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Encoding Structural Ambiguity in Rat Serial Pattern: The Role of Phrasing

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Rats, like humans, appear sensitive to the structure of the elements of sequences. In the present study, we examined the effects of phrasing a structurally ambiguous pattern as either a series of “runs” or “trills.” A pattern phrased as runs was easier to learn than when it was phrased as trills, a result that resembles a similar “runs bias” reported in the human sequential learning literature. Whereas rats learning the runs-phrased pattern showed rapid learning and little tendency to make trills errors, rats learning the trills-phrased version of the pattern produced inflated rates of both trills and runs errors. The results show that rats represented the runs- and trills-phrased versions of the pattern differently. These results add to the evidence that, in addition to serving as discriminative cues, phrasing cues can bias pattern perception in rat serial pattern learning resulting in memorial representations characterized by multiple interpretations of the same pattern. The results also fit well with recent behavioral and neurobehavioral studies implicating multiple concurrent psychological and neural processes in rat serial pattern learning.

Nonhuman animals, like humans, appear sensitive to the structure of the elements of serial patterns, that is, patterned sequences of events, even when the structure relates nonadjacent elements of the serial patterns (Fountain, 1990; Fountain & Benson, Jr., 2006; Fountain, Krauchunas, & Rowan, 1999; Fountain & Rowan, 1995a; 1995b; Fountain, Rowan, & Benson, Jr., 1999). Research on humans has shown that inserting cues into serial patterns (“phrasing cues”) biases people to group pattern elements into cognitive “chunks” indicated by the positioning of the phrasing cues (Bower, 1970; Restle, 1972; 1976; Restle & Brown, 1970; Simon, 1974). Phrasing thus biases how people detect and encode pattern structure by biasing people to interpret sequences of events in terms of the structure that emerges from this chunking process. These processes are readily observed when people learn serial patterns that are structurally ambiguous, that is, in sequences where pattern structure can be readily interpreted in more than one way (e.g., Restle, 1976).

Work on the effects of phrasing in rat serial pattern learning has shown that phrasing cues appear to have similar effects in rats (Fountain, 1990; Fountain, Henne, & Hulse, 1984; Fountain & Rowan, 1995b). For example, Fountain et al. (1984) examined how rats learn to anticipate food quantities presented on successive trials in a T-maze in consistent serial patterns. They positioned spatial, temporal, or both

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cues at the boundaries of chunks defined by the simplest interpretation of pattern structure. These cues all facilitated pattern learning relative to an unphrased pattern condition. Furthermore, when spatial cues were positioned either at the boundaries of these chunks (“good phrasing”) or were “misplaced” in the middle of these chunks (“bad phrasing”), rats learned patterns with good phrasing faster than rats with unphrased patterns, whereas rats learned patterns with bad phrasing slower than rats with unphrased patterns.

In a second study using a different paradigm, Fountain (1990) examined how rats learned to track a series of flashing lights in a 6-light horizontal array by pressing corresponding levers positioned under the lights. In one study, two groups of rats learned the same structurally ambiguous patterns with different arrangements of temporal pauses between trials as phrasing cues. Rats in two groups learned the same pattern with phrasing cues that emphasized either a “runs” interpretation of the pattern or a “trills” interpretation. After training, when phrasing cues were removed, rats made errors consistent with a runs or trills representation of the pattern depending on their phrasing cue condition.

In another study using a third paradigm, Fountain & Rowan (1995b) examined how rats learned to anticipate the successive positions of correct leverpress responses in a circular 8-lever array in an octagonal operant chamber (Fountain, Benson, & Wallace, 2000; Fountain & Benson, Jr., 2006; Fountain & Rowan, 1995a; 1995b; 2000; Fountain et al., 1999). In this paradigm, all 8 levers are presented at the beginning of each trial. Correct responses are immediately reinforced via brain stimulation reward (BSR), that is, brief electrical stimulation of the hypothalamus. Incorrect responses are corrected by removing all incorrect levers and requiring a correct response followed by BSR before continuing to the next trial. Fountain & Rowan (1995b) required rats to learn very similar sequences phrased as either runs or trills and containing a single pattern element that was inconsistent with pattern structure, that is, a “violation element.” In the pattern phrased as runs, rats had difficulty learning a violation of the run structure, but had little difficulty learning an element in the same position that was consistent with the run structure. In the pattern phrased as trills, rats had difficulty learning a violation of the trill structure, but had little difficulty learning an element in the same position that was consistent with the trill structure. These results supported the view that phrasing had biased rule learning processes involved in rats’ interpretation of pattern structure and, ultimately, their memorial representation of the serial pattern.

