Operating Characteristics of the Implicit Learning System Supporting Serial Interception Sequence Learning

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The memory system that supports implicit perceptual-motor sequence learning relies on brain regions that operate separately from the explicit, medial temporal lobe memory system. The implicit learning system therefore likely has distinct operating characteristics and information processing constraints. To attempt to identify the limits of the implicit sequence learning mechanism, participants performed the serial interception sequence learning (SISL) task with covertly embedded repeating sequences that were much longer than most previous studies: ranging from 30 to 60 (Experiment 1) and 60 to 90 (Experiment 2) items in length. Robust sequence-specific learning was observed for sequences up to 80 items in length, extending the known capacity of implicit sequence learning. In Experiment 3, 12-item repeating sequences were embedded among increasing amounts of irrelevant nonrepeating sequences (from 20 to 80% of training trials). Despite high levels of irrelevant trials, learning occurred across conditions. A comparison of learning rates across all three experiments found a surprising degree of constancy in the rate of learning regardless of sequence length or embedded noise. Sequence learning appears to be constant with the logarithm of the number of sequence repetitions practiced during training. The consistency in learning rate across experiments and conditions implies that the mechanisms supporting implicit sequence learning are not capacity-constrained by very long sequences nor adversely affected by high rates of irrelevant sequences during training.

Keywords: implicit memory, sequence learning, statistical learning

Perceptual-motor sequence learning has been considered a canonical task for observing implicit learning since the seminal study by Nissen and Bullemer (1987) using the serial reaction time (SRT) task. Amnesic patients exhibit spared learning of a covertly embedded repeating sequence in a choice reaction time task despite damage to their medial temporal lobe memory system and an accompanying deficit in explicit, conscious knowledge (Nissen & Bullemer, 1987; Reber & Squire, 1994, 1998). The information learned by healthy participants is often outside awareness (e.g., Sanchez, Gobel, & Reber, 2010) and reflects the fact that performance improves even though participants in implicit perceptual-motor sequence learning studies are typically not informed about what they are learning. Rather than depending on conscious knowledge of the embedded repeating sequence, perceptual-motor sequence learning is often described as the gradual development of simple stimulus-response associations (Graybiel, 2008; Yin & Knowlton, 2006), which may be combined via statistical learning mechanisms into sequence knowledge (Perruchet & Pacton, 2006).

A large number of studies have used the SRT task to examine implicit perceptual-motor sequence learning (see, Abrahamse, Jiménez, Verwey, & Clegg, 2010). These studies have generally used sequences that require learning of relatively higher-order statistics, typically second-order conditionals (SOC; Reed & Johnson, 1994). In an SOC sequence, the smallest relevant statistical structure is a three-item trigram; in order to predict an item in the sequence, information about the preceding two items must be available. The learning mechanism is required to continuously incorporate additional information about recent stimuli or responses with current stimulus-response associations, possibly through a chunking mechanism (Graybiel, 1998).

Computational models that attempt to capture human perceptual-motor sequence learning have either incorporated chunking mechanisms (Servan-Schreiber & Anderson, 1990) or used simple recurrent network (SRN) models (Cleeremans & McClelland, 1991; Cleeremans, Servan-Schreiber, & McClelland, 1989) that use interitem statistics to essentially extract a distributed representation of chunks. While there has been some debate about whether chunk learning is the best description of the sequence learning mechanism (Jiménez, 2008; Kirsch, Sebald, & Hoffmann, 2010; Koch & Hoffmann, 2000), alternate descriptions have tended to emphasize statistics such as relational patterns (Koch & Hoffmann, 2000) or transitional probabilities (Hunt & Aslin, 2001) that often incorporate similar ideas. The statistical learning that underlies sequence learning has also been studied in other contexts, such as language (Saffran, 2003; Saffran, Aslin, & Newport, 1996) and visual perception (Fiser, 2009), and may be a domain-general characteristic of underlying mechanisms (Hunt & Aslin, 2001; Perruchet & Pacton, 2006).

One of the challenges for statistical learning models is that there are a large number of potential statistics to maintain in order to identify which regularities are important for predicting future experiences or behavior. Most SRT studies of sequence learning have assessed sequences up to 12 items in length (which is the shortest possible SOC sequence with four alternative choice responses), or used probabilistic sequences that do not depend entirely on deterministic SOC statistics (Cleeremans & McClelland, 1991; Howard & Howard, 1997; Jiménez, Mendez, & Cleeremans, 1996; Schvaneveldt & Gomez, 1998). However, learning of more complex statistical regularities has been observed (Fiser & Aslin, 2002; Howard & Howard, 1997; Hunt & Aslin, 2001; Remillard & Clark, 2001; Schvaneveldt & Gomez, 1998), including up to sixth-order conditionals (Remillard, 2008, 2010). Using a new paradigm for studying perceptual-motor sequence learning, the serial interception sequence learning (SISL) task, the amount of statistical information required to maintain can be systematically increased in order to examine whether sequence learning rate slows as a function of statistical load and whether there is a level of statistical adversity that hinders learning.

The SISL task is based on the structure of the SRT in that visual cues are used to pace participants through a repeating sequence of motor actions without their awareness of the embedded repeating sequence. Instead of making a choice reaction time response, participants make an interception response to a vertically moving cue by pressing a response button as the cue passes through a target zone. As can be seen in Figure 1, the SISL task is unique from the SRT in that upcoming responses are visible on the screen
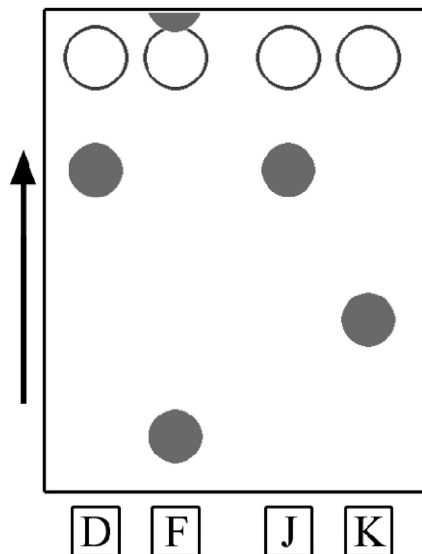

Figure 1. The SISL task. Circular cues scroll vertically across a screen toward one of four target zones marked as rings. Participants press the corresponding key(s) (D, F, J, or K) on the keyboard and attempt to time their responses so that the key is pressed just as the cue moves through the target zone. As shown, the participant would be timing the press of the "D" and "J" keys to coincide with the cues arriving at the vertical circle and immediately planning subsequent responses, "K" then "F". Dual-button responses, such as DJ, were only used in Experiments 1 and 2. In Experiment 3, the targets were at the bottom of the screen and the circles scrolled downward.

so that participants can prepare subsequent responses and are required to control the timing between the current response and those forthcoming. This preview creates a constantly changing visuospatial array that likely recruits various cortical motor areas during performance and learning (Bosco, Carrozzo, & Lacquaniti, 2008; Port, Kruse, Lee, & Georgopoulos, 2001). The perceptual characteristics of the SISL task make it possible that there is a contribution to task learning from perceptual-learning mechanisms, such as those that support contextual cuing (Chun & Jian, 1998), in addition to sequence learning mechanisms. In the SISL task, participants can rapidly learn a 12-item repeating sequence (of four motor actions, just as in the SRT task) largely in the absence of explicit awareness (Sanchez et al., 2010). The task can also be modified to incorporate interresponse timing, which then becomes part of the learned sequence (Gobel, Sanchez, & Reber, 2011).

In Experiments 1 and 2 here, the task is further extended by allowing for multiple keypress responses: pressing two response keys simultaneously to a pair of moving cues. This extension provides a set of 10 possible motor actions (four single-keypress responses and six double-keypress combination responses) that can be combined to create long repeating sequences that do not require learning conditional probabilities higher than second-order. In Experiment 1, participants performed the task with covert embedded repeating sequences ranging from 30 to 60 items in length. Experiment 2 extended these results with sequences from 60 to 90 items long across two training sessions on separate days. The key question across these experiments is whether sequence learning continues even when the target repeating sequence is exceptionally long, by prior research standards. If the information-processing capacity of the implicit perceptual-motor sequence learning system is constrained by sequence length, significant learning will likely not be observed for long sequences. If learning is observed across sequence lengths, the rate of learning will be examined to identify whether increasing sequence length slows the rate of learning. Because there is more information to track in longer sequences, a capacity limit in the learning mechanism should lead to a reduction in learning rate as sequence length increases.

