendix B

Sample Consent Form Study 1

LABORATORY FOR MOTOR LEARNING AND NEURAL PLASTICITY
CONSENT FORM TO PARTICIPATE IN RESEARCH

Title of project: The Effect of Practice Pattern on the Acquisition, Short-Term Retention and Transfer of Multi-Finger Sequences

Researchers: Dr. Virginia Penhune (Principal Investigator), Tal Savion-Lemieux (Graduate Student), Anthony Hopley (Research Assistant)

This is to state that I agree to participate in a program of research being conducted in the Laboratory for Motor Skill Learning and Neural Plasticity in the Department of Psychology at Concordia University.

A. PURPOSE

The purpose of this study is to advance our knowledge of how we learn precise motor skills, similar to playing the piano. In the future, this knowledge may be beneficial in settings in which optimal learning of fine motor skills is important, including expert music performance and motor rehabilitation.

B. PROCEDURES

This experiment includes 2 testing sessions. The first session lasts approximately 45 minutes. In this session, you will learn to reproduce two sequences of key-presses on an electronic keyboard. You will do this by following along with a visual stimulus presented to you on the computer. You will then be asked to practice the sequences for approximately 30 minutes. On the following day, you will be asked to return to the laboratory and practice the sequences for approximately 15 minutes. It is very important that you refrain from practicing the sequence between sessions. It is also very important that you refrain from drinking alcohol 24 hours prior to each testing session. On each day, you will be asked a series of questions about the quality and quantity of your sleep the night before. If you were recruited through the participant pool, you will receive two participant pool credits for participating in this research study. If you were not recruited through the participant pool, you will be compensated for your time and willingness to contribute to this research study.

Advantages and disadvantages: Participation in this study has no personal benefits. On a long term basis, the study may help us gain knowledge about motor skill learning. There are no physical risks associated with participation in this experiment. The only disadvantage of participation is the time you will spend doing the test and traveling to and from the laboratory. The investigator may end the study at any time for purely scientific reasons. In this case, compensation will be made for the part of the study completed.

C. CONDITIONS OF PARTICIPATION

I understand that my participation is entirely voluntary and that I am free to withdraw my consent and discontinue my participation at anytime without negative consequences. I further understand that all records and test results of this study will be kept strictly confidential. No one but the experimenters will have access to any information about me or my performance. In addition, my name will not be used in any report or publication.

I HAVE CAREFULLY STUDIED THE ABOVE AND UNDERSTAND THIS AGREEMENT. I FREELY CONSENT AND VOLUNTARILY AGREE TO PARTICIPATE IN THIS STUDY.

Name

Signature Date

Witness' Signature Date

For further information about this study either before or after it is completed, please feel free to contact:
Dr. Virginia Penhune 848-2424 x 7535 (vpenhune@vax2.concordia.ca) and/or her associates at 848-2424 x 7567. If you have questions about your rights as a research participant, please contact Adela Reid, Research Ethics and Compliance Officer, Concordia University, at 514-848-2424 x7481 or by email at Adela.Reid@concordia.ca.

Appendix C

Sample Consent Form Study 2

LABORATORY FOR MOTOR LEARNING AND NEURAL PLASTICITY
CONSENT FORM TO PARTICIPATE IN RESEARCH

Title of project: Neuronal Basis of Human Motor Skill Retention
Researchers: Dr. Virginia Penhune
Donald Watanabe
Tal Savion-Lemieux
Nicole Lalonde

This is to state that I agree to participate in a program of research being conducted in the Laboratory for Motor Skill Learning and Neural Plasticity in the Department of Psychology at Concordia University.

A. PURPOSE

The purpose of this study is to advance our knowledge of how the brain learns precise motor skills, similar to playing the piano. In the future, this knowledge may also increase our understanding of brain disorders resulting from disease or injury.

B. PROCEDURES

This experiment includes 6 testing sessions. The first session lasts approximately 30 minutes. In this session, you will be taught to make a sequence of finger taps in time with a visual stimulus presented on the computer. You will be asked to reproduce the sequence by tapping in synchrony with the visual stimulus using a single mouse key. You will then be asked to practice this sequence for approximately 15 minutes. On the following 5 days, you will be asked to return to the lab and practice the same sequence for approximately 15 minutes. It is very important that you refrain from practicing the sequence between sessions. It is also very important that you refrain from drinking alcohol 24 hours prior to each testing session. You will be compensated $20 for your time and willingness to contribute to this research study.

