

Developmental contributions to motor sequence learning

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Abstract 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 10 intermixed trials of a Repeated (REP) sequence and four trials of Random (RAN) sequences. Performance was assessed by examining changes in 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. Additionally, participants completed Recognition and Recall tests, to 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 behavioral 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 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. Taken together, the dissociation observed with our two behavioral 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 behavioral 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.

Keywords Motor skill learning · Developmental invariance · Children · Serial · Reaction time · Consolidation · Sensitive period

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 behavioral and neural underpinnings of motor skill learning in adults (For review, see: Hikosaka et al. 2002; Robertson et al. 2004; Doyon and Benali 2005; Krakauer

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and Shadmehr 2006); however, very little is known about how children acquire new motor skills. Recent evidence from pediatric structural neuroimaging research shows on-going changes in brain systems important for motor learning (Paus et al. 1999; Sowell et al. 1999, 2004; Gogtay et al. 2004; Barnea-Goraly et al. 2005; Mackie et al. 2007; Wilke et al. 2007). Thus, maturational changes in the brain coincide with and likely underlie changes in motor abilities across development. 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. A variant of the serial reaction time (SRT) paradigm was used to assess motor learning (Nissen and Bullemer 1987) and 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 (Karni et al. 1998; Hikosaka et al. 2002; Korman et al. 2003; Doyon and Benali 2005; Krakauer and 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 and Shadmehr 2006). This stage has been argued to be sleep-dependent (Fischer et al. 2002; Walker et al. 2003; Robertson et al. 2004; Krakauer and Shadmehr 2006). The third stage occurs throughout the remaining sessions (days or weeks) where slower and more gradual gains eventually lead to plateau in performance (Karni et al. 1998; Hikosaka et al. 2002; Korman et al. 2003; Doyon and Benali 2005; Savion-Lemieux and 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. 2003; Savion-Lemieux and 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 (Hikosaka et al. 1999; Doyon and Benali 2005). 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 and 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 et al. 2001), reaching (Kuitz-Buschbeck et al. 1998; Takahashi et al. 2003) and aiming (Contreras-Vidal et al. 2005; Smits-Engelsman et al. 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 (Meulemans et al. 1998; Badan et al. 2000; De Guise and Lassonde 2001; Ferrel et al. 2001; Thomas and Nelson 2001; Thomas et al. 2004; Dorfberger et al. 2007). 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 at all ages, as evidenced by increases in accuracy and decreases in reaction time. However, there is an absence of consistent developmental differences between groups (Meulemans et al. 1998). Furthermore, to our knowledge, only two previous studies have looked at motor sequence learning in children across multiple consecutive days (Dorfberger et al. 2007; Fischer et al. 2007). Both of these studies specifically examined sleep-dependant consolidation. The studies used widely differing paradigms, with Dorfberger using an explicit finger-to-thumb opposition task and Fischer implementing a highly implicit variant of the SRT. Both studies found similar learning for children and adults, but contrasting results for consolidation, with Dorfberger showing that younger children (7- and 10-year-olds) showed greater freedom from interference, and thus greater consolidation in the explicit task, while Fischer showed that children (between 7- and 11-years-old) showed smaller off-line gains, and thus poorer consolidation in the implicit task. Differences in experimental paradigms, as well as different age groups make it difficult to generalize from these studies.

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 indicate that the brain continues to develop into middle childhood and adolescence, and that these maturational changes coincide with the development of motor abilities (Paus et al. 1999; Sowell et al. 1999, 2004; Gogtay

et al. 2004; Barnea-Goraly et al. 2005; Mackie et al. 2007; Wilke et al. 2007). In particular, these studies show that global gray 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 gray 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 (Paus et al. 1999; Barnea-Goraly et al. 2005; Wilke et al. 2007). It has been hypothesized that these increases may underlie decreases in nerve conduction time that are observed with development. Furthermore, in 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 (Reber 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 among 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 invari-

ance model (Meulemans et al. 1998), other studies have showed age-related differences in explicit rather than implicit learning (Thomas and Nelson 2001) and have proposed that both systems develop in parallel across childhood (Thomas et al. 2004). Further, as described above, studies of sleep-dependent consolidation have also shown mixed results (Dorfberger et al. 2007; Fischer et al. 2007).

