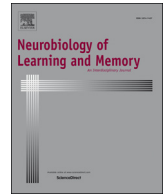




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## Short communication

## Serial pattern retention in male and female rats

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## ABSTRACT

Serial pattern learning is a model paradigm for studying parallel-processing in complex learning in rats. The current experiment extends the paradigm to the study of sequential memory by examining forgetting curves for the component element types that make up a serial pattern. Adult male and female rats were trained in a serial multiple choice (SMC) task in which rats learned a serial pattern of nose-poke responses in a circular array of 8 receptacles mounted on the walls of an octagonal operant chamber. The pattern was 123–234–345–456–567–678–781–818, where digits represent the clockwise positions of successive correct receptacles. Previous work has shown that chunk-boundary elements (the first element of each 3-element chunk), within-chunk elements (the second and third elements in all but the last chunk), and the violation element (the last element of the pattern) are learned via different cognitive mechanisms. After each rat was trained to an 85% correct performance criterion on the violation element, we then assessed serial pattern retention at 24-h, 2-week, and 4-week retention intervals. For chunk-boundary and within-chunk elements, forgetting was observed only at the 4-week retention interval. Sex differences were observed; females performed better than males on within-chunk elements at 24-h and 4-week retention intervals. For the violation element, significant forgetting was observed earlier at the 2-week retention interval as well as at the 4-week retention interval. Thus, pattern elements that were learned slower were forgotten faster. The experiment provides a proof of concept for evaluating forgetting curves separately for the multiple memory systems rats appear to employ concurrently in this paradigm, a method that may prove useful in characterizing the impact of relevant neurobiological manipulations on forgetting in multiple sequential memory systems.

## 1. Introduction

Without additional practice, memories fade over time (Nelson, 1971; Spitzer, 1939; Wixted & Ebbesen, 1991). The longer the retention interval between training and testing, the more forgetting is likely to be observed (Spear, 1978). Memory of a prior event can be assessed by conducting retention tests at multiple retention intervals to characterize a forgetting curve. Describing a forgetting curve is a well-established method for studying forgetting in humans and animals (Ebbinghaus, 1987; Guanowsky, Misanin, & Riccio, 1983; Loftus, 1985; Murre & Dros, 2015; Schneck & Warden, 1929; Spear, 1978). The primary goal of this study was to apply this method to assess forgetting in a serial pattern learning paradigm for rats.

Serial pattern learning is a model paradigm for studying parallel-processing in complex learning in rats (Fountain et al., 2012). The serial multiple choice (SMC) task is a serial pattern learning and memory task that rats learn by encoding multiple types of information including stimulus-response (S-R) associations, abstract rules, serial position information, timing, and spatial information (Fountain, Rowan, &

Wollan, 2013; Kunder & Fountain, 2014; Muller & Fountain, 2010, 2016; Wallace, Rowan, & Fountain, 2008). In the SMC task, rats learn a sequence of responses in a circular array of manipulanda. One commonly-studied serial pattern is the highly-structured 24-element serial pattern, 123–234–345–456–567–678–781–818–repeat. This pattern consists of three element types: chunk-boundary elements, within-chunk elements, and violation elements. The first element of each chunk is termed the chunk-boundary element. Rats use phrasing cues such as pauses (indicated by dashes in the pattern above) as discriminative cues that signal chunk-boundary elements (Fountain, et al., 2013; Kunder & Fountain, 2014; Muller & Fountain, 2010; Stempowski, Carman, & Fountain, 1999; Wallace, et al., 2008). Evidence also indicates that rats use counting/timing processes to anticipate the serial position of chunk-boundary elements (Muller & Fountain, 2010, 2016). Chunk-boundary elements are followed by within-chunk elements that are encoded by abstract rule learning (Fountain & Rowan, 1995a, 1995b; Fountain, Rowan, & Carman, 2007; Kunder & Fountain, 2011; Muller & Fountain, 2010). Finally, the pattern may also contain a violation element, defined as an element that is inconsistent with pattern

