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Sequence Structure Has a Differential Effect on Underlying Motor Learning Processes

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Current methods to understand implicit motor sequence learning inadequately assess motor skill acquisition in daily life. Using fixed sequences in the serial reaction time task is not ideal as participants may become aware of the sequence, thereby changing the learning from implicit to explicit. Probabilistic sequences, in which stimuli are linked by statistical, rather than deterministic, associations can ensure that learning remains implicit. Additionally, the processes underlying the learning of motor sequences may differ based on sequence structure. Here, the authors compared the learning of fixed and probabilistic sequences to randomly ordered stimuli using a modified serial reaction time task. Both the fixed and probabilistic sequence groups exhibited learning as indicated by decreased response time and variability. In the initial stage of learning, fixed sequences exhibited both online and offline gains in response time; however, only the offline gain was observed during the learning of probabilistic sequences. These results indicated that probabilistic structures may be learned differently from fixed structures and have important implications for our current understanding of motor learning. Probabilistic sequences more accurately reflect motor skill acquisition in daily life, offer ecological validity to the serial reaction time framework, and advance our understanding of motor learning.

Keywords: motor skill acquisition, online and offline learning, probabilistic sequence learning, serial reaction time task, variability

Motor sequences can be acquired implicitly, such that there is no conscious knowledge that a sequence is being learned (Reber, 1967, 1989; Seger, 1994; Stadler

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& Frensch, 1998). The implicit motor sequence learning literature has prominently used fixed sequences with deterministic structures; however, these are not conducive to understanding how learning occurs in real life where we continuously make statistical associations between events unconsciously that change in a dynamic environment (Cleeremans & McClelland, 1991; Cleeremans, Servan-Schreiber, & McClelland, 1989; Reber, 1989). Thus, fixed sequences alone are inadequate to assess the processes required to learn motor skills outside the laboratory.

The most common paradigm to assess implicit motor sequence learning in the laboratory is the serial reaction time task (Nissen & Bullemer, 1987). Participants respond to the location of a stimulus on a computer screen by pressing the corresponding key as quickly as possible. Participants are unaware that the stimuli follow a fixed repeating sequence. Learning is inferred from a shorter response time to the repeating sequence than a novel sequence (Nissen & Bullemer, 1987; Robertson, 2007). Due to this repetition, participants are likely to become consciously aware of the presence of a sequence, thus changing the nature of learning from implicit to explicit (Howard et al., 2004; Howard & Howard, 1997; Nissen & Bullemer, 1987; Reed & Johnson, 1994; Song, Howard, & Howard, 2007). In order for learning to remain implicit, the underlying stimulus structure must be complex enough to escape conscious awareness (Reber, 1989), a condition that often does not hold for fixed sequences.

Previous studies have reported the critical role of sequence structure in learning (Bennett, Howard, & Howard, 2007; Curran, 1997; Dennis, Howard, & Howard, 2006; Howard et al., 2004; Jiménez, Méndez, & Cleeremans, 1996; Reed & Johnson, 1994) and have used different types of probabilistic sequences (Cleeremans & McClelland, 1991; Peigneux et al., 2000; Schvaneveldt & Gomez, 1998; Song et al., 2007; Stadler, 1992). Cleeremans et al. used a finite-state grammar to create a probabilistic sequence for the serial reaction time task and found that participants had shorter response times during predictable trials compared with unpredictable trials, suggesting learning of the finite-state grammar rules (Cleeremans & McClelland, 1991). Schvaneveldt and Gomez (1998) used a different approach where two 4-item sequences appeared with a probability of either 80% or 20% and found that response times were shorter for probable compared with improbable transitions. Howard et al. modified the serial reaction time task into a more complex alternate serial reaction time task in which each item of a fixed sequence occurred in alternation with a random item (e.g., a sequence 1-2-3-4 would appear as 1-*r*-2-*r*-3-*r*-4, where *r* is randomly picked from one of the four items) and found shorter response times to higher frequency triplets compared with lower frequency triplets (Feeney, Howard, & Howard, 2002; Howard & Howard, 1997, 2001). Although different types of probabilistic sequences were used in these studies, the results consistently indicated that participants were sensitive to the relative probabilities of the stimuli.