In a third experiment, a 12-item repeating sequence was embedded with various amounts of nonrepeating 12-item segments during training in order to identify the effect of statistical noise on learning rate. The addition of nonrepeating segments provides a different challenge for sequence learning than extending the sequence length. The nonrepeating segments were constructed so that all possible SOCs occur equally often, as well as first-order conditionals and response frequency. Under these conditions, the predictability of the next response decreases as the amount of nonrepeating sequence trials during training increases, because increasing nonrepeating segment trials directly increases the amount of practice with nonrepeating SOC probabilities. If the implicit skill learning mechanism depends solely on simple statistics (e.g., the ratio of trained and untrained probabilities), learning should be increasingly slowed as the amount of noise increases, because the statistics are less predictive at higher noise.

Across all three experiments, a key question is whether the rate of learning is affected by the manipulations of sequence length or interpolated nonrepeating (noise) sequences. In each experiment, the sequence-specific learning at the end of the one- or two-hour

training session is reported. However, an important alternative way to characterize the learning rate is to examine the amount of sequence-specific learning that occurs as a function of the experience with the sequence as measured by the number of repetitions. The learning rate data across all three experiments are reevaluated as a function of the number of sequence repetitions in a cross-experiment analysis after Experiments 1–3.

Experiment 1 Method

Participants

Seventy-six Northwestern University undergraduates (50 women, 26 men, $M_{age} = 18.6$ years) received course credit for participating.

The SISL Task

Participants observed cues (blue circles), which scrolled vertically up a computer monitor in one of four horizontal locations toward corresponding yellow target rings at the top of the screen (see Figure 1). Participants were instructed to press the associated key (D, F, J, or K) when a circle overlapped as closely as possible with its target ring. One or two cues could be in the target area simultaneously, requiring single or double keypress responses. There were a total of 10 possible responses (four single-key, six possible dual-key combinations). Responses were scored as correct if the participant pressed only the correct corresponding key(s) while the cue was within a given distance from the target zone (roughly 180 ms from perfect overlap). Feedback was provided via the target rings flashing green to correct keypresses and red to errors as well as a score bar located above the target rings, which increased in size by 10% for correct responses and decreased by 2% for errors.

Cues initially moved with a velocity of 11.4 degrees/s and reached the target zones 2.0 s after first appearing at the bottom of the screen. The interval between cues was initially 500 ms, so that three to four cues appeared at a time on the screen, allowing for planning of upcoming responses. During training, percent-correct performance was assessed after every 50 trials and the overall speed of the cues was adjusted to increase or decrease the difficulty of the task adaptively. Performance at 90% correct or better decreased the time-to-target by 50 ms, while 70 to 89% correct decreased it by 25 ms. Performance at 11 to 30% increased time-to-target by 25 ms, and performance of 10% or lower decreased it by 50 ms. The interstimulus interval was adjusted with cue velocity such that the visual distance between cues remained constant through training.

Participants were not informed that the cues followed a repeating sequence of 30-, 40-, 50-, or 60-items in length on 80% of the training trials. The training sequences were constructed with similar constraints to the SOC structure described in Reed and Johnson (1994). The sequences had no repeated items (e.g., no K-K), no completion runs (e.g., no D-F-J-K), and no paired items repeated in a sequence (e.g., if K-D was a part of the sequence, it would not appear elsewhere in the same sequence). The double-motor operator items (DF, DJ, DK, FJ, FK, and JK) were treated as separate responses, so that items which included overlapping

motor operators (e.g., F-DF-DK) were not considered item repetitions.

Procedure

Participants were randomly assigned to one of four sequence-length training conditions and one of three repeating sequences within each condition. Before training, participants received 24 random trials of practice to familiarize themselves with the SISL task. The training phase of the experiment consisted of four 750-trial blocks (3000 trials total) with short, self-terminated rest breaks between blocks. Each block consisted of 600 trials of the trained sequence and 150 trials of nonrepeating sequence segments (20% of trials), resulting in 20, 15, 12, or 10 sequence repetitions per block (30-, 40-, 50-, and 60-item sequence lengths, respectively). The blocks were structured so that a novel segment occurred after every one or two trained sequence repetitions, and each new training block began with a novel segment. This block structure masked the first and the last item of each sequence to inhibit explicit sequence knowledge. The nonrepeating segments were 15, 10, 25, or 15 items in length across conditions (30, 40, 50, and 60 items, respectively). The sequences and novel segments were constructed following the same constraints, but the novel segments did not repeat. The nonrepeating segments used the 10 responses equally often (as in the training sequences) but had minimal overlap with the training sequences at the SOC (trigram) level (810 unique trigrams were available while avoiding response repetition).

After training, three tests of sequence knowledge were administered. First, participants performed an implicit knowledge test using the SISL task, consisting of the three repeating sequences for their sequence length condition (one trained, two novel). Each sequence was performed four times in the 40- to 60-length conditions and eight times in the 30-item condition in order to roughly maintain session duration across conditions. The order of the sequences was randomized and no indication of breaks between the sequences was given. Implicit sequence knowledge was assessed by comparing SISL performance on the practiced sequence with the two foil sequences.

After the implicit test of sequence knowledge, participants were informed that there had been a repeating sequence during training and were given a recognition test. However, due to a programming error, the recognition test was not administered properly and the resulting data were unusable. Participants were also given a free recall test in which participants saw the screen with only the yellow targets and used the keyboard to indicate their best guess as to what they thought the repeating sequence had been. Participants were required to generate 30 responses. The sequences provided during the recall test were compared with the trained sequence, the two foil sequences from the implicit test, and two unseen, novel sequences; the longest matching subsequence was identified for each.

Experiment 1 Results

Sequence Training Performance

Sequence-specific learning, calculated as the percent-correct performance difference between the trained sequence and the

novel segments during training, was analyzed with a mixed 4 × 4 analysis of variance (ANOVA) of length group (30, 40, 50, and 60 items) and training block. A trend analysis revealed a linear increase in sequence-specific learning across the four training blocks, $F(1, 72) = 53.82, p < .001, \eta^2 = .41$ (Figure 2a), resulting in the trained sequence being performed significantly better ($M = 57.41\%, SE = 1.16\%$) than the novel segments ($M = 50.46\%, SE = 1.26\%$) during the last block of training. All groups exhibited similar sequence learning throughout training because there was neither a main effect of length condition nor a significant interaction.

Implicit Sequence Knowledge Posttest

At test, all of the sequence length groups performed better on the trained sequence ($M = 56.74\%, SE = 1.44\%$) than on the foil sequences ($M = 51.05\%, SE = 1.42\%$), $F(1, 72) = 38.44, p < .001, \eta^2 = .31$. However, the percent-correct performance difference at test decreased linearly across conditions as the sequence lengths increased, $F(1, 72) = 11.40, p < .01, \eta^2 = .14$, indicating more sequence-specific knowledge of the shorter sequences. The performance difference between the trained sequence and mean of the foil sequences was significant in the 30-item ($M = 11.00\%, SE = 1.99\%$), $t(14) = 5.52, p < .001$, 40-item ($M = 7.45\%, SE = 2.43\%$), $t(17) = 3.06, p < .01$, and 50-item ($M = 4.86\%, SE = 2.07\%$), $t(18) = 2.35, p < .05$, conditions (Figure 2b). The performance difference during training was not observed for the 60-item condition at test, and the slight performance improvement for the trained sequence was not reliable ($M = 1.71\%, SE = 1.54\%$), $p = .28$.