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structure (viz., the terminal element of the last “818” chunk in the pattern above). The violation element is typically the most difficult element to learn because no single pattern item or rule predicts the location of the violation element in the pattern. To master the violation element, rats employ “multiple-item memory” (cf. Capaldi, Verry, & Nawrocki, 1982) consisting of as many as seven prior pattern elements or features, and other spatial or temporal cues (Kundey & Fountain, 2010; Muller & Fountain, 2010, 2016). Additional support for the claim that rats use multiple cognitive processes concurrently to learn such patterns comes from previous work showing that the different element types described above are also differentially sensitive to the effects of adolescent drug exposure on adult rat learning (Pickens, Rowan, Bevins, & Fountain, 2013; Rowan et al., 2015), to acute N-methyl-D-aspartate blockade (Fountain & Rowan, 2000), and to muscarinic cholinergic blockade (Chenoweth and Fountain, 2015, 2016; Fountain, et al., 2013).

While it is well-established that rats can encode and retain a variety of different types of information in serial pattern learning (Fountain et al., 2013; Kundey & Fountain, 2014; Muller & Fountain, 2010; Stempowski et al., 1999; Wallace et al., 2008), rats’ long-term retention has not been assessed for the different element types that can make up a serial pattern. The primary question considered here was whether it is possible to characterize forgetting curves for individual serial pattern element types. We know that different element types are learned at different rates, so a second question was whether differential rates of encoding of chunk-boundary, within-chunk, and violation elements lead to differential retention. The third question was whether sex differences will be observed in retention that parallel those observed in acquisition, where male rats learned chunk-boundary and violation elements faster than females (cf. Pickens et al., 2013). To answer these questions, male and female rats were trained in the SMC task with the pattern described above until each rat reached a high criterion of performance on all element types, then retention was assessed at 24-h, 2-week, and 4-week retention intervals.

## 2. Methods

### 2.1. Subjects

Twenty-six naïve Long Evans hooded rats (*Rattus norvegicus*), 15 males and 11 females, were single-housed in polycarbonate “shoebox” cages (40 cm wide × 85 cm long × 40 cm high) at postnatal day 90 (P90) and given *ad libitum* access to food (LabDiet5P00 - ProLabRMH3000). Rats had restricted access to water beginning on P94 for the duration of the experiment. Following testing each day, rats received 5 minutes of *ad libitum* water. Rats were reinforced with water droplets for correct responses in operant chambers. Rats were kept on a 14:10-h light-dark cycle with testing conducted during the light portion of the cycle.

### 2.2. Apparatus

Shaping chambers of clear Plexiglas (15 × 30 × 30 cm) had stainless steel wire mesh flooring and a nose-poke receptacle (2.5-cm diameter black PVC pipe end caps) centered on one end wall 5.0 cm above the floor. The nose-poke receptacle was equipped with an infrared emitter-detector pair and a white LED cue light centered in the back of the receptacle. Octagonal chambers were also constructed of clear Plexiglas (15 cm wide × 30 cm tall walls with 40 cm between opposite walls) and had stainless steel wire mesh flooring and a nose-poke receptacle centered 5.0 cm above the floor on each chamber wall. A syringe containing distilled water was connected to each receptacle by Tygon tubing (VWR Scientific, Performance Plastics 1/32-inch, #R-3603) with an inline solenoid (Parker Hannifin 003-1264-900 24V) for delivering water reward. For each correct response, a 0.025 ml water droplet was delivered to the bottom of the nose-poke receptacle.

### 2.3. Shaping and acquisition

For shaping, at the beginning of each trial, the receptacle light was illuminated. When the rat made a nose-poke response, the receptacle light was turned off and a droplet of water was delivered. A 1-s inter-trial interval separated trials on Day 1 and a 2-s inter-trial interval separated trials on following days. Criterion for being included in the study was set at 240 responses within 1 h on each of these two consecutive days.