Multiple timescales underlie motor learning, with a slow learning process that drives improvement during rest (and occurs over hours or days) and a fast, transient process that improves performance during the practice session (Newell, Mayer-Kress, Hong, & Liu, 2009; Newell, Mayer-Kress, & Liu, 2001). Studies have further characterized the fast learning processes of motor sequences by examining progressive changes in response times during learning (Bönstrup, Iturrate, Hebart, Censor, & Cohen, 2020; Bönstrup et al., 2019; Du & Clark, 2020; Du, Prashad, Schoenbrun, & Clark, 2016; Du, Valentini, Kim, Whitall, & Clark, 2017). These learning processes may be online (i.e., the continuous trial-by-trial learning of the sequence during the performance of the task) or offline (i.e., the learning between practice blocks or during rest) in nature and may contribute differentially to different sequence structures. Offline learning has traditionally been thought to reflect the slow learning process by consolidation of newly acquired memory (Brashers-Krug, Shadmehr, & Bizzi, 1996; Robertson, Pascual-Leone, & Miall, 2004) that is independent of the practice sessions in the serial reaction time task and occurs over the course of hours or days (Newell et al., 2001; Reis et al., 2009) and during sleep (Censor, Sagi, & Cohen, 2012; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Walker et al., 2003). More recently, however, studies have reported that offline learning can occur at the level of seconds and contributes to the early acquisition of motor sequences (Bönstrup et al., 2019, 2020; Du et al., 2016, 2017) as an early memory boost (Hotermans, Peigneux, Maertens de Noordhout, Moonen, & Maquet, 2006). We have also previously found that groups performing fixed sequences exhibited greater online learning, while those performing probabilistic sequences exhibited offline learning, but no online learning (Du et al., 2016).

Furthermore, few have assessed how additional measures of learning (e.g., transfer of learning, response time variability) compare between sequence structures. Transfer of learning and decreased variability provide provide an evaluation of whether performance can be maintained in different contexts or variations of the skill (Cohen & Sternad, 2009; Newell, 1991; Newell & Shapiro, 1976; Wulf & Schmidt, 1997) and, despite being largely undervalued in the serial reaction time framework, they are essential for assessing motor learning.

Thus, the aims of this study were to (a) directly compare fixed and probabilistic sequences with stimuli appearing in a random order in a modified serial reaction time task, (b) characterize the underlying learning processes of the different sequence types, (c) investigate the transfer of learning from the assigned sequence to a novel sequence, and (d) examine changes in variability during learning. For the probabilistic sequences, we generated a first-order transitional probabilistic structure, where the present state influenced the subsequent state based on predefined transitional probabilities between states. Over trials, we hypothesized that participants would unconsciously learn the probabilistic rules underlying the sequence (e.g., two is most likely to be followed by six). We also included a condition in which stimuli appeared in a randomized order to characterize performance changes that would result from the motor component of the task, independent of learning a sequence structure, allowing for an examination of learning-related changes in performance. Specifically, we predicted that (a) the fixed and probabilistic sequence groups would exhibit decreased mean response times between the first learning block and the last learning block, increased mean response times to randomly ordered stimuli, and decreased mean response times to novel sequences; (b) in the random group, response times would remain constant for all of the blocks in the task; (c) variability would decrease with learning in the fixed and probabilistic sequence groups, but not the random group; and (d) that the fixed sequence group will exhibit both online and offline learning, while the probabilistic sequence group will exhibit only offline learning.

Materials and Methods

Participants

Thirty female right-handed adults were randomly assigned to one of three groups: fixed sequence (mean age: 20.0 ± 1.18), probabilistic sequence (mean age: 20.5 ± 1.25), and randomly ordered stimuli (mean age: 20.2 ± 1.37). The procedures performed in this study were approved by the Institutional Review Board at the University of Maryland, College Park and all participants signed consent forms prior to their participation. Each participant received $10 after the completion of the experiment. All participants completed the Global Physical Activity Questionnaire (Armstrong & Bull, 2006) to account for the relationship between physical activity and cognition (Hillman, Erickson, & Kramer, 2008) and potential effects on motor learning (Rhee et al., 2016; Snow et al., 2016; Statton, Encarnacion, Celnik, & Bastian, 2015), a spatial version of the *n*-back task to assess working memory (Jaeggi, Buschkuehl, Jonides, & Perrig, 2008), and a computer skills questionnaire to assess familiarity with the number pad on the computer keyboard. Participants were also screened for neurological and motor impairments through a health questionnaire. No significant differences were found between the groups in age, $F(2, 29) = 0.40$, $p = .67$, physical activity, $F(2, 29) = 0.91$, $p = .41$, or *n*-back score, $F(2, 29) = 0.86$, $p = .43$.

Serial Reaction Time Task

Participants were seated in front of a computer monitor (21″) and keyboard (keys size 13 × 15 mm, keys were 6 mm apart vertically and horizontally and 8 mm apart diagonally). A modified serial reaction time task was used that consisted of nine white squares organized in a 3 × 3 matrix on the computer screen (37 × 37 mm each). Participants placed the index finger of their right hand on the center button on the number pad of the keyboard. The relationship between the squares on the screen and the buttons on the number pad was spatially compatible, that is, the top right square corresponded to the top right button. At the beginning of each trial, one of the eight squares turned blue and the participant pressed the key that corresponded to the location of the stimulus and then returned to the home position. Each key was presented an equal number of times (i.e., 20 times per block) for all groups to avoid differences between groups based on key locations. A response-to-stimulus interval between 300 and 1,000 ms was selected randomly for each trial to prevent participants from anticipating the appearance of the subsequent stimulus as well as to prevent any confounding effects from the length of the response-to-stimulus interval (Willingham, Greenberg, & Thomas, 1997). No visual feedback of the hands was given to participants as a wooden board blocked the view of their finger position.