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. We used these particular age groups given the results of recent pediatric neuroimaging studies that have shown maturational brain changes between the ages of 6 and 10 years (Gogtay et al. 2004; Sowell et al. 2004; Wilke et al. 2007), which parallel the development of motor abilities. We used a consistent 2-year separation between age groups in order to be able to identify any incremental changes that might occur. In the MFST, participants had to "catch an animal," appearing in one of the 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. Further, we postulated that learning on this task could be broken down into two components. As such, performance was assessed by exploring changes in 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. 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 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, 0–9 months), 8 ($n = 12$; $M = 8$ years, 7 months; range = 8 years, 3–8 months), and 10 years ($n = 13$; $M = 10$ years, 3 months; range 10 years, 2–9 months) were recruited. A fourth comparison

group of university undergraduates ($n = 15$; $M = 24$ years, 5 months; range = 20–34 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 behavioral differences in motor skill performance between adult musicians and non-musicians, adult participants in the present study were selected to have less than 3 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 were 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 (Pitcher et al. 2003; Kooistra et al. 2005; O'Driscoll et al. 2005). 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 Bullemer (1987) classical SRT task. In the MFST, participants reproduced 10-element sequences of key presses on a MIDI-compatible electronic keyboard (M-Audio O₂, 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 colored frames (5 cm²), 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 cm²)



Fig. 1 Experimental setup

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. As such, participants were not instructed to respond “as fast as possible,” as is typically the case in classical SRT studies (e.g., Meulemans et al. 1998; Thomas and Nelson 2001; Thomas et al. 2004). 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 four 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 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 brief Familiarization phase. Each familiarization block consisted of 12 repetitions of one simple and predictable sequence (Sequence A: index, middle, ring, pinkie; Sequence B: pinkie, ring, middle, index). Each block was repeated twice. Some children in the two youngest groups required additional familiarization on the first day, 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 h 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, three 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 Edinburg Handedness Inventory (Oldfield 1971). On Day 2, participants again completed the Familiarization phase, followed by two 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.

Behavioral 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. Anticipatory responses were included in the measure because previous studies have shown that anticipation increases with learning (e.g., Savion-Lemieux and Penhune 2005). In order for participants to perceive themselves as being synchronous with the stimulus as instructed, they would have to anticipate their response. 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.

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

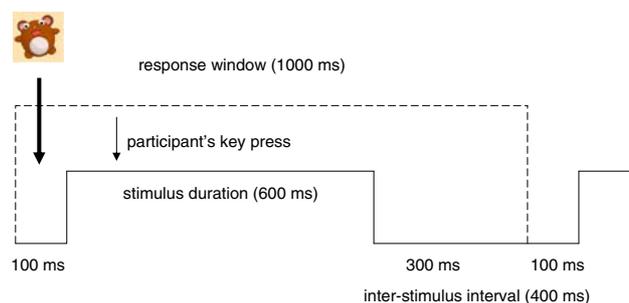


Fig. 2 Scoring method for accuracy and response synchronization of key presses

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 10 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 either behavioral measures ($P \geq 0.165$). Similarly, when comparing children with and without piano training, no significant differences were found on either behavioral measures ($P \geq 0.576$), indicating that piano training in the Child groups did not influence performance on the MFST. Therefore, behavioral 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 four 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 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.