During Acquisition, all rats learned the same 24-element pattern, 123–234–345–456–567–678–781–818–, where digits indicate the clockwise position of the correct receptacle in the circular array and dashes indicate 3-s pauses that served as phrasing cues before chunk-boundary elements and as the inter-pattern interval. At the beginning of the trial, all nose-poke receptacles were illuminated and remained illuminated until the rat made a choice. If the correct receptacle was chosen, receptacle lights extinguished and the rat was reinforced. If the incorrect receptacle was chosen, a correction procedure began where all the incorrect nose-poke receptacles extinguished and only the correct receptacle remained illuminated, forcing the rat to make the correct response before continuing with the next trial where all lights are illuminated again. Testing progressed in this manner until 10 patterns had been completed. Because prior studies indicated that the violation element in this pattern would be learned much slower than all other pattern elements, all rats were trained until they met a criterion of 85% correct responses on the violation element on two consecutive days of training.

### 2.4. Retention tests

Retention tests were administered after 24-h, 2-week, and 4-week retention intervals. The second day of criterion was used as a measure of 24-h retention. Rats were then tested for serial pattern retention 4 weeks after the last day of training. Next, rats were retrained to 85% criterion, then were tested after a 2-week retention interval.

## 3. Results

Retention was assessed at 24-h, 2-week, and 4-week retention intervals in male and female rats. Better retention of the violation element was observed at the 24-h test than at 2- and 4-week retention tests ( $p < .05$ ). Better retention was observed at the 2-week retention test compared to the 4-week retention test ( $p < .05$ ). Performance on chunk-boundary and within-chunk element retention was significantly poorer at the 4-week retention test than at 24-h and 2-week retention tests ( $p < .05$ ).

### 3.1. Acquisition and Re-acquisition of the violation element

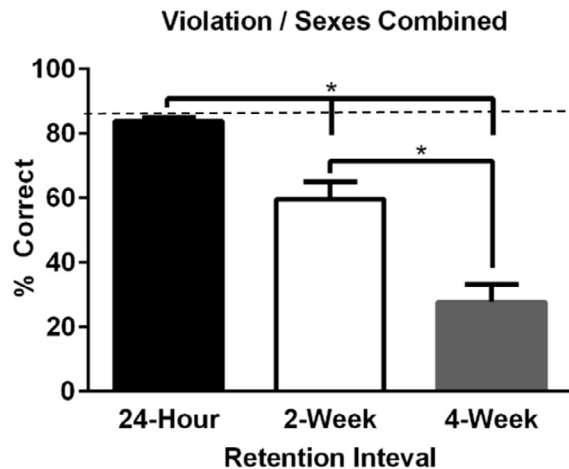
To assess sex differences in acquisition, a repeated measures ANOVA was conducted comparing days-to-criterion results. A significant main effect of sex was found,  $F(1, 24) = 4.35, p = .048$ , partial  $\eta^2 = .15$ . Males required an average of 21.13 days to reach 85% criterion in acquisition, which was significantly quicker than females that required an average of 32.18 days ( $p < .05$ ). There was a marginally significant interaction of acquisition phase X sex,  $F(1, 24) = 3.78, p = .064$ , partial  $\eta^2 = .14$ .

### 3.2. Forgetting curves

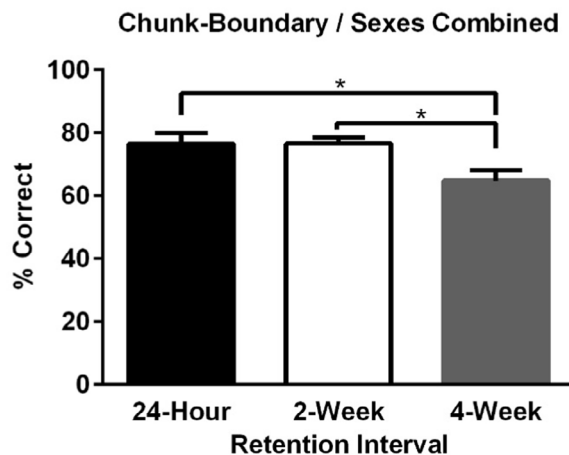
#### 3.2.1. Forgetting curve for the violation element