Participants were randomly assigned to either a 16-item fixed second-order conditional sequence (Reed & Johnson, 1994), probabilistic sequence, or were presented with stimuli in a random order. We created the probabilistic sequence based on a probabilistic transitional matrix representing a first-order Markov process. The transitional matrix generated sequences that resembled a deterministic, but not repeating, sequence (e.g., if Stimulus 2 occurred, there was a 60% probability that the next stimulus was 6, a 30% probability that the next stimulus was 8, and a 2% probability that the next stimulus was 1, 3, 4, 7, or 9). We told participants that the experiment will test how quickly they respond to visual stimuli, but did not inform them that a sequence existed, regardless of their assigned group. We constrained the probabilistic and randomly ordered stimuli such that the same stimuli did not repeat in consecutive trials and each stimulus appeared an equal number of times in each block (i.e., 20 times per block).

All groups performed a total of eight blocks, each consisting of 160 trials (see Figure 1). The first block for all groups was a baseline block (B0), consisting of 160 trials in which the stimuli appeared in a random order. The next four blocks (B1–B4) were learning blocks consisting of the fixed or probabilistic sequence in the fixed or probabilistic sequence groups, respectively. Block 5 (B5) consisted of 160 trials of stimuli occurring in a random order and Block 6 (B6) consisted of the same assigned sequence from B1 to B4. An increase in response time in B5 and a decrease in B6 would indicate learning (Robertson, 2007). Lastly, Block 7 (B7) consisted of a different sequence that was constructed from the same underlying structure as the assigned sequence to assess the transfer of learning. If the response times decreased from B5 to B7, it would suggest that participants were able to transfer their learning. A unique sequence was assigned to each participant to ensure that the results were not intrinsic to the sequence used, but could be generalized to all sequences (DeCoster & O'Mally, 2011). In the randomly ordered stimuli group, stimuli occurred in a random order in all eight blocks. Participants were given a 2-min mandatory break between each block. The experiment was performed using Presentation® software (version 18.1; www.neurobs.com).

The participant's response time (i.e., amount of time taken to press the corresponding button after the stimulus was presented) and accuracy were recorded for each trial. It is important to emphasize that response time, and not reaction time, was recorded. Response time includes both reaction time and movement time. Thus, in this task, movement time (i.e., amount of time taken to move the index finger from the home position to the corresponding button after the participant's initial reaction to the stimulus) was embedded in the recorded response time.

Posttest

All participants completed a posttest after the eight blocks to determine if learning remained implicit. First, participants were asked the following question: "The stimulus movement is best described as" with the following options: "a) Random, b) Some positions occurred more often than others, c) The movement was often predictable, d) The same sequence of movements would often appear, and e) The same sequence of movements occurred throughout the entire experiment" (Curran, 1997). Second, participants completed a recognition test to assess explicit recall of the sequence (Destrebecqz & Cleeremans, 2001) consisting of two parts: (a) participants were presented with six-item chunks from their assigned sequence as well as random chunks and were asked to rate their confidence on a scale of 1–5 (where 1 was *Confident that I **have not** seen it before* and 5 was *Confident that I **have** seen it before*) and (b) participants were presented with the entire 16-item sequence that they were assigned as well as other novel sequences and they were asked to rate them on the same scale.

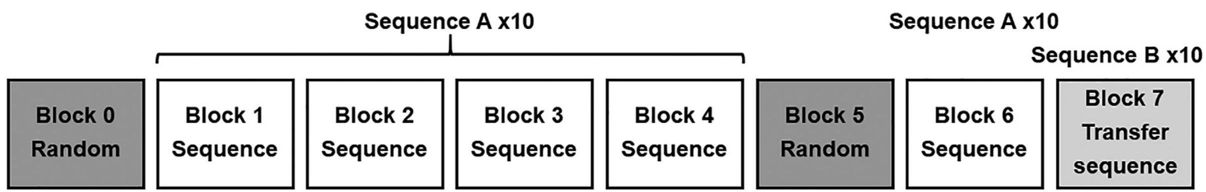

Figure 1 — The experimental paradigm used for the three groups. All groups started with a baseline (B0), then the fixed and probabilistic groups performed the learning blocks (B1–B4) and ended with a random block (B5) followed by another sequence block (B6) and a transfer block (B7). Each block consisted of 160 trials. Participants were given a 2-min break between each block. Participants in the fixed and probabilistic groups were given a unique fixed or probabilistic sequence, respectively. Participants in the random group were presented with stimuli in a random order for all blocks.