Explicit Sequence Knowledge Posttest

The sequences generated by the participants as they attempted to recall the trained sequence matched the trained sequence ($M = 3.37$ items, $SE = .11$) better than the foil sequences ($M = 2.87$ items, $SE = .04$), $F(1, 72) = 17.68, p < .001, \eta^2 = .18$. A significant interaction was found between the matched subsequence lengths (novel/foil vs. trained) and the sequence length condition, $F(3, 72) = 3.17, p < .05, \eta^2 = .10$, suggesting that explicit knowledge varied across the groups. A recall score for each condition was calculated as the difference between the length of the longest matching subsequence to the trained sequence and the mean length to the foil sequences. The recall score in the 30-item condition was only marginal ($M = .62, SE = .31$), $t(14) = 2.01, p = .06$, and neither the 40-item ($M = .26, SE = .16$), $t(17) = 1.65, p > .10$, nor the 60-item ($M = .10, SE = .15$), $t < 1$, length groups produced a sequence that matched the trained sequence better than the foils. Only participants in the 50-item condition had a significant recall score ($M = 1.01, SE = .32$), $t(18) = 3.16, p < .01$, generating a matched subsequence to the trained sequence of 3.89 items in length ($SE = .30$).

Nonspecific Learning and Performance Effects

Nonspecific learning was assessed by average cue velocity (or time in seconds from the cue entering the screen to crossing the target zone), which was adjusted adaptively during training, dependent on the individual participant's performance level. Cue velocity, averaged over the first block, was 1.92 seconds ($SE = .01$) across all conditions. The cue velocity increased in a linear
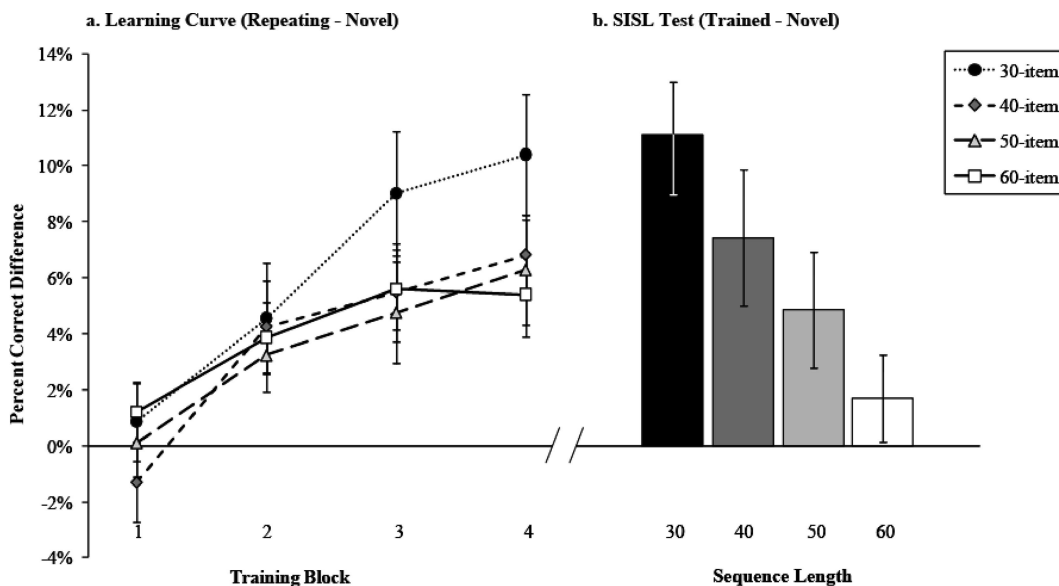

Figure 2. Experiment 1 sequence-specific learning curve and test performance. Each training block consisted of 750 trials separated by a short rest break. The learning curve (a) shows the gradual sequence learning throughout training. The percent-correct difference is the difference between the percent correct on the repeating sequence trials and the nonrepeating novel trials within a block. The percent correct difference at test (b) is the percent correct difference between the trained sequence trials and the novel sequence trials. Error bars reflect the standard error of the mean.

fashion significantly across training, $F(1, 72) = 261.08$, $p < .001$, $\eta^2 = .78$, and did not differ significantly across groups (see Table 1).

To assess whether participants' error rates reflect sequential dependencies (streaks of correct or incorrect responses), a probability ratio was calculated for each participant as the probability of a correct response versus an incorrect response, following a correct response. A ratio greater than one indicates that correct responses tend to be followed by correct responses. The ratio was consistently greater than one, and generally consistent among the 30-item ($M = 2.40$, $SE = .25$), 40-item ($M = 2.62$, $SE = .36$), 50-item ($M = 1.96$, $SE = .12$), and 60-item ($M = 2.28$, $SE = .17$) groups on the trained test sequences, $F(3, 72) = 1.35$, $p = .26$. During performance of foil sequences at test, the ratio was maintained ($M = 2.25$, $SE = .08$), suggesting that this effect is a general performance characteristic of the SISL task and is not associated with sequence knowledge.

An analysis of the 10 individual motor operators was conducted to compare the single- and double-keypress responses (prior perceptual-motor sequence learning tasks have generally relied on single-keypress response paradigms). A one-way ANOVA indicated reliable differences in the performance rates across the 10 operators during SISL test trained sequence performance, Greenhouse-Geisser correction, $F(7.37, 552.62) = 13.92$, $p < .001$, $\eta^2 = .16$. Four of the possible double-button responses were performed at higher rates ($M = 58.55\%$, $SE = 1.37\%$) than all other possible responses: the index and middle finger combination for both the left and right hands (DF and JK), as well as the two index fingers (FJ) and two middle fingers (DK). Single-button responses were performed better ($M = 54.39\%$, $SE = 1.52\%$) than the other two double-button responses (DJ, FK; $M = 50.47\%$, $SE = 1.91\%$). This same pattern of operator performance was also present during the foil performance at test, and was present early in training (averaged across performance during the first block), indicating that this phenomenon is also a nonspecific performance effect.

Experiment 1 Discussion

Participants were able to learn repeating sequences that were 30, 40, or 50 items long within a single training session. While only marginal learning was observed of the 60-item sequences, the single training session may have been too short to provide enough repetitions of the sequence for reliable learning to emerge. Increasing the complexity of the task to require a mix of single- and double-button responses did not appear to interfere with participants' ability to learn the embedded repeating sequences (compared to previous reports). In addition to identifying reliable sequence-specific learning, participants also exhibited task-based, nonspecific performance effects such as higher performance on a subset of the two-button response operators and a sequential dependency effect, whereby correct responses tended to be followed by additional correct responses. Participants performing the SISL task sometimes experience performance streaks of correct responses, akin to the "hot hand" in sports (Gilovich, Vallone, & Tversky, 1985). The enhanced performance for a subset of the double-button responses may reflect a more general motor effect for responses that depend on the same finger for both hands (index finger for FJ, middle finger for DK) or two fingers from the same hand (DF, JK), such as the motor overflow effect (Liederman & Foley, 1987).

These results found sequence learning for much longer repeating sequences than have previously been studied, and the limitation on the learnable length of a repeating sequence appears to have been constrained by the 1-hr training session. To assess the possibility that sequence learning was mainly constrained by training time, Experiment 2 extended the length of training across two sessions and examined learning for even longer repeating sequences. Also, Experiment 1 found some evidence of explicit knowledge, which may have been underestimated due to missing the sensitive test of sequence recognition. Experiment 2 includes a recognition test, as well as the recall test, to better assess explicit awareness of very long sequences during training.

Experiment 2 Method

Participants

Fifty-eight undergraduates from Northwestern University received course credit for participating. Two participants were removed from the analyses due to a lack of performance during the SISL test (not responding to over half of the trials), resulting in 56 participants (31 women, 25 men, $M_{age} = 18.9$ years).

The SISL Task

The SISL task parameters used for Experiment 2 were identical to those for Experiment 1, except for minor modifications to the adaptive velocity parameters. In Experiment 2, performance was assessed after each repetition of the trained sequence so that novel sequence segment performance did not affect cue velocity. Performance of 80% correct or better decreased the time-to-target by 50 ms, and performance 65 to 79% correct decreased the time-to-target by 25 ms. Performance between 26 and 64% correct increased the time-to-target by 25 ms, and performance 25% or below increased it by 50 ms. Cue velocity at the end of training determined the constant velocity during the SISL and recognition tests. The training sequences and novel segments were constructed following the guidelines from Experiment 1.