Fig. 1A shows forgetting curves for the violation element. To assess differences in forgetting of the violation element at different retention intervals, we conducted a 2 (Sex) × 4 (Retention Day) repeated measures ANOVA on data from four days. The four days included in the analysis were Day 1 of criterion, the day of the 24-h retention test (i.e.,

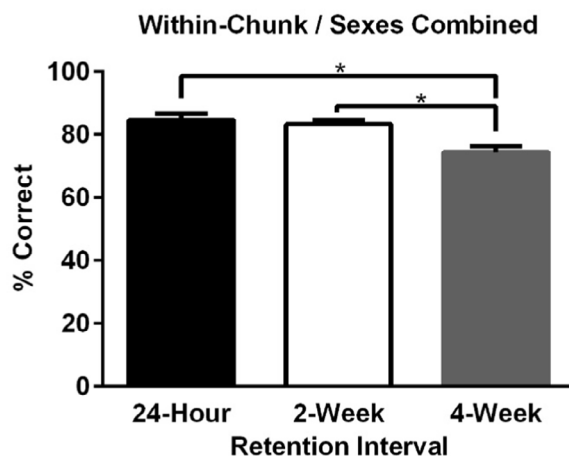
A



B



C



**Fig. 1.** (A) Retention of the violation element for male and female rats combined. Significantly better violation element retention was observed at the 24-h retention test (Day 2 of criterion) than at the 2-week ( $p = .001$ ) and 4-week retention tests ( $p < .01$ ), and better retention was observed at the 2-week retention test than at the 4-week retention test ( $p < .01$ ). Dashed line indicates 85% criterion. Performance on Day 1 of criterion was 86.2%. Error bars:  $\pm$  SEM. \* $p < .05$  for comparisons indicated. (B) Retention of chunk-boundary elements for male and female rats combined. Significantly better chunk-boundary element retention was observed at the 24-h (Day 2 of criterion) and 2-week retention tests than at the 4-week retention test ( $ps = .01$ ), but there was no significant difference in retention between the 24-h retention test and the 2-week retention test ( $p > .05$ ). Performance on Day 1 of criterion was 75.4%. Error bars:  $\pm$  SEM. \* $p < .05$  for comparisons indicated. (C) Retention of within-chunk elements for male and female rats combined. Significantly better retention was observed at the 24-h (Day 2 of criterion) and 2-week retention tests than at the 4-week retention test ( $ps < .05$ ). There was no significant difference in retention between the 24-h retention test and 2-week retention test ( $p > .05$ ). Performance on Day 1 of criterion was 85.1%. Mean  $\pm$  SEM. \* $p < .05$  for comparisons indicated.

Significant Difference (LSD) tests comparing rats' retention at 24 h, 2 weeks, and 4 weeks indicated significant differences in violation element retention for all comparisons. Violation element retention was significantly better at the 24-h retention test than at 2-week and 4-week retention tests ( $p = .001$ ), and performance was better at the 2-week retention test than at the 4-week retention test ( $p < .01$ ). Thus, forgetting curves were observed for the violation element and no sex differences were observed.