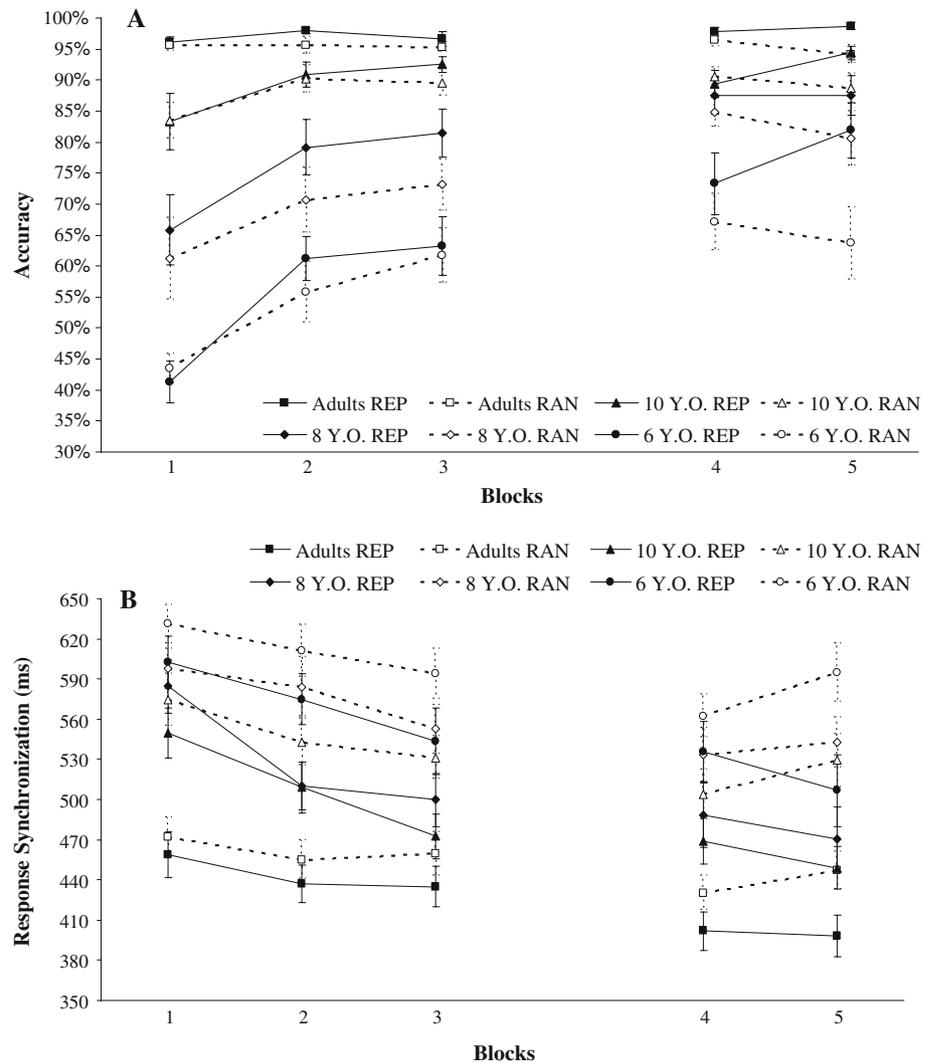
REP versus RAN: Day 1

When comparing percent correct, on the REP and RAN sequences, between the groups across the three blocks of practice on Day 1 (Fig. 3a), there was a significant main effect of Sequence Type $F(1, 49) = 10.833$, $P = 0.002$ indi-

cating 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 $F(1.7, 83.32) = 33.032$, $P < 0.001$ was also found, such that overall Block 1 was significantly less accurate than Blocks 2 and 3 ($P < 0.001$). As predicted, there was a significant main effect of Group $F(3, 49) = 51.69$, $P < 0.001$. Post hoc planned comparisons revealed that the Adult and 10-year-old groups did not significantly differ ($P = 0.318$), whereas the two youngest groups were significantly different from each other and from the Adults and 10-year-olds ($P < 0.001$). There was also a significant Block \times Group interaction $F(5.1, 83.32) = 5.462$, $P < 0.001$. Post hoc comparisons revealed that on all blocks, groups were significantly different from each other ($P < 0.016$), except the Adults and 10-year-olds ($P > 0.064$), 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 ($P = 0.05$), and 8-year-olds and 6-year-olds showed significant improvements when comparing Block 1 to the other two blocks ($P < 0.001$). 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 \times Block, Sequence \times Group, and Sequence Type \times Block \times Group interactions were found ($P \geq 0.058$) for percent correct.