Advantages and disadvantages: Participation in this study has no personal benefits. On a long term basis, the study may help us gain knowledge about brain functioning. There are no physical risks associated with participation in this experiment. The only disadvantage of participation is the time you will spend doing the test and traveling to and from the laboratory. The investigator may end the study at any time for purely scientific reasons. In this case, compensation will be made for the part of the study completed.

C. CONDITIONS OF PARTICIPATION

I understand that my participation is entirely voluntary and that I am free to withdraw my consent and discontinue my participation at anytime without negative consequences. I further understand that all records and test results of this study will be kept strictly confidential. No one but the experimenters will have access to any information about me or my performance. In addition, my name will not be used in any report or publication.

I HAVE CAREFULLY STUDIED THE ABOVE AND UNDERSTAND THIS AGREEMENT. I FREELY CONSENT AND VOLUNTARILY AGREE TO PARTICIPATE IN THIS STUDY.

____
Name

____
Signature Date

____
Witness signature Date

For further information about this study either before or after it is completed, please feel free to contact: Dr. Virginia Penhune at 848-7535 (vpenhune@vax2.concordia.ca)

Appendix D

Sample Consent Forms Study 3

CONSENT FORM TO PARTICIPATE IN RESEARCH (ADULT FORM)

Title of project:	Developmental contributions to motor skill learning
Researchers:	Virginia Penhune, Ph.D. (principle investigator) Tal Savion-Lemieux, Ph.D. Candidate (graduate student) Andrea Ming-Si Lee (undergraduate student) Jennifer Anne Bailey (undergraduate student)

This is to state that I agree to participate in a program of research being conducted in the Laboratory for Motor Learning and Neural Plasticity in the Department of Psychology at Concordia University.

A. PURPOSE

I have been informed that the purpose of this study is to advance our knowledge of how precise motor skills, similar to playing the piano, are learned and retained across the life-span.

B. PROCEDURES

This experiment includes two consecutive lab visits (24 hours apart). Each visit will last approximately one hour. In the first visit, I will play a computer learning game using an electronic keyboard. In this learning game, I will be instructed to "catch the animal" (appearing in one of four squares presented next to one another in a row on a computer) as quickly and accurately as possible, by pressing one of four keys on an electronic keyboard using four fingers of the right hand. I will be asked to asked to play this computer learning game for approximately 25 minutes (breaks will be provided to prevent fatigue and boredom). I will also be asked to give definition of words and remember series of numbers. In the second visit, I will be asked to play the same computer learning game as on the first visit for 25 minutes. I will also be asked to complete another computer activity. On this activity, letters will be presented on a computer screen and I will have to press as quickly as I can the space bar after each letter presentation, except the letter X. At the end of the second visit, I will be compensated $5 and will be offered a small prize for my time and willingness to contribute to this research study.

Advantages and disadvantages: Participation in this study has no personal benefits. There are no physical risks associated with participation in this experiment. Breaks will be provided to prevent fatigue and boredom. The only disadvantage of participation is the time you will spend doing the test and travelling to and from the laboratory. The investigator may end the study at any time for purely scientific reasons. In this case, compensation will be made for the part of the study completed.

C. CONDITIONS OF PARTICIPATION

I understand that my participation in this study is entirely voluntary and that I am free to withdraw my consent and discontinue participation at anytime without negative consequences. I further understand that all records and test results of this study will be kept strictly confidential. No one but the experimenters will have access to any information about me or my performance. In addition, my name will not be used in any report or publication.

I HAVE CAREFULLY STUDIED THE ABOVE AND UNDERSTAND THIS AGREEMENT. I FREELY CONSENT AND VOLUNTARILY AGREE TO PARTICIPATE IN THIS STUDY.

Name (please print): ____

Signature: ____ Date: __________________

Witness' Signature: _____________________________________ Date: __________________

For further information about this study either before or after it is completed, please feel free to contact Dr. Virginia Penhune at 514-848-2424 x. 7535 or by email vpenhune@vax2.concordia.ca, or Tal Savion-Lemieux at 514-848-2424 x. 7567 or by email t_savion@alcor.concordia.ca.