Other studies seem to contradict this interpretation of the processes mediating phrasing effects in rats. In the food quantity serial pattern literature, Capaldi and colleagues have argued that phrasing cues serve as discriminative cues that control rats’ responses in serial patterns (Capaldi, Birmingham, & Miller, 1999; Capaldi, Verry, Nawrocki, & Miller, 1984). Furthermore, they reported evidence that phrasing cues, like other salient discriminative cues, can overshadow other associative cues in serial patterns (Capaldi et al., 1999; Capaldi et al., 1984). Work involving the octagonal chamber paradigm just described has also provided evidence supporting the same conclusions (Fountain et al., 2000; Stempowski, Carman, & Fountain, 1999). For example, Stempowski et al. (1999) examined the effects of two phrasing cues that differed in how well they cued the response required after the phrasing cue and showed that phrasing cue removal produced deficits propor-

tional to how well rats performed with the phrasing cue present before cue removal. Fountain, Benson, and Wallace (2000) showed that the effects of phrasing cues were directly proportional to the number of times rats experienced each cue independent of their organization. Results of all these studies and other studies (Fountain, 2006; Fountain, Wallace, & Rowan, 2002) indicate that phrasing cues routinely serve as discriminative cues in rat serial pattern learning.

Finally, it should be noted that research supporting both of these ideas—that phrasing biases rule learning processes (the perception and encoding of pattern structure) versus phrasing as response eliciting discriminative cues—implicitly assumed that rats used a single process for learning serial patterns, namely, rule learning versus discrimination learning, respectively. Recent evidence has strongly favored the idea that rats use multiple psychological and brain processes concurrently in serial pattern learning (Fountain, 2006; Fountain & Benson, Jr., 2006; Fountain & Rowan, 2000; Fountain et al., 2002). This notion motivated a closer examination of phrasing effects in structurally ambiguous patterns to look for additional evidence that phrasing cues do indeed bias rats' perception of pattern structure in the same paradigm where it is well established that phrasing cues serve as discriminative cues. Such an outcome would provide a rapprochement of the otherwise conflicting models that have been developed to describe phrasing effects in rat serial pattern learning.

Structurally ambiguous patterns are likely to provide the best context for studying whether or not phrasing induces biases in the perception of pattern structure. In the present study, rats learned essentially the same structurally ambiguous pattern that was phrased into 4-element chunks of either runs or trills. Differential acquisition of the phrased patterns can be construed as evidence for a bias to learn one rule over the other. Results were also carefully examined to determine the rates of runs and trills errors in acquisition for both phrasing conditions, along with rates of perseverations and other errors. Specifically, we examined the results to determine whether phrasing cues biased rats in the two phrasing conditions to make differentially more errors consistent with the structure implied by the phrasing cues experienced in each condition. Finally, we examined the results for evidence to support or refute the idea that rats may have represented their serial patterns as composed concurrently of both runs and trills befitting the structural ambiguity of the patterns.

Method

Subjects

The subjects were 12 naïve male hooded rats (*Rattus norvegicus*) at least 90 days of age at the time of surgery. All rats were implanted with bipolar electrodes (MS301, Plastic Products, Roanoke, VA) for hypothalamic BSR (coordinates, skull level: 4.5 mm posterior, 1.5 mm lateral, 8.5 mm below the surface of the skull). Prior to surgery, rats were deeply anesthetized by 35.56 mg/kg ketamine and 3.56 mg/kg xylazine i.p. injection. Rats also received antibiotics (60,000 units penicillin i.m.) following surgery to reduce the chance of infection. They were carefully monitored for infection following surgery and were allowed at least 1 week for recovery from surgery. Rats were housed in individual cages with food and water freely available. They were maintained on a 15:9-hr light-dark cycle. Testing occurred during the light portion of the cycle. Both food and water were freely available in the home cage.