For response synchronization (Fig. 3b), a similar pattern of results was observed. There was a significant main effect of Sequence Type $F(1, 49) = 70.487$, $P < 0.001$ 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 $F(1.81, 88.75) = 51.017$, $P < 0.001$, such that there were significant improvements in response synchronization across the three blocks of practice ($P \leq 0.001$). As expected, there was a significant main effect of Group $F(3, 49) = 15.312$, $P < 0.001$. Post hoc planned comparisons revealed that Adults performed significantly more synchronously than all child groups ($P > 0.005$). Moreover, 10-year-olds’ responses were significantly more synchronized than 6-year-olds’ responses ($P = 0.041$). There was also a significant Sequence Type \times Block interaction $F(1.88, 92.31) = 4.916$, $P = 0.011$, with post hoc analyses indicating that overall key presses were significantly faster on the REP sequence on all blocks ($P \leq 0.002$), suggesting an early emergence of “sequence-specific” learning. Lastly, there was a significant Block \times Group interaction $F(5.43, 88.75) = 2.735$, $P = 0.021$, such that overall Adults were significantly faster than Children on all blocks ($P \leq 0.006$). Interestingly, by

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



Block 3, Adults and 10-year-olds showed no significant differences in performance ($P = 0.132$), 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 ($P \leq 0.06$), indicating that the Adults were performing at ceiling whereas the Child groups showed within-day learning. No significant Sequence Type \times Group and Sequence Type \times Block \times Group interactions were found ($P \geq 0.110$).

REP versus RAN: consolidation

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. 3a), a significant main effect of Sequence Type $F(1, 49) = 8.991$, $P = 0.004$ 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 $F(1, 49) = 12.39$, $P = 0.001$, indicating overall consolidation. As predicted, there was a significant main effect of Group $F(3, 49) = 31.309$, $P < 0.001$. Post hoc planned comparisons revealed that 6-year-olds made significantly more errors than all groups ($P < 0.001$), and 8-year-olds, but not 10-year-olds, were significantly less accurate than Adults ($P < 0.001$, $P = 0.426$, respectively). Lastly, there was a significant Block \times Group interaction $F(3, 49) = 4.129$, $P = 0.011$. Post hoc planned comparisons revealed that only 8-year-olds and 6-year-olds showed significant improvements in performance between the two blocks ($P \leq 0.002$). No significant Sequence Type \times Block, Sequence Type \times Group, and Sequence Type \times Block \times Group interactions were observed ($P \geq 0.137$).

For response synchronization (Fig. 3b), overall performance on the REP sequence was more synchronous than on the RAN sequences $F(1, 49) = 66.089$, $P < 0.001$ (M REP =

480.713 ms, M RAN = 520.997 ms). Furthermore, there were significant improvements in response synchronization across the two blocks of practice $F(1, 49) = 22.769$, $P < 0.001$, indicating overall consolidation. Lastly, there was a significant main effect of Group $F(3, 49) = 11.028$, $P < 0.001$, where planned comparisons showed that Adults were significantly more synchronous than all Child groups ($P \leq 0.05$). Moreover, 10-year-olds significantly differed from 6-year-olds ($P = 0.051$). No significant interactions were noted ($P \geq 0.346$).

REP versus RAN: Day 2

When comparing group accuracy, on the REP and RAN sequences, across the two blocks of practice on Day 2 (Fig. 3a), there was a significant main effect of Sequence Type $F(1, 49) = 32.667$, $P < 0.001$, 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 \times Block interaction $F(1, 49) = 13.703$, $P = 0.001$. Post hoc analyses comparing performance on each sequence type across the two blocks indicated significant improvements on the REP sequence ($P = 0.002$), but marginally significant decrements on the RAN sequences ($P = 0.059$). As expected, there was a significant main effect of Group $F(3, 49) = 18.357$, $P < 0.001$, such that 6-year-olds were significantly less accurate than all groups ($P \leq 0.004$) and 8-year-olds were significantly less accurate than Adults ($P = 0.013$). Finally, there was a significant Sequence Type \times Group interaction $F(3, 49) = 5.519$, $P = 0.002$, such that only the 6-year-old and 8-year-old groups showed sequence-specific learning ($P \leq 0.023$). No other significant interactions were found.