Procedure

Experiment 2 took place over two 1-hr sessions, separated by 48 hours. Participants were randomly assigned to a sequence length of

Table 1
Mean (SE) Values

Sequence length	Trained sequence performance	Novel/foil performance	Cue velocity
Last block of training			
30 items	58.84% (1.94)	48.44% (2.39)	1.41 (0.10)
40 items	55.00% (3.31)	48.19% (2.66)	1.43 (0.07)
50 items	59.55% (1.78)	53.26% (2.97)	1.46 (0.07)
60 items	56.63% (2.01)	51.22% (2.07)	1.59 (0.06)
SISL test			
30 items	53.08% (3.66)	42.08% (3.22)	1.36 (0.10)
40 items	59.93% (3.57)	52.48% (2.83)	1.40 (0.07)
50 items	57.84% (2.14)	52.99% (3.06)	1.40 (0.07)
60 items	55.74% (2.40)	54.04% (1.94)	1.54 (0.05)

60, 70, 80, or 90 items. Within each sequence-length group, participants were randomly assigned to train on one of three possible sequences. Before training, participants received 24 random practice trials to familiarize themselves with the SISL task. The training phase consisted of nine 675- or 700-trial blocks, which were separated by self-terminated rest breaks; six blocks of training were conducted on day one and three on day two. Training was immediately followed by implicit and explicit tests of sequence knowledge. The 60- and 80-item sequence length conditions used 700-trial training blocks with novel nonrepeating segment lengths of 15 and 20 items, respectively. The 70- and 90-item sequence length conditions featured 675-trial training blocks with novel segment lengths of 35 and 45 items, respectively. Novel segments were included after every one or two trained sequence repetitions to maintain a rate of 20% nonrepeating sequence trials.

The implicit SISL test was administered directly after training (and a self-terminated rest break) and consisted of each of the three sequences (trained sequence and two novel foils) performed four times. After the implicit test, participants were made aware of the repeated sequence during training and completed an explicit recognition test. During the recognition test, participants watched and responded to five sequences—the three possible repeating sequences and two novel foils—and immediately rated each sequence on a scale from −10 (*sure the sequence had not been the trained sequence*) to 10 (*sure the sequence had been the trained sequence*) as to how likely it was that it had been practiced initially, with 0 rated as *unsure*. Participants had the SISL training and test structure explicitly explained to them so they understood that they were attempting to recognize the sequence during training, not the sequences that appeared later, during the test phase. Participants were then given a recall test during which they attempted to recall as much of the trained sequence as possible in 30 responses, as in Experiment 1.

Experiment 2 Results

Sequence Training Performance

Sequence-specific learning during training, calculated as the percent-correct difference between the sequence performance and the novel segment performance during training, was analyzed with a 4 × 9 ANOVA of length condition (60, 70, 80, and 90 items) and training block (see Table 2). There was a linear increase in sequence-specific learning throughout training, $F(1, 52) = 20.98$ $p < .001$, $\eta^2 = .24$, such that by the end of training (averaged across the last block) there was a significant difference between the performance on the trained sequences ($M = 60.76\%$, $SE = 1.14\%$) and the novel segments ($M = 55.75\%$, $SE = 1.36\%$), $F(1, 52) = 27.30$, $p < .001$, $\eta^2 = .29$. An interaction between sequence-length group and block suggests that the groups did not learn the same amount in each block, $F(3, 52) = 4.97$, $p < .01$, $\eta^2 = .17$ (see Figure 3a). Less sequence knowledge was exhibited by groups receiving longer sequences during training, $F(1, 52) = 15.16$, $p < .001$, $\eta^2 = .22$.

Implicit Sequence Knowledge Posttest

At test, the performance difference between the trained sequence and mean of the foil sequences was significant in the

Table 2
Mean (SE) Values

Sequence length	Trained sequence performance	Novel/foil performance	Cue velocity
Last block of training			
60 items	59.12% (2.43)	49.05% (3.09)	1.24 (0.09)
70 items	62.46% (1.42)	55.82% (2.56)	1.23 (0.08)
80 items	61.75% (0.97)	56.87% (2.23)	1.17 (0.05)
90 items	60.00% (3.17)	60.65% (2.18)	1.30 (0.07)
SISL test			
60 items	63.24% (3.04)	55.24% (2.50)	1.24 (0.09)
70 items	61.84% (2.27)	52.18% (2.88)	1.23 (0.09)
80 items	66.78% (1.24)	60.73% (1.27)	1.16 (0.05)
90 items	61.02% (2.83)	59.57% (2.53)	1.29 (0.06)

60-item ($M = 8.01\%$, $SE = 2.69\%$), $t(13) = 2.97$, $p < .05$, 70-item ($M = 9.66\%$, $SE = 1.88\%$), $t(12) = 5.12$, $p < .001$, and 80-item ($M = 6.05\%$, $SE = 1.41\%$), $t(12) = 4.28$, $p < .01$ conditions (Figure 3b). However, the difference at test in the 90-item condition was not reliable ($M = 1.46\%$, $SE = 2.02\%$), $t < 1$. Across all groups, performance was better for the trained sequence ($M = 63.76\%$, $SE = 1.26\%$) than the foil sequences ($M = 57.04\%$, $SE = 1.25\%$), $F(1, 52) = 37.22$, $p < .001$, $\eta^2 = .37$, but sequence-specific knowledge decreased with increasing sequence length, $F(1, 52) = 6.55$, $p < .05$, $\eta^2 = .11$.

Explicit Sequence Knowledge Posttest

Participants provided higher confidence ratings to their trained sequence ($M = 2.72$, $SE = .66$) than to the mean of the foil sequences ($M = -.25$, $SE = .32$) during the recognition test, $F(1, 52) = 15.65$, $p < .001$, $\eta^2 = .23$. There was neither a main effect of sequence-length group nor an interaction effect, $Fs < 1$. However, recognition rating did not correlate with sequence performance on the implicit test, $r = -.03$. On the recall test, participants were unable to generate a sequence that matched the trained sequence ($M = 3.29$, $SE = .10$) reliably better than the mean of the foil sequences ($M = 3.17$, $SE = .04$), $F < 1$. This result was consistent across the four conditions because there was no main effect of sequence length or an interaction, $Fs < 1$.

Nonspecific Learning and Performance Effects

As in Experiment 1, the cue velocity also increased linearly across training, $F(1, 52) = 431.71$, $p < .001$, $\eta^2 = .89$, and the variance between sequence length conditions was not significant (see Table 2). The sequential dependency ratios were also similar to Experiment 1. The ratio during trained sequence performance at test ($M = 2.07$, $SE = .07$) did not vary across sequence length conditions, $F < 1$, and was slightly lower than during foil sequence performance ($M = 2.23$, $SE = .08$), $t(55) = 2.70$, $p < .01$, suggesting this effect was not sequence-specific. The pattern of performance across the 10 motor operators in Experiment 2 was also similar to Experiment 1. The same four double-button motor operators (DF, JK, DK, FJ) were performed with a reliably higher accuracy rate ($M = 66.93\%$, $SE = 1.74\%$) than both the other double-button ($M = $
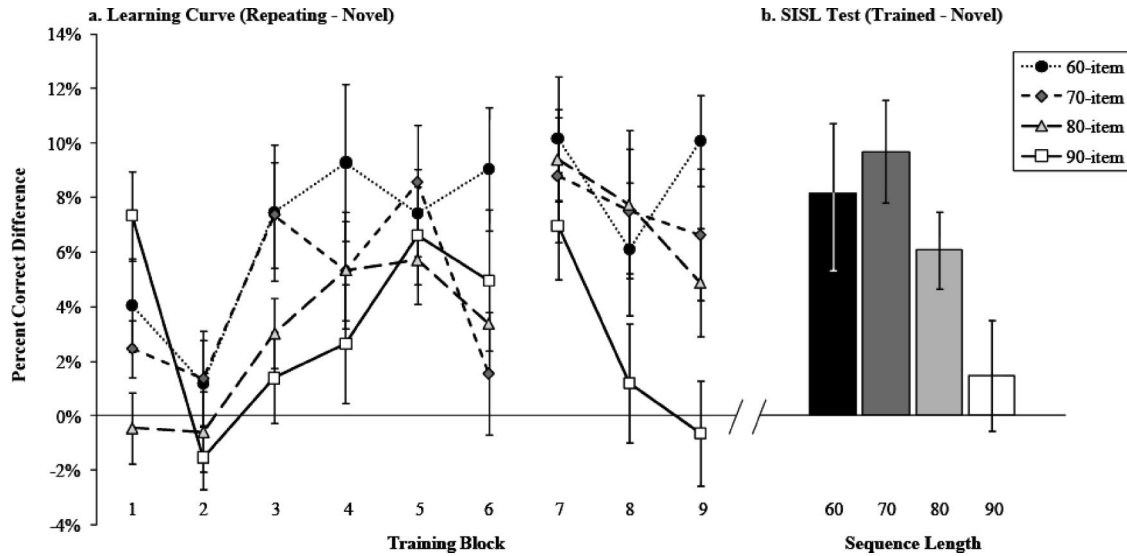
Figure 3. Experiment 2 sequence-specific learning curve and test performance. Each training block consisted of 675 or 700 trials separated by a short rest break. The learning curve (a) shows the gradual sequence learning throughout training. The percent-correct difference is the difference between the percent correct on the repeating sequence trials and the nonrepeating novel trials within a block. The gap between blocks 6 and 7 represents the 48-hr time delay between sessions. The percent-correct difference at test (b) is the percent correct difference between the trained sequence trials and the novel sequence trials. Error bars reflect the standard error of the mean.