Data Analysis

Response times were trimmed according to the individual participant's mean and standard deviation. Response times greater or less than 2.5 *SD*s from their mean were excluded for the analyses (Ratcliff, 1993; Whelan, 2008). Mean response times for each block were calculated and averaged across participants in each group. Learning was inferred by a significant decrease in response times from B1 to B4, an increase from B4 to B5 (stimuli in random order), and a decrease from B5 to B6 (stimuli in assigned sequence). Transfer of learning was inferred if there was a significant decrease from B5 to B7 (stimuli in a different sequence of the same structure as the assigned sequence). Incorrect responses were excluded from the analysis.

Within-subject variability around the individual participant's mean was calculated and then averaged across each block and each group. B0 and B5 were excluded from this calculation to avoid inflation of the mean variability due to longer response times in these blocks.

To characterize the progressive behavioral changes during sequence learning, the mean response times for every 16 response times (i.e., the length of the fixed sequence) within a block were calculated. These means were used to measure online and offline changes in response time and to infer learning. Specifically, the online gain or loss was quantified by subtracting the mean response times of the last 16 trials within each block from the first 16 trials of the same block. The presence of online learning was inferred from a gain in this difference score (i.e., positive values). A subtraction of the mean response times of the first 16 trials in the current block from the last 16 trials in the preceding block was used to quantify an offline gain or loss. Similar to online learning, the presence of offline learning was inferred through a gain in this difference score. The average online and offline gains across the first four learning blocks were calculated for each participant.

Mixed factorial analyses of variance (ANOVAs) were used to compare differences in response time and variability between the blocks and groups. A mixed factorial ANOVA was also used to compare differences between online and offline learning between the groups. Bonferroni post hoc tests were used to decompose any significant effects. In addition, we had specific hypotheses about the direction of change in response times, so we conducted separate pairwise comparisons on the contrasts of interest (i.e., B1 vs. B4, B4 vs. B5, B5 vs. B6 to assess learning, and B5 vs. B7 to assess transfer). To compare differences in ratings in the posttest, Kruskal–Wallis *H* tests were used to compare responses to the stimulus movement question and whether participants recognized their assigned sequence. Wilcoxon signed-rank tests were used to compare the ratings to chunks from the assigned sequence and random chunks and the ratings to the assigned sequence and other novel sequences within the fixed and probabilistic sequence groups. Statistical significance was defined at $p < .05$. The data were processed using custom scripts written in MATLAB (version 8.4; MathWorks, Natick, MA) and SPSS Statistics (version 22; IBM, Armonk, NY).

Results

Accuracy

All groups exhibited high levels of accuracy with 2% or fewer errors. Thus, we did not use accuracy as a measure of learning and did not analyze accuracy further. Low error rates are consistent with previous studies (Robertson, 2007; Willingham, Nissen, & Bullemer, 1989).

Mean Response Time

A two-way mixed factorial (3 × 8) ANOVA on Sequence Type (fixed, probabilistic, random) × Block (0–7) on the response times with Block as the within-subject variable indicated a main effect for Block, $F(7, 189) = 37.1$, $p < .001$, partial $\eta^2 = .58$. There was no main effect of Sequence Type, $F(2, 27) = 2.4$, $p = .11$, partial $\eta^2 = .15$, and no significant interaction, $F(14, 189) = 0.83$, $p = .64$, partial $\eta^2 = .058$. Pairwise comparisons between contrasts that were determined a priori revealed significant differences between B1 and B4 in the fixed sequence group ($p < .001$, Cohen's $d = 0.88$), the probabilistic sequence group ($p < .001$, Cohen's $d = 0.95$), and the randomly ordered stimuli group ($p = .024$, Cohen's $d = 0.70$; Figure 2). There were also significant differences between B4 and B5 in the fixed sequence group ($p = .001$, Cohen's $d = 0.28$), but not in the probabilistic sequence group ($p = .38$, Cohen's $d = 0.088$) or the randomly ordered stimuli group ($p = .85$, Cohen's $d = 0.39$). Significant differences also appeared between B5 and B6 in the fixed ($p = .001$, Cohen's $d = 0.58$) and probabilistic ($p = .023$, Cohen's $d = 0.62$) sequence groups, but not in the randomly ordered stimuli group ($p = .54$, Cohen's $d = 0.13$).

Transfer of Learning

We assessed transfer of learning by comparing B5 (i.e., stimuli in a random order) and B7 (i.e., stimuli in a novel sequence created using the same underlying

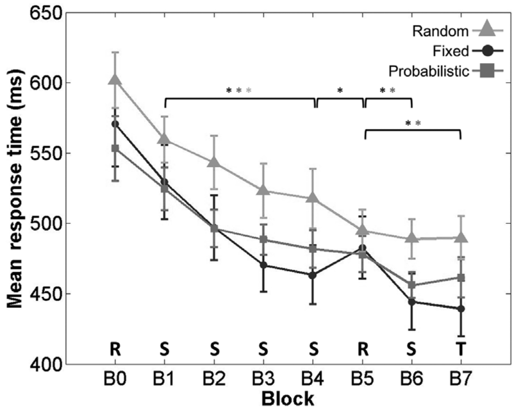

Figure 2 — Mean response time of each block for all three groups. The fixed and probabilistic sequence groups exhibit learning of the sequences, and the randomly ordered stimuli group exhibited a significant improvement in the motor component of the task. Error bars indicate *SE*. Note: Stimuli were presented in a random order for all blocks for the randomly ordered stimuli group. R = stimuli presented in a random order; S = stimuli presented in a sequential order of the assigned sequence; T = stimuli presented in a sequential order of a novel sequence. *Significance level of $p < .05$.