For response synchronization (Fig. 3b), there was a significant main effect of Sequence Type $F(1, 49) = 111.082$, $P < 0.001$, 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 \times Block interaction $F(1, 49) = 24.6$, $P < 0.001$. Post hoc analyses revealed significant improvements on the REP sequence, but significant decrements in performance on the RAN sequences ($P < 0.001$). No other interactions were observed ($P > 0.231$). There was also a significant main effect of Group $F(3, 49) = 10.552$, $P < 0.001$, such that Adults were significantly more synchronous than all Child groups ($P \leq 0.036$), but the Child groups did not differ from each other ($P \geq 0.093$). No other significant interactions were found. Given the seemingly large group differences reported for response synchronization, especially for the youngest age groups, we also calculated the proportional measure of response synchronization between the repeated and random sequences for each block of practice and for each participant (e.g., [Block 1

RAN – Block 1 REP]/[Block 1 RAN + Block 1 REP]; Thomas and Nelson 2001), to control for this group difference. As such, we conducted an additional 4×5 (Group \times Block; Group as the between-subject factor and Block as the within-subject factor) repeated measures ANOVA, with the new proportional measure of response synchronization. Results indicated no significant Group effect and no significant interaction. There was a significant Block effect $F(3, 155) = 14.5$, $P < 0.001$, such that Block 5 was significantly different from all blocks ($P < 0.001$), which is consistent with the results of the REP versus RAND analyses.

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. 4a), there was a significant main effect of Block $F(2, 92.58) = 43.336$, $P < 0.001$, such that overall there were significant improvements in performance across all blocks ($P \leq 0.046$). Furthermore, there was a significant main effect of Group $F(3, 49) = 42.963$, $P < 0.001$. Post hoc analyses revealed that only the Adult and 10-year-old groups did not significantly differ ($P = 0.181$), indicating that by Day 1, 10-year-olds reached Adult level of performance on this measure. Finally, there was a significant Block \times Group interaction $F(6, 92.58) = 7.221$, $P < 0.001$, such that only 8-year-olds and 6-year-olds showed significant improvements across blocks of practice ($P \leq 0.058$).

For response synchronization (Fig. 4b), there was a significant main effect of Block $F(1.81, 88.67) = 56.173$, $P < 0.001$, such that overall there were significant improvements in performance across all blocks ($P \leq 0.009$). Moreover, there was a significant main effect of Group $F(3, 49) = 11.562$, $P < 0.001$, such that Adults were significantly faster than all Child groups ($P \leq 0.011$). Lastly, there was a significant Block \times Group interaction $F(5.43, 88.67) = 2.689$, $P = 0.023$. Post hoc analyses revealed that Adults reached ceiling in performance by Block 2, 10-year-olds showed significant improvements across all blocks ($P \leq 0.007$), and 8-year-olds and 6-year-olds showed significant improvements between Block 1 and Blocks 2 and 3 ($P \leq 0.001$), but not between Blocks 2 and 3 ($P \geq 0.440$).

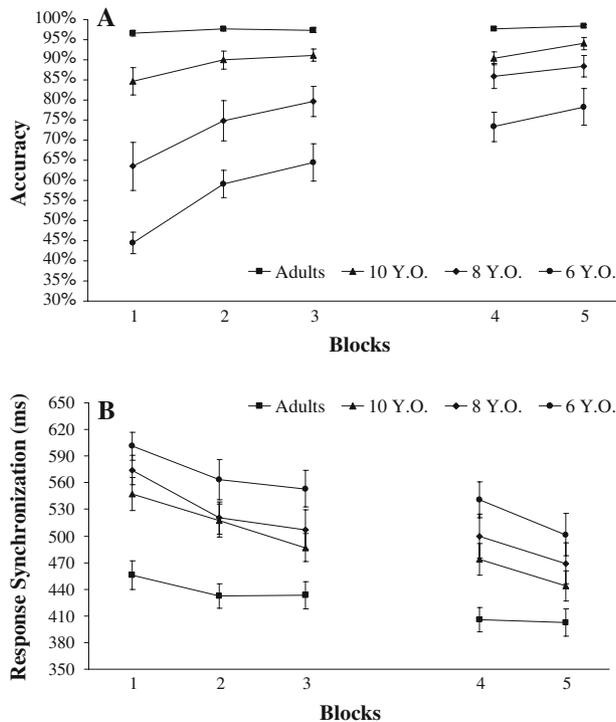


Fig. 4 Average accuracy (a) and response synchronization (b) data for all groups across five blocks of practice for all REP trials (14 trials per block)

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. 4a), results indicated overall consolidation $F(1, 49) = 15.445$, $P < 0.001$. There was also a significant main effect of Group $F(3, 49) = 24.135$, $P < 0.001$, such that 6-year-olds made significantly more errors than all groups ($P \leq 0.003$), and 8-year-olds made significantly more errors than Adults ($P = 0.001$). Finally, there was a significant Block \times Group interaction $F(3, 49) = 6.647$, $P = 0.001$, with post hoc comparisons indicating that only 8-year-olds and 6-year-olds showed significant improvements across the two blocks ($P \leq 0.002$), suggesting that Adults and 10-year-olds reached ceiling in performance on this measure.