58.49%, *SE* = 2.36%) and single-button operators (*M* = 57.53%, *SE* = 1.96%). This pattern of motor operator performance was observed in the foil performance at test, again indicating this was not a sequence-specific effect.

Experiment 2 Discussion

The results from Experiment 2 confirm that sequences of 60 to 80 items can be learned in two hours of training. While learning was not robust for the 90-item sequences, it is not clear whether this reflects a capacity constraint on implicit sequence learning or simply the fact that even over two hours of training, participants could not complete a sufficient number of repetitions of the 90-item sequence. The SISL test results of Experiment 2 are similar to those of Experiment 1 in that the sequence-specific learning effects were reduced for longer sequences. However, with a fixed amount of training time, shorter sequences repeated more often than the longer sequences during training. Of particular note, the 60-item sequence was not reliably learned in a single session in Experiment 1, but with additional practice over two sessions, sequences of this length were reliably learned. Participants also exhibited some recognition memory for the long sequences practiced in Experiment 2. However, recall scores indicated that, unsurprisingly, participants could not reproduce a substantial portion of these long sequences. Due to the difficulty of memorizing an entire 60- to 80-item sequence (especially at the pace of the SISL task), it seems likely that participants were recognizing short fragments of the repeating sequence and that test performance did not depend materially on explicit sequence knowledge.

The ability to learn these exceptionally long repeating sequences poses a question of what knowledge participants have acquired. It is possible the participants learned the entirety of the sequence as a single element, but prior sequence-learning research has suggested learning occurs in shorter chunks, such as three-item trigrams. In a typical 12-item SOC sequence, the trigram is the smallest element that can be used to reliably predict the next cue. Although the repeating sequences used here were constructed with similar constraints, the 10 possible motor responses dictate that a fully SOC sequence would be 90-items long, and shorter sequences could be learned with a combination of bigram and trigram information. Although sequence-specific learning expressed at test decreased as sequence length increased, the current analysis does not address whether the learning rate is slower for longer sequences because the longer sequences were repeated less frequently during training (but see below). If there is a limit to the response contingencies that can be simultaneously learned, longer sequences might be more challenging and learned more slowly.

Another method for creating this kind of challenge is to increase the relative rate of the nonrepeating segments to make the task of predicting the next sequence item more difficult. In Experiment 3, participants trained on a traditional 12-item SOC sequence, but with varying amounts of interspersed nonrepeating segments, ranging from 20 to 80% of the training trials. If the statistical learning mechanism is maintaining simple SOC statistics, the conditions with increased amounts of nonrepeating segments should be more difficult, because trigrams not embedded in the repeating sequence will be occurring with much higher frequency, making the sequence-specific statistics less predictable. In this

case, the learning rate should be slower as the percentage of nonrepeating segments increases.

Experiment 3 Method

Participants

Forty-seven undergraduates (16 women, 31 men, $M_{age} = 19.3$ years) from Northwestern University received course credit for participating.

The SISL Task

Only single-key responses (D, F, J, K) were used, and minor visual changes were made to the SISL task. Cues scrolled down from the top of the screen toward targets near the bottom of the screen (closer to the keyboard) and a frame was placed around the task. Feedback about performance was provided by a performance meter on the left side of the cue-response area (correct and incorrect responses moved the meter by 2 pixels) and a score on the right side of the cue-response area that increased with correct responses (correct responses when the target was in the optimal location yielded a larger score increase than when the target was somewhat offset). The initial scrolling velocity was 10 degrees/s (364 pixels/s) so that the cues would reach the target zone 1600 ms after first appearing on the screen. The adaptive velocity followed the same guidelines as Experiment 2, but was based on performance after every 60 trials.

Procedure

Participants were randomly assigned to one of four "noise" conditions (20, 40, 60, and 80% nonrepeating, novel segments during training) and to one of three 12-item SOC training sequences. A timing sequence of short- and long-interstimulus intervals (2.5 and 5 cue lengths, respectively) was embedded with each sequence order and was the same (S-L-L-S-L-S-L-S-S-L-L-S) for every sequence and noise segment iteration. Prior to training, participants received 24 random practice trials to familiarize themselves with the SISL task. Training consisted of six 480-trial blocks separated by self-terminated rest breaks, resulting in 2880 trials of training. The training blocks were structured so that training and nonrepeating novel segments were always presented in their entirety (all 12 trials in order) and were evenly dispersed over every 60 trials. The novel segments never repeated and were randomly selected from a list of unique 12-item SOC sequences.

The five sequences chosen for the implicit and recognition tests were selected in order to evenly distribute the amount of trigram overlap between the sequences. All five sequences overlapped each other by two to four trigrams (e.g., training sequences 1 and 2 both had the trigrams D-F-D and D-K-F). Reversals (e.g., D-F-D, K-J-K) were also controlled for so that each sequence contained between three and four reversals, so to minimize performance consequences previously seen in the SRT task (Jiménez, Vaquero, & Lupianez, 2006).

After training, participants received the same implicit sequence knowledge test as in Experiments 1 and 2. The implicit test was one 540-trial block consisting of 15 repetitions of each of the three

possible 12-item training sequences (trained sequence and two foils). Sequences were presented in groups of five repetitions each (60 trials). Sequence-specific performance improvements were measured as the percent-correct difference between the mean performance on the trained sequence and the mean performance on the two novel sequences. The recognition test was administered as it was in Experiment 2, and included the three possible training sequences along with two completely novel, unseen SOC sequences. Each sequence was shown in one 24-trial block, which consisted of two repetitions of the sequence. For the sequence generation recall test, participants were required to make 24 motor responses.

Experiment 3 Results

Sequence Training Performance

Sequence-specific learning, calculated as the percent-correct difference between the repeating sequence performance and the novel segment performance during training, was analyzed with a 4×6 ANOVA of noise condition (20, 40, 60, and 80%) and training block (performance averaged every block). The sequence-specific performance benefit increased gradually in a linear trend throughout training, $F(1, 43) = 6.19, p < .05, \eta^2 = .11$ (see Figure 4), so that by the end of training (averaged across the last block) participants were reliably performing the trained sequence ($M = 59.15\%$, $SE = 1.24\%$) better than the novel segments ($M = 53.90\%$, $SE = 1.12\%$), $F(1, 43) = 19.19, p < .001, \eta^2 = .28$. The main effect of noise condition, $F(3, 43) = 12.13, p < .001, \eta^2 = .25$, reflects the fact that less sequence-specific knowledge was expressed by participants in the higher noise conditions, which is also seen in a reliable difference in performance on the final block, $F(1, 43) = 6.75, p < .05, \eta^2 = .13$.