### 3.2.2. Forgetting curve for chunk-boundary elements

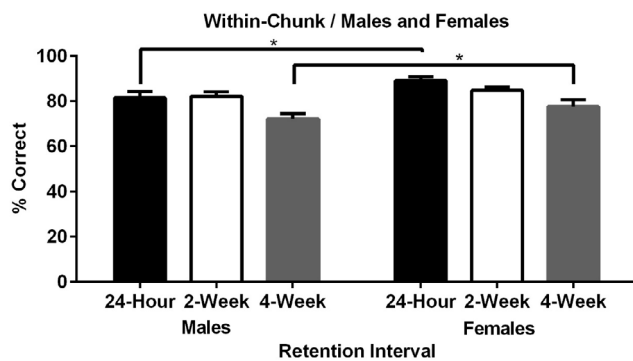
Fig. 1B shows forgetting curves for the chunk-boundary elements. To assess differences in forgetting of chunk-boundary elements at different retention intervals, we conducted a 2 (Sex)  $\times$  4 (Retention Day) repeated measures ANOVA on data from four days. As in the earlier analysis for the violation element, the four days included in the analysis were Day 1 of criterion, the day of the 24-h retention test (i.e., Day 2 of criterion), the day of the 2-week retention test, and the day of the 4-week retention test. The ANOVA revealed a significant main effect of Retention Day,  $F(3, 72) = 6.25$ ,  $p = .001$ , partial  $\eta^2 = .21$ , but no other main effects or interactions were significant ( $ps > .05$ ). LSD tests comparing rats' retention at 24 h, 2 weeks, and 4 weeks indicated chunk-boundary element retention was significantly better on Day 1 of criterion and on the 24-h and 2-week retention tests than on the 4-week retention test ( $p = .022$ ,  $p = .012$ , and  $p = .007$ , respectively). Thus, a shallower forgetting curve was observed for chunk-boundary elements and no sex differences were observed.

### 3.2.3. Forgetting curve for within-chunk elements

Fig. 1C shows forgetting curves for the within-chunk elements. To assess differences in forgetting of within-chunk elements at different retention intervals, we conducted a 2 (Sex)  $\times$  4 (Retention Day) repeated measures ANOVA on data from four days. As in the earlier analysis for the violation and chunk-boundary elements, the four days included in the analysis were Day 1 of criterion, the day of the 24-h retention test (i.e., Day 2 of criterion), the day of the 2-week retention test, and the day of the 4-week retention test. The ANOVA revealed a significant main effect of Day,  $F(3, 72) = 17.53$ ,  $p < .01$ , partial  $\eta^2 = .42$ , and a significant effect of Sex,  $F(1, 24) = 4.20$ ,  $p = .05$ , partial  $\eta^2 = .15$ , but no other main effects or interactions were significant ( $ps > .05$ ). LSD tests comparing rats' retention at 24 h, 2 weeks, and 4 weeks indicated within-chunk element retention was significantly better on Day 1 of criterion and on the 24-h and 2-week retention tests than on the 4-week retention test ( $ps < .01$ ). Thus, a shallower forgetting curve was observed for within-chunk elements, but a marginally significant sex difference was observed.

Fig. 2 shows comparisons of forgetting curves for the within-chunk

Day 2 of criterion), the day of the 2-week retention test, and the day of the 4-week retention test. The ANOVA revealed a significant main effect of Retention Day,  $F(3, 72) = 54.24$ ,  $p < .01$ , partial  $\eta^2 = .69$ , but no other main effects or interactions were significant ( $ps > .05$ ). Because sex differences were not observed, Fig. 1 shows retention of the violation element with data for male and female rats combined. Least



**Fig. 2.** Retention of within-chunk elements comparing male and female rats. Significantly better retention was observed for females compared to males at the 24-h test (Day 2 of criterion) and at the 4-week retention test ( $p < .05$ ). Other differences were not significant ( $p > .05$ ).

elements for male and female rats. Based on the foregoing ANOVA results indicating a marginally significant sex difference in rats' retention of within-chunk elements, planned comparisons were conducted. Females had significantly better retention of within-chunk elements than males on the 24-h retention test (Day 2 of criterion) and the 4-week retention test ( $p < .05$ ). Performance did not differ between males and females on the 2-week retention test ( $p > .05$ ).

#### 4. Discussion

Much of the previous research on complex sequential behavior in nonhuman species has focused on the cognitive and neural underpinnings of rats' and, more recently, pigeons' ability to learn complex patterned sequences in the SMC paradigm (Fountain et al., 2013; Garlick, Fountain, & Blaisdell, 2017; Kunder & Fountain, 2014; Muller & Fountain, 2010, 2016; Stempowski et al., 1999; Wallace et al., 2008). In contrast, the current experiment with rats focused on forgetting of well-learned serial patterns. Specifically, the primary question in this experiment was whether it is possible to describe forgetting curves for the individual element types of a serial pattern. Not only was this approach successful in establishing a proof of concept for studying retention of complex behavior, but the work also revealed potentially important conceptual differences between learning and memory for the same sequential information. For example, the pattern of sex differences observed in the reported forgetting curves differs in significant ways from the pattern of sex differences previously reported in acquisition of the same task (cf., Pickens et al., 2013). This outcome lays the groundwork for a new method for characterizing the cognitive and neural mechanisms responsible for complex sequential behavior in an animal model. These results also indicate that studies of forgetting of sequential behavior are likely to provide new perspectives on both cognitive and neural mechanisms involved in complex sequential behavior.