For response synchronization (Fig. 4b), a similar pattern of results emerged, such that overall there were significant improvements across the two blocks of practice $F(1, 49) = 8.126$, $P = 0.006$. A significant main effect of Group $F(3, 49) = 9.473$, $P < 0.001$, revealed that Adults were significantly faster than the two youngest Child groups ($P \leq 0.009$), and 10-year-olds were marginally faster than the 6-year-olds ($P = 0.068$) 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 \times Group interaction was observed ($P = 0.275$).

REP: Day 2

When comparing percent correct between the groups across the two blocks of practice on Day 2 (Fig. 4a), there was a significant main effect of Block $F(1, 49) = 13.431$, $P = 0.001$, indicating improvements in performance across blocks. Moreover, there was a significant main effect of Group $F(3, 49) = 15.78$, $P < 0.001$, such that 6-year-olds were significantly less accurate than all other groups ($P \leq 0.014$), and 8-year-olds were significantly less accurate than Adults ($P = 0.014$) but not 10-year-olds ($P = 0.945$), indicating that by Day 2, 8-year-olds reached 10-year-olds' level of performance. No significant Block \times Group interaction was observed ($P = 0.275$).

For response synchronization (Fig. 4b), there was a significant main effect of Block $F(1, 49) = 42.495$, $P < 0.001$, revealing significant improvements across the two blocks of practice. Moreover, there was a significant main effect of Group $F(3, 49) = 7.156$, $P < 0.001$, such that only the Adults were significantly faster than the two youngest Child groups ($P < 0.024$). Lastly, there was a significant Block \times Group interaction $F(3, 49) = 4.444$, $P = 0.008$, with post hoc analyses indicating that all Child groups showed continued improvements across the two blocks of practice ($P < 0.001$).

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 behavioral measures (Fig. 5). 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 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 \times Group interaction $F(3, 49) = 14.394$, $P < 0.001$. 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 ($P < 0.027$) who did not differ from each other ($P > 0.05$). When comparing both measures for each group, we found that there were no

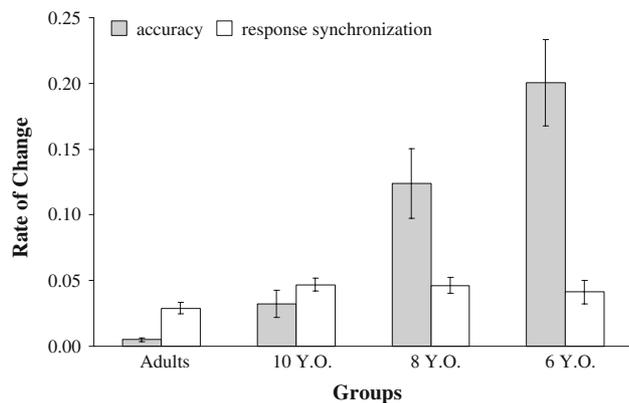


Fig. 5 Comparison of absolute rate of change between the first and last blocks of practice, relative to the first block of practice, for accuracy and response synchronization for all groups

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 ($P < 0.05$).

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. 6a) or Recall tests (Fig. 6b; $P > 0.05$).