If at any time you have questions about your rights as a research participant, please contact Adela Reid, Research Ethics and Compliance Officer, Concordia University, at 514-848-2424 x. 7481 or by email Adela.Reid@concordia.ca.

CONSENT FORM TO PARTICIPATE IN RESEARCH (Parent Version)

Title of project:	Developmental contributions to motor skill learning
Researchers:	Virginia Penhune, Ph.D. (principle investigator) Tal Savion-Lemieux, M.A. (graduate student) Andrea Ming-Si Lee (undergraduate student)

This is to state that I agree to participate in a program of research being conducted in the Laboratory for Motor Learning and Neural Plasticity in the Department of Psychology at Concordia University.

A. PURPOSE

I have been informed that the purpose of this study is to advance our knowledge of how precise motor skills, similar to playing the piano, are learned and retained across development. Results of this experiment will also allow us to evaluate the existence of a possible "sensitive" or "critical" period for motor learning in childhood, similar to that observed for learning a language.

B. PROCEDURES

This experiment includes two consecutive lab visits (24 hours apart). Each visit will last approximately two hours. In the first visit, my child will learn, by trial and error, to reproduce a sequence of key presses on an electronic keyboard using four fingers of the right hand. My child will be cued to press one of four keys by a visual stimulus presented on the computer screen. The visual stimulus consists of an animal appearing in one of four rectangular coloured bars presented sequentially (next to one another in a row) on a computer screen. My child will be instructed to "catch the animal" as quickly and accurately as possible. The animal will jump from one bar to another until a sequence of ten key presses has been completed. My child will be asked to practice this sequence for approximately 20 minutes (frequent breaks will be provided to prevent fatigue and boredom). My child will then be asked to complete several other activities including: copying geometrical designs on a paper with a pencil; re-creating a design from a booklet using red-and-white blocks while being timed; and giving definitions of words. In the second visit, my child will be asked to play the same "catch the animal" game as on the first visit for 20 minutes. My child will then be asked to complete several other activities including: pressing on the space bar after letters are presented at varying speeds, except when the letter 'X' appears; repeating numbers in either the same or reverse order as presented aloud by the experimenter; and recalling numbers in ascending order and letters in alphabetical order from a sequence of numbers and letters read aloud by the experimenter.

My child will be given a small toy at the end of *each* lab visit. In addition, I will be compensated $40.00, at the end of the second visit, for my time and willingness to contribute to this research study.

Advantages and disadvantages: Participation in this study has no personal benefits. There are no physical risks associated with participation in this experiment. Frequent breaks and snacks will be provided to your child to prevent fatigue and boredom. The only disadvantage of participation is the time that your child will spend doing the test and travelling to and from the laboratory. The investigator may end the study at any time for purely scientific reasons. In this case, compensation will be made for the part of the study completed.

C. CONDITIONS OF PARTICIPATION

I understand that my child's participation in this study is entirely voluntary and that I am free to withdraw my consent for myself and my child and discontinue participation at anytime without negative consequences. I further understand that all records and test results of this study will be kept strictly confidential. No one but the experimenters will have access to any information about my child or my child's performance. In addition, my child's name will not be used in any report or publication.

I HAVE CAREFULLY STUDIED THE ABOVE AND UNDERSTAND THIS AGREEMENT. I FREELY CONSENT AND VOLUNTARILY AGREE TO HAVE MY CHILD PARTICIPATE IN THIS STUDY.

Child Name (please print): ______________________________________

Parent's Name (please print): ____________________________________

Parent's Signature: ____ Date: ___________________

Witness' Signature: ____ Date: ___________________

For further information about this study either before or after it is completed, please feel free to contact Dr. Virginia Penhune at 514-848-2424 x. 7535 or by email vpenhune@vax2.concordia.ca, or Tal Savion-Lemieux at 514-848-2424 x. 7567 or by email t_savion@alcor.concordia.ca.

If at any time you have questions about your rights and your child's rights as a research participant, please contact Adela Reid, Research Ethics and Compliance Officer, Concordia University, at 514-848-2424 x. 7481 or by email Adela.Reid@concordia.ca.