Implicit Sequence Knowledge Posttest

At test, the 20% group exhibited the largest sequence-specific benefit of 12.38% ($SE = 2.90\%$), $t(11) = 4.27, p = .001$, while the 40 and 60% groups also displayed significant learning ($M = 9.91\%$, $SE = 1.90\%$), $t(11) = 5.22, p < .001$; ($M = 7.78\%$, $SE = 2.12\%$), $t(11) = 3.66, p < .01$, respectively. The 80% group had a positive sequence-specific performance increase ($M = 3.51\%$, $SE = 2.10\%$), but the performance difference was not significant, $t(10) = 1.67, p = .13$. Overall, participants performed better on their trained sequence ($M = 59.28\%$, $SE = 1.65$) than on the novel foil sequences at test ($M = 50.89\%$, $SE = 1.29\%$), $F(1, 43) = 53.21, p < .001, \eta^2 = .51$, but the sequence-specific benefit decreased as noise percent increased, $F(1, 43) = 7.68, p < .01, \eta^2 = .15$.

Explicit Sequence Knowledge Posttest

Participants provided similar confidence ratings for the trained sequences ($M = 1.47$, $SE = .79$) and the four foil sequences ($M = 1.41$, $SE = .43$) on the recognition test. A 2×4 mixed ANOVA of sequence type (trained and foils) and noise condition (20, 40, 60, and 80%) found that these ratings did not vary across groups or produce an interaction, $Fs < 1$, suggesting that participants could not recognize the sequence they had practiced during train-
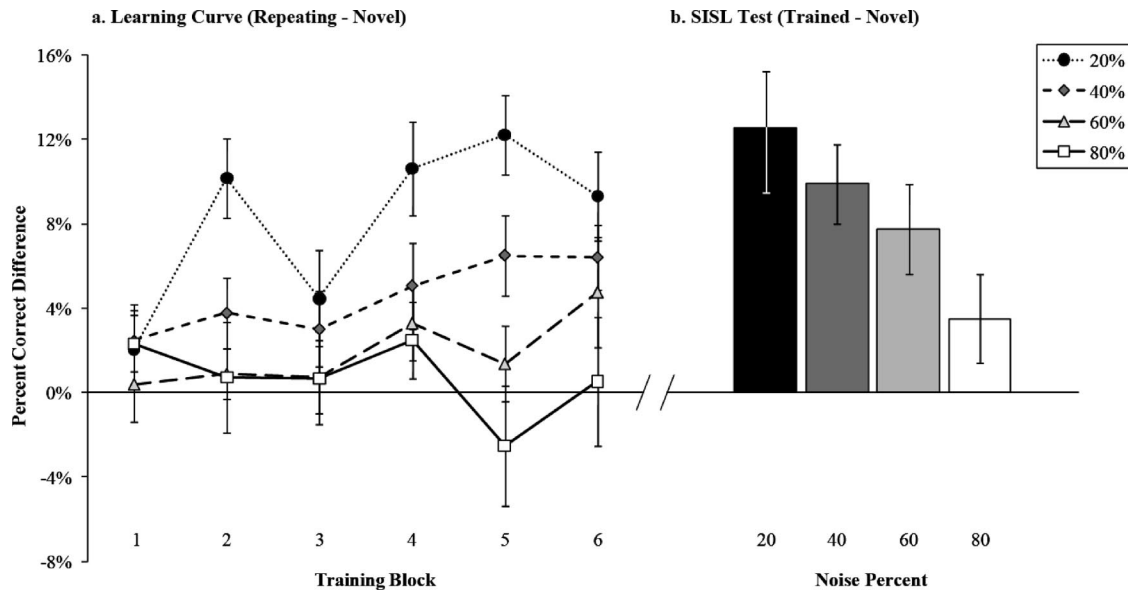
Figure 4. Experiment 3 sequence-specific learning curve and test performance. Each training block consisted of 480 trials separated by a short rest break. The learning curve (a) shows the gradual sequence learning throughout training. The percent-correct difference is the difference between the percent correct on the repeating sequence trials and the novel, nonrepeating sequence trials within a block. The percent-correct difference at test (b) is the percent correct difference between the trained sequence trials and the novel sequence trials. Brackets reflect the standard error of the mean.

ing. Participants did provide slightly lower confidence ratings to the novel sequences that were not seen during the SISL test ($M = .98$, $SE = .58$), but these ratings also did not differ from the ratings given to the trained sequence. The sequences generated during the recall test did not match the trained sequence ($M = 4.11$, $SE = .17$) better than the foil sequences ($M = 4.31$, $SE = .12$), and there was no main effect of sequence type, noise condition, or an interaction, $Fs < 1$, suggesting that participants could not recall the sequence they had learned.

Sequence-Independent Performance Effects

For all groups, the cue velocity increased linearly across training, represented as a decrease in the time (in seconds) for the cue to reach the target, $F(1, 43) = 301.81$, $p < .001$, $\eta^2 = .87$. There was neither a main effect of noise condition nor an interaction, $Fs < 1$. As seen in Table 3, the cue velocities differed at the end of training, but this was not statistically significant. The sequential dependency ratio remained consistent in Experiment 3, replicating the performance effect that was in the previous two experiments. If a participant gets a response correct, it roughly doubles the likelihood that that person will get the next response correct. Also in parallel with the previous experiments, the ratio during trained sequence performance at test ($M = 2.02$, $SE = .15$) did not differ from the ratio during foil performance ($M = 1.96$, $SE = .07$), $t < 1$.

Experiment 3 Discussion

Participants were able to learn the embedded repeating sequences even when most of the responses that they made were to nonrepeating (noise) trials. Significant learning was observed in

conditions in which 20, 40, and 60% of the training trials consisted of novel, nonrepeating SOC segment trials. There was some weak evidence for learning in the 80% condition as well, and it is possible that the embedded repeating sequence may simply not have been repeated enough during training to obtain reliable sequence-specific learning. Although the 12-item SOC training sequences were much shorter than the sequences used in the first two experiments, participants did not develop explicit knowledge of the sequence on which they exhibited performance improvements. The procedure used in Experiment 3 was similar to that used in Sanchez et al. (2010), which also produced a dissociation between explicit sequence knowledge and implicit performance.

In Experiment 3, as the amount of novel, nonrepeating segments during training increased across groups, the trained sequence per-

Table 3
Mean (SE) Values

Noise condition	Trained sequence performance	Novel/foil performance	Cue velocity
Last block of training			
20%	58.03% (0.97)	48.70% (2.15)	1.19 (0.06)
40%	60.13% (2.42)	53.73% (2.37)	1.20 (0.10)
60%	60.68% (2.35)	55.93% (2.47)	1.17 (0.09)
80%	57.77% (1.21)	57.24% (1.87)	1.33 (0.11)
SISL test			
20%	54.31% (4.36)	41.92% (2.44)	1.19 (0.06)
40%	59.67% (2.59)	49.77% (2.69)	1.19 (0.11)
60%	62.55% (3.08)	54.77% (2.32)	1.16 (0.10)
80%	60.61% (2.78)	57.10% (2.85)	1.32 (0.10)

formance during the SISL test decreased, suggesting less sequence-specific knowledge had been obtained. However, in all three experiments, the more challenging conditions of longer sequences or higher amounts of novel training trials also led to the embedded repeating sequence being repeated less often, so that test performance does not reflect learning rate as a function of experience with the repeating sequence. A key question about the mechanism that implicitly extracts sequential information is whether the rate of sequence learning is reduced in the more challenging conditions. For the longer sequences, there are potentially more critical interitem statistics to track. The longer sequences provide the opportunity to assess whether participants were learning only partial fragmentary elements of the longer sequences. For example, if participants were constrained by capacity to only learning up to 15 trigrams (an arbitrary capacity, for the sake of argument), they would learn half of the 30-item sequence, but only one sixth of the 90-item sequence. Performance during the repeating sequence at test would then incorporate a relatively larger number of unknown elements for longer sequences, leading to a smaller performance difference reflecting the lesser learning.