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 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 ($P > 0.05$). 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

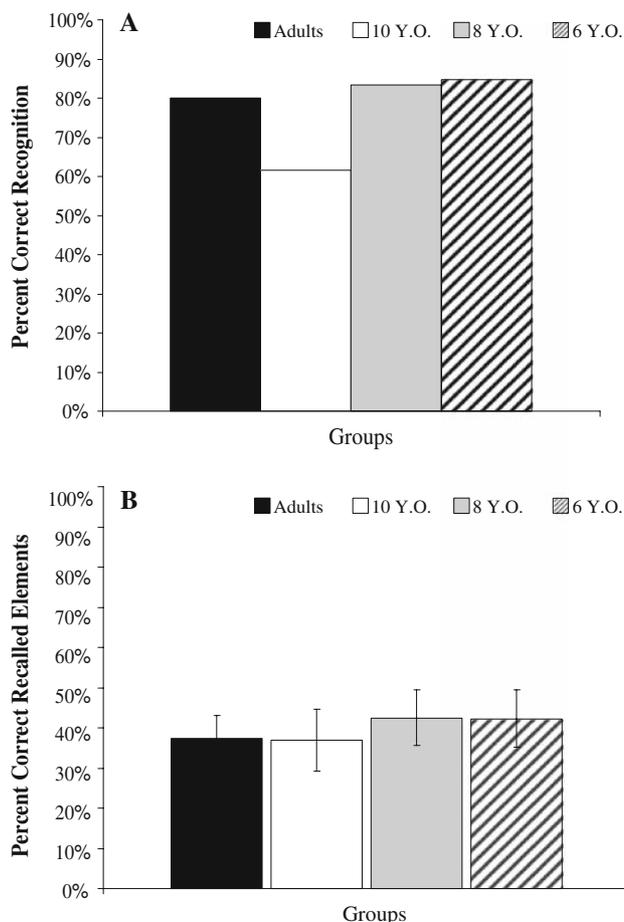


Fig. 6 Recognition (a) and Recall (b) data for 6-year-old, 8-year-old, 10-year-old, and Adults on Day 2. Recognition data are the percent of participants who correctly identified the REP sequence from a three alternative forced choice. Recall data show the average percent of correctly produced key-presses from the first 10 responses on the explicit recall test

CPT performance, computed on the basis of the ability to discriminate between target and false alarm stimuli; $P > 0.05$).

Discussion

The main goal of the current experiment was to examine developmental differences in motor sequence learning, across 2 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 behavioral 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 6-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 behavioral 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 and Nelson 2001; Thomas et al. 2004).

In contrast to the abundant literature on the progression of motor sequence learning in adults, only two previous studies have looked at motor sequence learning in children within the context of multiple days of practice (Dorfberger et al. 2007; Fischer et al. 2007). The studies used widely differing paradigms (Dorfberger: explicit finger-to-thumb opposition; Fischer: an implicit variant of the SRT) and found contrasting results showing better consolidation of the explicit task in younger children (Dorfberger) versus poorer consolidation of the implicit task (Fischer). The paradigm used in our experiment is more similar to Dorfberger's, and our results are consistent in showing both learning and off-line gains in all child groups.

Contrary to Dorfberger et al. (2007), we found a differential pattern of results for the two behavioral 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 behavioral 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, 2002; Savion-Lemieux and 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 gray and white matter densities, with primary sensory and motor regions developing earlier, and frontal and temporal-parietal association areas later (Paus et al. 1999, 2001; Gogtay et al. 2004; Sowell et al. 2004; Wilke et al. 2007). In particular, these studies show that global gray 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 gray 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 corticospinal system between childhood and late adolescence (Paus et al. 1999; Barnea-Goraly et al. 2005; 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 behavioral 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 (Sowell et al. 1999; Barnea-Goraly et al. 2005; Mackie et al. 2007). Taken together, the dissociation observed between our two behavioral 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 neighboring 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 (Wolff et al. 1983; Denckla 1973; Garvey et al. 2003). 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 less 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 and Schieber 2000; Reilly and Hammond 2000, 2006; Slobounov et al. 2002; Lang and Schieber 2004), 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 behavioral 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 prominent 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 (Reber 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). Further, Fischer's (2007) findings showing poorer consolidation on the SRT indicates that all aspects of implicit learning may not be invariant.

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 behavioral 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 (Reber 1993; Meulemans et al. 1998; Thomas and Nelson 2001; Thomas et al. 2004). 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 behavioral 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.

Of note, 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 and Newport 1989; Weber-Fox and 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 and Pollak 2005). Furthermore, behavioral 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 behavioral 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. Although the design of our current study does not allow us to evaluate the existence of a putative sensitive period in motor learning (particularly given the observed ceiling effects), we believe this hypothesis would be an interesting area for future investigation.

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 behavioral 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, on-going 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.

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