structure as the assigned sequence). Response times in B5 were significantly longer compared with B7 in the fixed ($p = .012$, Cohen's $d = 0.65$) and probabilistic ($p = .032$, Cohen's $d = 0.38$) sequence groups, but not in the randomly ordered stimuli group ($p = .14$, Cohen's $d = 0.10$).

Variability in Response Time

We calculated overall variability by averaging standard deviations of B1–B4, B6, and B7 for each group. There was no significant difference between the groups in overall variability as determined by a one-way ANOVA, $F(2, 27) = 0.93$, $p = .41$, $\eta^2 = .064$; however, overall variability does not provide insight on how performance variability changed with learning. Thus, to assess changes in variability with learning, we performed a two-way mixed factorial (3×6) ANOVA on Sequence Type (fixed, probabilistic, randomly) × Block (B1, B2, B3, B4, B6, B7) on the standard deviations of the response times with Block as the within-subject variable. There was a main effect of Block, $F(5, 135) = 7.2$, $p < .001$, partial $\eta^2 = .21$, but there was no main effect of Sequence Type, $F(2, 27) = 2.6$, $p = .09$, partial $\eta^2 = .16$, or interaction, $F(10, 135) = 0.53$, $p = .87$, partial $\eta^2 = .038$. The a priori determined pairwise comparisons revealed significant differences between B1 and B4 in the fixed ($p = .036$, Cohen's $d = 0.47$) and probabilistic ($p < .001$, Cohen's $d = 0.078$) sequence groups, but not in the randomly ordered stimuli group ($p = .31$, Cohen's $d = 0.23$). No other significant differences were found for any of the groups (Figure 3).

Dynamic Changes in Response Time Within and Between Blocks: Online and Offline Learning

To investigate online (i.e., within block) and offline (i.e., between block) learning, we performed a two-way mixed factorial (3×2) ANOVA on Sequence Type (fixed, probabilistic, randomly) × Learning (online, offline) on the response times with Learning as the within-subject variable. The results indicated a main effect of Learning, $F(1, 27) = 18.2$, $p < .001$, partial $\eta^2 = .40$ and a significant interaction, $F(2, 27) = 5.53$, $p = .010$, partial $\eta^2 = .29$, but no main effect of Sequence Type, $F(2, 27) = 0.99$, $p = .39$, partial $\eta^2 = .29$. In the post hoc analyses, we found overall greater offline learning compared with online learning ($p < .001$, Cohen's $d = 0.68$) across the groups. The significant interaction revealed that the probabilistic sequence group exhibited greater offline learning than the randomly ordered stimuli group ($p = .032$, Cohen's $d = 1.3$), but no differences emerged between the groups in online learning. We also found greater offline learning compared with online learning in the probabilistic sequence group ($p < .001$, Cohen's $d = 1.6$), but no difference in the fixed sequence ($p = .086$, Cohen's $d = 0.71$) and randomly ordered stimuli ($p = .60$, Cohen's $d = 1.4$) groups (Figure 4).

Posttest

After the completion of the task, participants were asked how they would describe the stimulus movement in the task (see "Methods" section for question). A Kruskal–Wallis H test found no significant differences in the responses between the groups, $\chi^2(2) = 3.8$, $p = .15$, $\eta^2 = .068$.

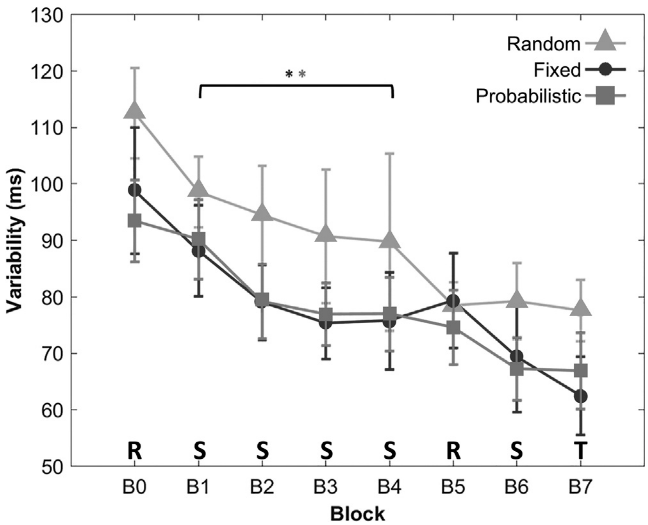

Figure 3 — Within-subject variability across blocks for the fixed sequence, probabilistic sequence, and randomly ordered stimuli groups. The fixed and probabilistic sequence groups exhibited a significant decrease in variability in the learning blocks, but the randomly ordered stimuli group did not. Error bars indicate *SE*. Note: Stimuli were presented in a random order for all blocks for the randomly ordered stimuli group. R = stimuli presented in a random order; S = stimuli presented in a sequential order of the assigned sequence; T = stimuli presented in a sequential order of a novel sequence. *Significance level of $p < .05$.