Likewise, for the higher noise conditions in Experiment 3, the novel segments during training make the statistics less predictable by increasing the rate of irrelevant contingencies, potentially posing a difficult problem for a simple statistical Bayesian learning mechanism of relative trigrams. For example, if the training sequence contained the trigram D-F-J, a mechanism could learn to predict J by noting that it follows the D-F pair with a much higher probability than either D or K. However, the novel segments during training contained the fragments D-F-D, D-F-J, and D-F-K at the same rates, reducing the ability to predict J within the repeating sequence following D-F. This would lead to a lower learning rate for a mechanism simply using Bayesian learning of probabilities up to SOC.

Learning rates as a function of trained repetitions of the sequence were not specifically presented in Experiments 1–3. The question of learning rate as a function of practiced repetitions is presented here as an analysis across all three experiments to emphasize commonalities in learning performance across experiments.

Operating Characteristics Across Experiments 1–3

Across the three experiments reported here, there were 12 experimental conditions in which learning was measured. For each condition, sequence learning was estimated by the average performance difference between the trained repeating sequence and novel foils during the posttraining test. Motor learning rate is generally considered nonlinear with practice, following an exponential or power learning curve (see, Heathcote, Brown, & Mewhort, 2000; Newell & Rosenbloom, 1981). Log-linear learning curves have been classically reported in the acquisition of motor skills (Crossman, 1959), and sequence learning has been shown to increase as a function of repetitions practiced (Karni et al., 1995). Therefore, it was hypothesized that the amount of sequence learning would be strongly related to the logarithm of the number of trained sequence repetitions. In addition, a thirteenth group was added (see Table 4 for the data used) based on learning rate information from Sanchez et al. (2010). No adjustments were

Table 4
Mean (SE) Values

Experiment	Sequence repetitions	SISL test score
Experiment 1		
30 item	80	11.00% (1.99)
40 item	60	7.45% (2.43)
50 item	48	4.86% (2.07)
60 item	40	1.71% (1.54)
Experiment 2		
60 item	81	8.01% (2.69)
70 item	72	9.66% (1.88)
80 item	63	6.05% (1.41)
90 item	54	1.46% (2.02)
Experiment 3		
20%	192	12.38% (2.90)
40%	144	9.91% (1.90)
60%	96	7.78% (2.12)
80%	48	3.51% (2.10)
Sanchez, Gobel, & Reber (2010)	192	10.11% (1.84)

made based on the variability among conditions such as sequence lengths, number of keypresses for each motor response, the percent of nonrepeating sequence trials during training, and/or cue velocity.

Despite differences in these experimental variables, performance improvements were remarkably consistent across learning conditions. A regression analysis of the logarithm of practiced repetitions ($Reps_{Log}$) by SISL test performance revealed sequence repetition to account for a significant amount of the variance across groups, $F(1, 11) = 22.67$, $p < .001$, $b = .13$ ($SE = .03$), adjusted $R^2 = .64$ (see Figure 5). $Reps_{Log}$ predicted performance better than using the linear count of sequence repetitions, adjusted $R^2 = .51$, or sequence length, adjusted $R^2 = .21$. A model using sequence length in addition to $Reps_{Log}$ was not a better predictor, adjusted $R^2 = .61$, than just the $Reps_{Log}$ model, $F < 1$, and did not improve the quality of the fit.

Bigram Analysis for Extended Sequences (Experiments 1 and 2)

With 10 possible responses, the sequences used in Experiments 1 and 2 that were shorter than 90 items in length were not fully SOC. All 90 potential bigrams (two-item pairs) cannot be fully represented in the sequences from 30 to 80 items long, making a certain proportion of bigrams unique to the trained sequence. Many of these trained bigrams recurred in the foils at test and provide a unique opportunity to examine bigram-level learning in these two experiments. The degree to which the bigrams recurred in the foils related directly to sequence length. For 30-item sequences, an average of 12.3 of the sequence bigrams were unique and 17.7 (59%) recurred in one or more of the foils. For the 60-item sequence conditions, 88% of bigrams also occurred during foil sequences (and for the 90-item sequence, all bigrams occur in targets and foils). Bigram performance was measured by assessing the percent correct of the second item in a particular bigram, because the second item is the response that is able to be statistically predicted (e.g., performance for bigram D-F was determined by correct responding to F).
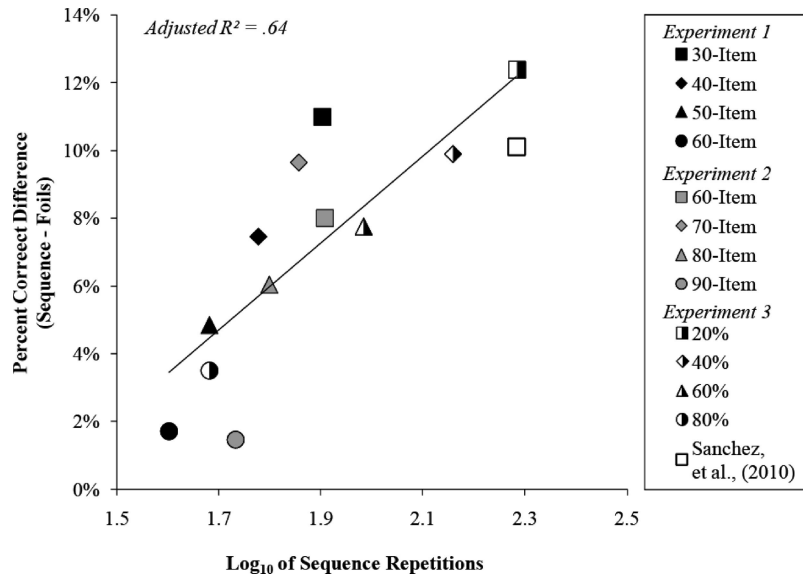
Figure 5. Scatterplot of the SISL test score by the $\log_{10}$ of trained sequence repetitions. The three experiments and previous data are distinguished by different marker fills. The SISL test performance as a log-linear function of trained sequence repetitions is better predictive than other variables, such as sequence length.

Across all participants in all conditions in Experiments 1 and 2, bigram-specific performance was compared when the participant was performing the bigram during the trained sequence and the foil sequences. Performance was reliably higher for the same bigram occurring in the trained sequence ($M = 59.70\%$, $SE = 1.03\%$) than during a foil sequence ($M = 54.32\%$, $SE = 1.02\%$), $t(131) = 6.70$, $p < .001$, indicating that participants learned statistics that were more complex than simple bigrams (bigram-level learning would lead to similar performance of the same bigrams regardless of context). However, in Experiment 1, performance of the recurring bigrams during foil sequences can also be compared to completely novel bigrams that were present during foil sequence performance (the longer sequences in Experiment 2 leave few novel bigrams). Participants performed reliably better on the bigrams that also occurred in the repeating sequences ($M = 52.1\%$, $SE = 1.47\%$) than on completely novel bigrams ($M = 49.9\%$, $SE = 1.46\%$), $t(75) = 3.45$, $p < .001$, indicating that there was some learning at the bigram level as well.

To assess the impact of bigram learning on overall learning rate, the cross-experiment regression comparing learning rate and the log of the number of repetitions was repeated with an additional predictor variable reflecting the percentage of the trained sequence that contained unique bigrams. Both variables, $Reps_{Log}$ and proportion of unique bigrams, contributed significantly to predicting the learning rate, ts > 3.46, ps < .01, and the adjusted r^2 for the overall fit was .82, suggesting that bigram learning likely contributed materially to sequence performance at test.

Discussion

Sequence-specific performance improvements increased logarithmically with each repeated performance of the sequence, seemingly independent of sequence length or surrounding novel segments during training. Although this analysis shows that learning rate is roughly similar across all conditions, careful examination of Figure 5 suggests that the learning rates observed in Experiments 1 and 2 may actually be slightly higher than Experiment 3. Of note, because of the 10 possible operators, sequences less than 90 items long were not fully SOC sequences and, therefore, participants appear to have benefitted from learning first-order conditional information (bigrams). Clearly, participants were also learning higher-order conditionals (and longer fragments), because longer sequences with less bigram-specific information were learned as well. The similarity in learning rate between sequences of very different lengths (30-item and 70-item, 40-item and 80-item) also indicates that the number of probabilities or fragments to be learned does not affect the learning rate. Increasing sequence length or irrelevant training trials does not lead to a slower learning rate, as might be expected with a simple statistical learning mechanism that is challenged by tracking many conditional probabilities (in long sequences) or discriminating predictive probabilities from surrounding noise.