Studies on animal retention in other paradigms show that performance on many tasks decreases over time. For example, Deweer, Sara, and Hars (1980) found that rats' memory of the location of reward in a T-maze faded over 25 days. Similarly, Alescio-Lautier and Soumireu-Mourat (1986) found that mice showed less memory in a go/no-go task when tested at longer retention intervals (14- to 30-day intervals) compared to shorter retention intervals (1- and 7-day intervals). Crystal and Alford (2014) demonstrated that rat episodic memory in a radial maze faded by 14 days. The current study's results demonstrate forgetting on a similar time-scale in a different cognitive task.

The second question that motivated this experiment was whether differential rates of encoding of chunk-boundary, within-chunk, and violation elements would lead to differential retention. Differential retention was observed. The violation element, which requires use of

multiple-item memory (Muller & Fountain, 2010) and was learned the slowest, showed the most forgetting. Chunk-boundary and within-chunk elements were learned successively faster and produced less forgetting, resulting in flatter forgetting curves. Forgetting of information learned via different cognitive mechanisms appeared to be forgotten at different rates. However, learning to criterion took longer for violation elements than for within-chunk and chunk-boundary elements, thus comparisons of forgetting are difficult because both chunk-boundary and within-chunk elements were likely overtrained. Despite potential overtraining, both chunk-boundary and within-chunk elements showed forgetting and provide baseline forgetting curves for future experiments. Overtraining effects will need to be addressed in future studies by training each element type separately to an appropriate criterion. Ideally, the order of retention tests should also be counterbalanced in future studies.

The third question was whether sex differences would be observed in retention that parallel those observed in acquisition. Previous research demonstrated that female rats learned chunk-boundary and violation elements slower than males (cf. Pickens et al., 2013). No similar effect was observed in retention; that is, female rats remembered the violation element just as long as males despite taking longer to learn it in the acquisition phase. Instead, significantly better retention of within-chunk elements was observed by females at the 24-h test and at the 4-week retention test compared to males. We have never observed a parallel sex difference in within-chunk element acquisition. Thus, the pattern of sex differences observed in the reported forgetting curves differs in significant ways from the pattern of sex differences previously reported in acquisition of the same task.

Although other studies have examined sequential memory in rats, pigeons, and primates (e.g., Fortin, Agster, & Eichenbaum, 2002; Kesner & Novak, 1982; Wright, Santiago, Sands, Kendrick, & Cook, 1985), this experiment examined long-term retention of multiple types of information in a complex cognitive task in nonhuman animals. Results indicate that, when tested for retention of a highly-structured pattern, rule learning and stimulus-response learning were less susceptible to forgetting compared to multiple-item learning. The results fit well with our view that serial pattern learning in rats recruits multiple concurrent cognitive processes, including rule learning, stimulus-response (S-R) learning, abstract rule learning, serial position learning, timing, and spatial learning (Fountain et al., 2013; Kunder & Fountain, 2014; Muller & Fountain, 2010, 2016; Wallace et al., 2008). These results, along with others involving pharmacological manipulations (Chenoweth et al., 2015, 2016; Fountain et al., 2013; Pickens et al., 2013; Rowan et al., 2015), also indicate that these processes can be dissociated and manipulated independently to analyze the cognitive and neural substrates of complex learning. This experiment provides a proof of concept for evaluating forgetting curves separately for the multiple memory systems rats appear to employ concurrently in this paradigm, a method that may prove useful in characterizing the impact of relevant neurobiological manipulations on forgetting in multiple sequential memory systems.

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