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RESEARCH ARTICLE

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

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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.

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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 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.

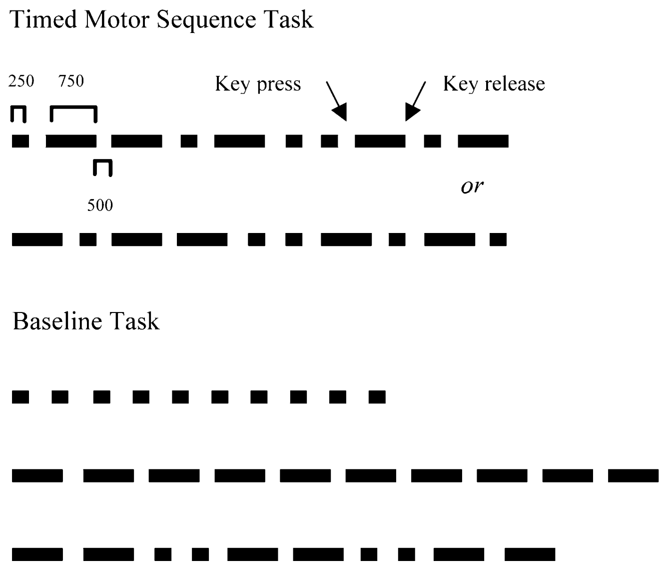

Fig. 1 Structure of the timed motor sequences and the baseline sequences. Sequences in both tasks comprised of white squares that appeared sequentially at the center of the computer monitor. *Top panel* illustrates the two different sequences used in the timed motor sequence task (TMST). *Bottom panel* 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

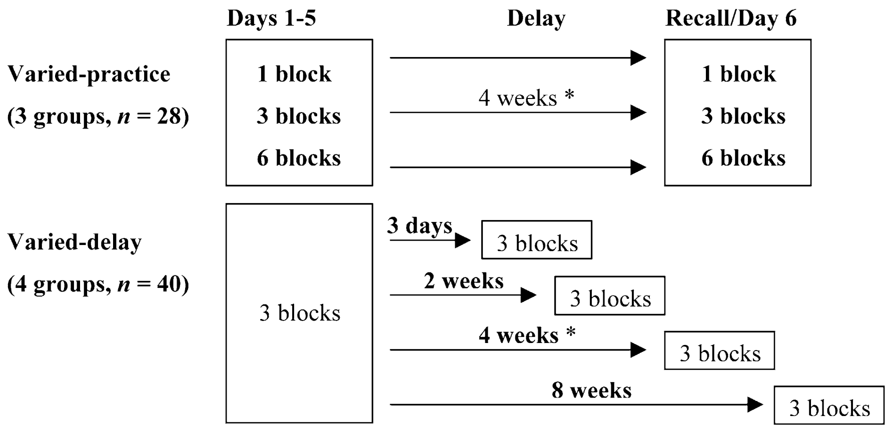

Fig. 2 Experimental design. *Top panel* shows the varied-practice condition where participants received either one, three, or six blocks of practice on the TMST, over five consecutive days (days 1–5), followed by a fixed 4-week delayed-recall session (day 6). *Bottom panel* shows the varied-delay condition 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, $F_{(2,24)}=5.118$,