A relatively simple statistical learning mechanism, such as one that learns bigrams and trigrams with practice, as in the SRN (Cleeremans & McClelland, 1991), can capture this result as long as there is enough representational capacity to track all the statistics. However, this type of mechanism should be impaired by the conditions in Experiment 3, where increasing the amount of noise would lead to slower learning. One possibility for the constant learning across noise conditions is that participants extract even higher-order statistics, such as third- or fourth-order conditionals. There are so many unique third- or fourth-order fragments that the repeating sequence may make the predictable relationships discriminable from the noise. This type of learning comes at the cost of representing these higher-order conditionals, a potential exponential increase in the information necessary to track. Evidence for optimal statistical representations has been previously reported

(Orbán, Fiser, Aslin, & Lengyel, 2008), and Remillard (2008, 2010) has reported motor sequence learning of up to sixth-order conditional probabilities after many hours of training, suggesting a large representational capacity. The similarity in learning rate across conditions in Experiment 3 suggests that third-order conditional learning may emerge even within the first hour of training.

General Discussion

Experiments 1 and 2 showed that the implicit sequence learning memory system is capable of learning sequences that far exceed the lengths that have been previously examined. Additionally, Experiment 3 showed that learning of a repeating sequence occurs even when irrelevant trials outnumber the relevant training sequence trials. Across all three experiments, learning rate was found to be an exponential function of training repetitions, suggesting that the number of practiced repetitions is the best predictor of learning and more important than sequence length or amount of irrelevant practice (nonrepeating segments) during training. This consistent learning rate across sequence lengths, number of motor operators, and number of training sessions may provide some constraints into the current theories of how memory development and consolidation operates in implicit perceptual-motor sequence learning. These results not only provide further evidence that implicit sequence learning persists across procedural variations (Chambaron, Ginhac, & Perruchet, 2006), but that it also persists at a constant rate independent of nonsequence specific parameters. This learning capability has been considered an important part of implicit statistical learning in domains from visual perception to language; associations will be identified as long as there are regularities in the environment (Fiser & Aslin, 2002; Saffran, 2003). The explicit memory system, in contrast, has difficulty with the acquisition and expression of knowledge in conditions where the regularities are not common enough to be consciously identified (Jiménez et al., 2006).

The absence of slowed learning due to sequence length may be another contrast of differential operating characteristics between implicit and explicit memory. In the effortful memorization of long lists of information, a list-length effect (Gronlund & Elam, 1994) is observed where the amount of information acquired is reduced, reflecting a bandwidth constraint on explicit memory acquisition. This type of effect predicts that participants would have a difficult time memorizing and retrieving the entirety of the very long sequences used in training here. Although it may have been confounded by the preceding implicit knowledge test, the sensitive recognition test used here would not necessarily have been affected by this explicit memory effect because it is only necessary to recognize a small fragment to exhibit above chance performance.

Identifying functional differences in the operation of these two kinds of memory may provide a better understanding into the basis of memory than attempts to simply dissociate the neural systems. Patient findings have shown dissociable systems, but in healthy participants both systems are operational and some awareness of the repeating sequence typically develops (Willingham, Greeley, & Bardone, 1993). This has generated an extended debate over the degree to which sequence knowledge is partly or completely unavailable to conscious awareness (Perruchet & Amorim, 1992; Shanks & St. John, 1994; Song, Marks, Howard, & Howard, 2009)

and also how the two memory systems may potentially interact. While implicit and explicit sequence knowledge are capable of developing in parallel (Willingham & Goedert-Eschmann, 1999), the relationship of sequence recognition to procedural performance is not necessarily advantageous (Song et al., 2009), suggesting a potentially complicated interaction between these memory systems.

In fact, the learning process in the SISL task may reflect a combination of both response-sequence learning (as seen in the SRT task) and a contribution from perceptual learning analogous to that seen in the contextual cuing paradigm (Chun & Jian, 1998). In the SRT task, items are presented individually and with a set response-to-stimulus interval, which extends the time between stimuli. However, in the SISL task, numerous stimuli are shown on the screen at a time (typically 4 to 5 cues) and this visuospatial array may influence the statistical dependencies used for learning. The possibility of combining complex perceptual learning with serial response sequence learning may contribute to the ability to learn long sequences (Experiments 1 and 2) and resist interference from the nonrepeating noise segments (Experiment 3). Prior studies that have examined the knowledge acquisition characteristics of implicit sequence learning mechanisms have used very extensive training protocols (Remillard, 2008, 2010; Remillard & Clark, 2001), up to around 20,000 trials of practice over 10 sessions. Those results support the idea that the implicit sequence learning mechanism can acquire high-order knowledge, but suggests it is acquired very slowly and laboriously. The current results extend this previous work by finding relatively sophisticated learning occurring within the first hour or two of training. The combination of perceptual and sequential information in the SISL task is common in real world skill acquisition (e.g., playing a song from sheet music) and may indicate that SISL is a good model task of this process.

The SISL task also elicits behavioral characteristics that may be relatively specific to certain kinds of sequence learning tasks, such as the sequential dependency in response accuracy. The sequential dependency ("hot hand") may reflect the initial elements of a kind of "flow" state (Csikszentmihalyi, 1990), which has been reported in highly expert skill performance (Chen, 2007; Ericsson & Ward, 2007). In Experiments 1 and 2, during which responses were frequently made with multiple fingers, evidence for a motor overflow effect was observed (Armatas & Summers, 2001; Armatas, Summers, & Bradshaw, 1994; Liederman & Foley, 1987) that likely reflects a SISL-specific performance characteristic. Despite the performance effects, the sequence-specific learning component persisted at a relatively constant log-linear rate.

The sequence learning component of the SISL task is believed to rely on corticostriatal circuits connecting the basal ganglia and motor cortex, which have been shown to be critical for supporting learning with the SRT task (e.g., Ashe, Lungu, Basford, & Lu, 2006; Doyon, 2008). While corticostriatal loops connect most areas of cortex to the basal ganglia (Middleton & Strick, 2000), each of these circuits are much less complex (Houk & Wise, 1995) than the entirety of the medial temporal lobe memory system. This relative simplicity suggests the possibility of constraints on the amount of information that can be processed and stored for implicit learning relative to explicit learning. The lack of a capacity constraint on learning that was observed here might suggest a complex kind of learning during SISL similar to the contextual

cueing phenomenon that occurs implicitly but appears to depend on the hippocampus (Chun & Phelps, 1999; Greene, Gross, Elsinger, & Rao, 2007). A neuroimaging study of SISL observed changes largely in cortical regions reflecting reduced activity for practiced sequences (Gobel, Parrish, & Reber, 2011). Increased activity was also observed in the ventral striatum and not the medial temporal lobe, although the lack of activity differences cannot definitively indicate the lack of involvement of a region.

These behavioral results open a large area of future work that can provide insight into the cognitive neuroscience of implicit sequence learning. The learning rate consistency across procedural variations suggests a possible homogeneity within implicit sequence learning mechanisms. Motor sequence learning develops through a multitude of connections with the basal ganglia, throughout cortical regions such as the motor, parietal, and frontal cortex, as well as with connections to the cerebellum (Ashe et al., 2006; Doyon et al., 2009; Doyon, Penhune, & Ungerleider, 2003; Hikosaka et al., 1999; Hikosaka, Nakamura, Sakai, & Nakahara, 2002; Penhune & Doyon, 2005). The SISL task also incorporates timing with order in interception responses (Gobel, Sanchez, & Reber, 2011) which may recruit other areas as well (Bosco et al., 2008; Gobel, Parrish, & Reber, 2011); yet all of these disparate mechanisms operate together and are likely to be responsible for the characteristics of sequence learning seen with this task.

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