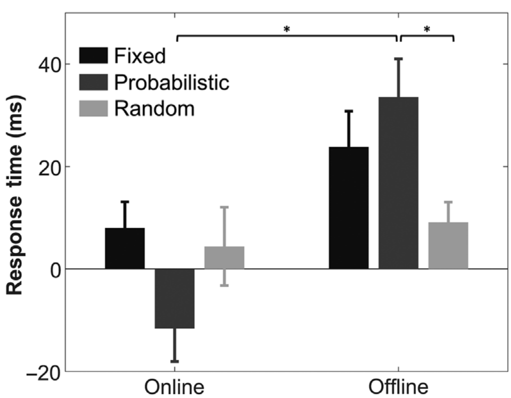

Figure 4 — Online and offline learning contributions to each sequence type. Positive response times are gains that suggest the presence of online or offline learning. There was a significant difference between online and offline learning in the probabilistic sequence group, but not the fixed sequence and randomly ordered stimuli groups. There were also significant differences between offline learning in the probabilistic sequence and the randomly ordered stimuli group. Error bars indicate *SE*. *Significance level of $p < .05$.

The posttest also required participants to rate their confidence on a scale of 1–5 whether they had seen the presented chunk in any of the blocks. Some of the chunks presented to participants were from the assigned sequence and some were novel chunks. In the fixed sequence group, there was a significant difference between the rating for the chunks from the sequence (mean rating = 3.2) and random chunks (mean rating = 2.8, $p = .042$, Cohen's $d = 0.76$). In the probabilistic sequence group, there were no significant differences between the ratings for the chunks (mean rating for chunks from assigned sequence = 3.2; mean rating for random chunks = 3.2, $p = 77$, Cohen's $d = 0.090$). A statistical comparison was not run for the randomly ordered stimuli group because there was no assigned sequence for this group (i.e., all stimuli occurred in a random order).

Participants were also shown entire sequences, one of which was their assigned sequence. There were no significant differences between the ratings for the entire sequences in both the fixed (mean rating of assigned sequence = 3.5; mean ratings of novel sequences = 2.5, $p = .072$, Cohen's $d = 0.88$) and probabilistic sequence (mean rating of assigned sequence = 2.9; mean rating of novel sequences = 3.0, $p = .63$, Cohen's $d = 0.17$) groups. However, based on these ratings, a significantly greater number of participants in the fixed sequence group (five participants) compared with the probabilistic sequence group (zero participants) correctly recognized their assigned sequence, $\chi^2(1) = 6.3$, $p = .012$, $\eta^2 = .30$.

Discussion

By directly comparing fixed and probabilistic sequence structures with randomly ordered stimuli, this study highlighted the different processes underlying the learning of probabilistic sequences. Participants exhibited learning of both fixed and probabilistic sequences in a variety of forms: reduction in response times, transfer of learning, and decreased variability. We found that the underlying learning processes are distinct for fixed and probabilistic sequences, such that both online and offline learning underlie the learning of fixed sequences, but only offline learning underlies the learning of probabilistic sequences. Together, these results offered a better understanding of motor learning in the serial reaction time task.

Using Probabilistic Sequences Enhances the Assessment of Motor Learning

The probabilistic sequences used in this study were generated using a Markov process. Markovian probabilistic sequences have been used previously and can be learned in the serial reaction time framework (Du et al., 2016). Here, we replicated and extended these findings by examining the variability in response time during the learning of Markovian probabilistic sequences and directly comparing the learning of this sequence structure with randomly ordered stimuli. Consistent with previous studies, the fixed sequence group exhibited learning of the assigned sequence and transfer of learning to a novel sequence as evidenced via a significant decrease in response time during the learning blocks (B1 and B4), an increase from B4 to B5, a decrease from B5 to B6, and a decrease between B5 and B7.