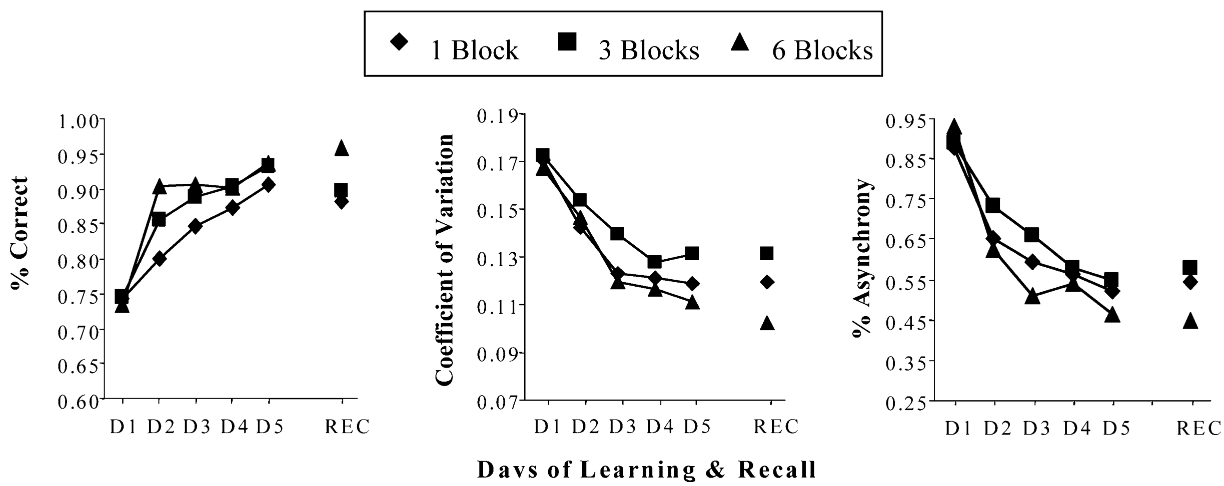

Fig. 3 Changes in performance for the TMST across days of practice (*D1–D5*) and at delayed-recall (*REC*) for the varied-practice groups. *Left graph* shows the change in percentage correct, *middle graph* shows changes in the coefficient of variation, and *right graph* shows changes in percent response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

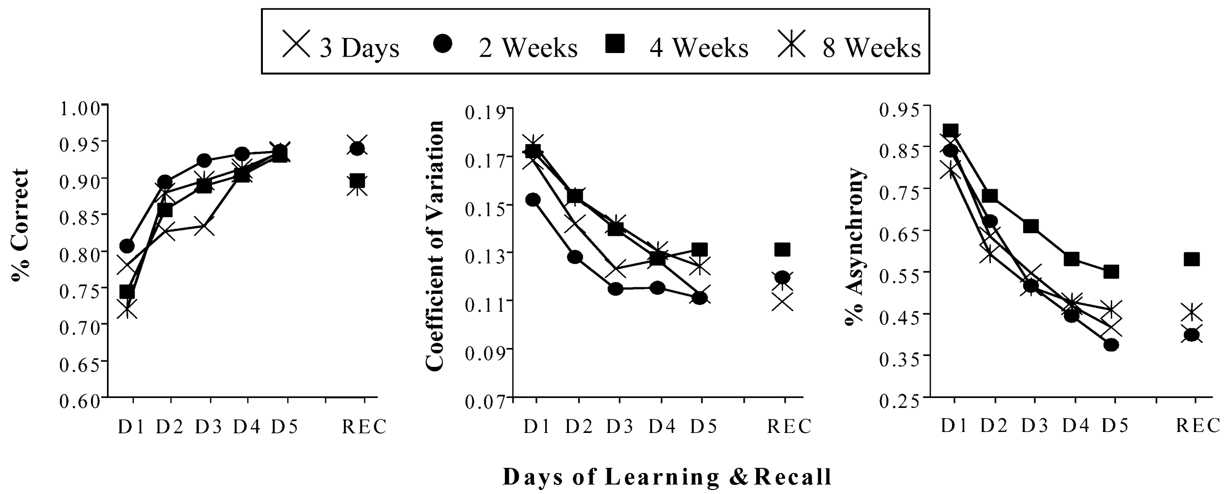

Fig. 4 Changes in performance for the TMST across days of practice (*D1–D5*) and at delayed-recall (*REC*) for the varied-delay groups. *Left graph* shows the change in percentage correct, *middle graph* shows changes in the coefficient of variation, and *right graph* shows changes in percent response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

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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