Importantly, the probabilistic sequence group also exhibited a decrease in response time through the learning blocks (B1–B4), a significant decrease from B5 to B6, and a significant decrease from B5 to B7 indicating both learning of the sequence and transfer of learning to a novel sequence. However, we were surprised to find that the probabilistic sequence group did not exhibit a significant increase in response time from B4 to B5. This finding indicates that participants were not perturbed by the appearance of randomly ordered stimuli in B5 and may reflect prior findings that increased variability during practice results in a greater rate of learning, despite poorer performance (Kitago & Krakauer, 2013; Seidler, 2007). This difference between fixed and probabilistic sequences may be akin to blocked versus variable practice. Variable practice provides a high contextual interference experience that improves learning compared with blocked practice (Li & Wright, 2000; Shea & Morgan, 1979) and may underlie the improved performance in B5 in the probabilistic group as they experienced increase task variability during B1–B4 due to the nature of probabilistic sequences. Thus, the learning of probabilistic sequences may represent learning that is more resilient to interference (Bönstrup et al., 2019; Robertson et al., 2004). This interference may also highlight the association between stimuli as evidenced by the substantial decrease in response times after the random block. As such, the extraction of information from a complex sequence may become more salient after the random block, making the relationship between stimuli in the subsequent block (B6) more prominent, albeit unconsciously, compared with the randomly ordered stimuli in B5. Monitoring the environment and extracting associations between related stimuli unconsciously is essential for motor learning as it occurs outside the laboratory. Thus, these findings suggest that along with fixed sequences including probabilistic sequences enhances the ecological validity of the serial reaction time task.

Different Processes Underlie the Learning of Fixed and Probabilistic Sequences

While mean block times provide overall trends of the response time, they do not reflect dynamic changes within a block. These dynamic changes are important to examine the underlying learning processes. Consistent with the literature (Du et al., 2016), online learning emerged as an important learning process in the fixed sequence group, but not in the probabilistic sequence group. Online learning is comprised of a trial-by-trial update of the sequence structure (Bornstein & Daw, 2012, 2013; Verstynen et al., 2012) and may be more cognitively expensive, by demanding attentional and working memory requirements, as the structure becomes more complex. For example, unlike learning a fixed sequence, in the probabilistic sequence group, online learning requires continuous updating of the estimation of the six-by-six transitional probabilities between the items while performing the task (Bornstein & Daw, 2012, 2013; Laming, 1969). Since the probabilistic sequence was more complex, online learning and maintenance of performance during the block could be too cognitively demanding and may explain the performance deterioration within the blocks. In addition, such online deterioration could subsequently result in misleading offline improvement in response time, leading to an assumption that offline improvements in probabilistic sequence learning resulted from reactive inhibition (Török, Janacsek, Nagy, Orbán, & Nemeth, 2017). Our results, however, indicate that this online deterioration does not appear to be due to fatigue since performance in the randomly ordered stimuli group would decline as well if fatigue were the cause and are consistent with recent findings (Bönstrup et al., 2019, 2020).

The presence of offline learning in both the fixed and probabilistic sequence groups suggests that the learning process continues to occur during the breaks and manifests as better performance in the subsequent block. Offline learning has previously been found to occur as a memory boost (Hotermans et al., 2006; Schmitz et al., 2009) or consolidation (Brown & Robertson, 2007; Handa, Rhee, & Wright, 2016; Robertson et al., 2004) at least 30 min to hours after a new sequence was learned. However, only a few studies have explored offline learning during the initial stage of learning the execution of motor sequences (Bönstrup et al., 2019, 2020) and learning the sequential orders of movements (Du & Clark, 2020; Du et al., 2016, 2017). In the present study, we were able to replicate our previous findings that offline learning underlies the learning of probabilistic sequences (Du et al., 2016). It is important to note, however, that due to differences in the tasks used in different studies, the underlying learning processes may be different. For example, Bönstrup and colleagues used a short sequence that participants knew prior to the start of the task and participants learned how to execute the task quickly (i.e., Bönstrup et al. [2019, 2020], while we used the serial reaction time task that focuses on the learning of the sequential order of movement by participants who are unaware of the presence of a sequence (Du et al., 2016). Thus, the nature of this rapid form of offline learning and why it takes place during the initial stage of motor sequence learning remain to be determined (Du & Clark, 2020; Du et al., 2016, 2017). In addition, the differential presence of online and offline learning in the fixed and probabilistic sequences suggests that these are two distinct processes, but further evidence is required to fully understand the processes underlying the fast, transient phase of motor learning.

Variability Is Important to Assess Learning

Previous studies using the serial reaction time task have focused on comparing mean response times to assess learning, but not the change in within-subject variability of response times, even though a reduction in motor performance variability has been a hallmark of motor learning (Cohen & Sternad, 2009; Wulf & Schmidt, 1997). The fixed and probabilistic sequence groups exhibited a reduction in variability during the learning blocks, but not the randomly ordered stimuli group. These results are consistent with previous findings that variability in motor performance decreases with learning (Cohen & Sternad, 2009; Newell, 1991; Newell & Shapiro, 1976). Variability represents motor exploration that is regulated by the motor system (Dhawale, Smith, & Ölveczky, 2017), tends to be larger during the beginning of the task, and can improve motor learning (Herzfeld & Shadmehr, 2014; Wu, Miyamoto, Castro, Ölveczky, & Smith, 2014). As learning progresses, the exploration, and thus variability, decreases (Dhawale, Miyamoto, Smith, & Ölveczky, 2019). We found reduced variability in both the fixed and probabilistic sequence groups, suggesting that variability is not affected by sequence structure, but that a reduction in variability is an important indicator of learning. Accordingly, the randomly ordered stimuli group's within-subject variability did not change since there was no sequence to be learned.

Implications for Future Serial Reaction Time Task Studies

Probabilistic sequences allow for the investigation of implicit learning processes that are less likely to be contaminated by explicit awareness of the sequence. These characteristics offer a compelling reason to use probabilistic sequences for the study of motor skill learning while addressing methodological problems with wide implications for future serial reaction time task studies.

The posttest indicated that participants who were assigned probabilistic sequences were less likely to differentiate chunks from their assigned sequence from other random chunks, but participants assigned to fixed sequences were able to identify chunks from their sequences. Additionally, although there was no difference in the mean ratings for the assigned sequences compared with the novel sequences in both fixed and probabilistic sequence groups, five participants were able to correctly identify their assigned fixed sequence, but no participants were able to correctly identify their assigned probabilistic sequence. The identification of parts of the assigned sequence, but not the entire sequence, suggests chunking, which is often found in sequence learning as it reduces working memory load (Bo & Seidler, 2009; Wymbs, Bassett, Mucha, Porter, & Grafton, 2012). This difference in the conscious awareness of chunks of the assigned sequence between the groups suggests that the knowledge of the sequence became explicit, and thus, learning did not remain implicit throughout the task in the fixed sequence group, but did remain implicit in the probabilistic sequence group. This finding is significant as participants can become aware of the sequence at different times in the learning process, thereby contaminating implicit learning in an unquantifiable manner. This confound is particularly problematic when applying neuroimaging methods to the serial reaction time framework to study the neural correlates of implicit learning since it is difficult to separate explicit and implicit learning using fixed sequences. Thus, the probabilistic structure is more likely to ensure implicit sequence learning by preventing confounding effects from explicit learning, thus providing a method to better assess the neural underpinnings of implicit motor sequence learning. Additionally, more complex sequences are more likely to be learned implicitly. A recent study found that when participants learned a fixed sequence in a dual task condition (i.e., with distraction) that reduced the engagement of explicit memory, online learning vanished while offline learning remained (Du & Clark, 2020), suggesting that offline learning is not an outcome of the complex structure of sequences. On the other hand, increased online learning in fixed sequences may be related to the emergence of explicit knowledge (Du et al., 2016). Similar effects of explicit knowledge on trial-by-trial learning in motor adaptation have also been reported (Malone & Bastian, 2010).

While previous studies have used similar methods to generate probabilistic sequences, such as a finite-state grammar (Jimenez & Mendez, 1999; Jiménez et al., 1996) and the alternate serial reaction time task (Feeney et al., 2002; Howard & Howard, 2001; Song et al., 2007), few studies have used probabilistic sequences generated by Markov processes to assess sequence learning with the classical serial reaction time framework. This method resulted in more complex and entirely probabilistic sequences and used the whole generated sequence to assess learning and trial-by-trial changes in response time. This study demonstrates that examining these dynamic trial-by-trial changes is critical to our understanding of underlying learning processes. Furthermore, the learning of these sequences may be more resilient to interference, perhaps due to the inherent variability in their structure. The ability to manipulate probabilities and determine the effects of different types of sequences on motor sequence learning may be useful in understanding the learning processes in greater depth. Most importantly, probabilistic sequences reflect the learning acquired in daily life, since ultimately our aim is to better understand motor skill learning that is adaptive to changes in the environment.

Interestingly, the randomly ordered stimuli group also displayed a continuous decrease in response time in the early blocks (B1–B4), but not in the subsequent blocks. Since there was no sequence to learn, the consistency in response time in the later blocks is not surprising. The modified serial reaction time task we used here included a more significant motor component (compared with a traditional serial reaction time task) that improved with practice, contributing to the reduction in response time in the early blocks. Previous serial reaction time task studies used fewer stimuli and responses than the modified version used here and practice effects are more likely to affect more complex tasks (Nissen & Bullemer, 1987). Thus, the improvement in the motor component of the task also highlights the importance of decomposing response time to better understand the separate contributions of reaction and movement time (Du & Clark, 2016; Moisello et al., 2009).

Conclusion

In sum, this study directly compared the learning of different types of sequence structures by examining their underlying learning processes, changes in variability, and transfer of learning to a novel sequence. We replicated and extended our previous findings that the initial stage of learning of probabilistic sequences involved only offline learning, while the learning of fixed sequences involved both online and offline learning. As probabilistic sequences add ecological validity to the serial reaction time framework to assess motor learning, as it occurs in daily life outside of the laboratory, the differential involvement of these learning processes in different sequence structures has important implications for our current understanding of motor learning. Further investigating the underlying learning processes is critical in understanding optimal parameters of motor learning and how learning changes developmentally and in clinical populations. This paper represents an essential starting point toward a deeper understanding of the dynamic motor learning process.

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