Apparatus

Two shaping chambers (30 X 30 X 30 cm), each equipped with a single retractable response lever mounted 5.0 cm above the floor and a commutating device centrally located in the ceiling, were used for shaping the lever-press response for BSR. Each box was constructed from clear Plexiglas with a floor of stainless steel rods. Each was enclosed in a sound attenuating shell made of particleboard (20 X 60 X 65 cm). These shaping chambers were housed in a room separate from those of the test chambers.

The training chamber (Fountain & Rowan, 1995a; 1995b; Fountain et al., 2002) was octagonal in shape with clear Plexiglas walls 15 cm wide by 30 cm tall and measured approximately 40 cm between parallel walls. The chamber rested upon a floor of hardware cloth. A retractable response lever was centered on each wall 5.0 cm above the floor. Each lever required approximately 0.15-N force for activation. Rats in the testing chamber were connected to a stimulator by way of a flexible cord (Plastic Products MS304) and a commutating device centrally located in the ceiling of the chamber. Two such operant chambers were each located in separate testing rooms (approximately 2.0 X 2.6 m) illuminated throughout testing by fluorescent lighting. The only major distal cues in the rooms were wall-mounted electrical outlet panels on two walls and a door on a third wall. Mounted above each chamber was a closed circuit television camera so that the rats' activity could be monitored throughout testing. The experiment was controlled from an adjoining room by a microcomputer and interface (interface and Med-State Software, Med Associates, Inc., Fairfield, VT).

Procedure

Throughout all phases of the experiment, rats received reinforcement consisting of a single 250-ms BSR "pulse" of a 60-Hz sinusoidal pulse train from a constant current source of 40-90 μ A. In all procedures, rats received one such pulse for each correct response.

After at least 1 week's recovery from surgery, rats were shaped to lever press for BSR in a shaping chamber. At the beginning of the session, the lever was inserted into the chamber and remained inserted throughout the 30-min session. Rats were required to make at least 1000 lever press responses within a 30-min session and received up to 2 sessions to meet criterion. Rats that failed to meet the criterion were excluded from the study. After 12 adult male hooded rats were shaped to lever press for BSR pulses, they were randomly divided into 2 groups and trained daily in the octagonal operant chamber. In a discrete-trial 8-choice procedure with correction, all 8 levers were inserted into the chamber at the beginning of each trial. If a correct choice was made, all levers were retracted and BSR was administered. For incorrect choices, all levers but the correct lever were withdrawn and the rat was required to produce the correct response to obtain BSR before continuing to the next trial. On each trial, the lever chosen and the latency to the first response were recorded.

Rats in both groups learned the same pattern: 1234345656787812, where integers refer to the clockwise position of the levers in the octagonal chamber. Rats were randomly assigned to two phrasing conditions:

Runs group (N=6)

1234-3456-5678-7812-...

Trills group (N=6)

1212-3434-5656-7878-...

Integers refer to the clockwise position of the levers in the octagonal chamber. All ITIs were 1 s in duration except where dashes indicate 3-s phrasing cues between Runs or Trills chunks. Rats received 20 patterns without interruption each day for 14 consecutive days. It should be noted that, given that there were no interruptions between patterns, the two sequences of responses each day were identical for the two phrasing conditions with the exception that the final two elements of the entire day, "12", of the Runs pattern were moved to the beginning of daily testing for the Trills pattern to make the initial chunk complete for the Trills phrasing pattern.

Results

On each trial, rats' first choice of lever was recorded and scored as correct or incorrect, with incorrect responses immediately followed by the correction pro-

cedure. Figure 1 shows acquisition curves for the two phrasing groups over the 14 days of the experiment. The results show that the Runs pattern was significantly easier to learn than the Trills pattern. In all reported analyses, main effects and interactions were considered significant if $p < .05$. An analysis of variance (ANOVA) was conducted on rats' daily mean percent errors (pooled across elements of the pattern). The ANOVA indicated significant main effects for phrasing, $F(1,10) = 5.56$, and days, $F(13,130) = 32.07$, and a significant interaction for Phrasing X Days, $F(13,130) = 2.80$. Planned comparisons based on the appropriate error term from the ANOVA demonstrated that Runs rats made significantly fewer errors than Trills rats on Days 1–7.

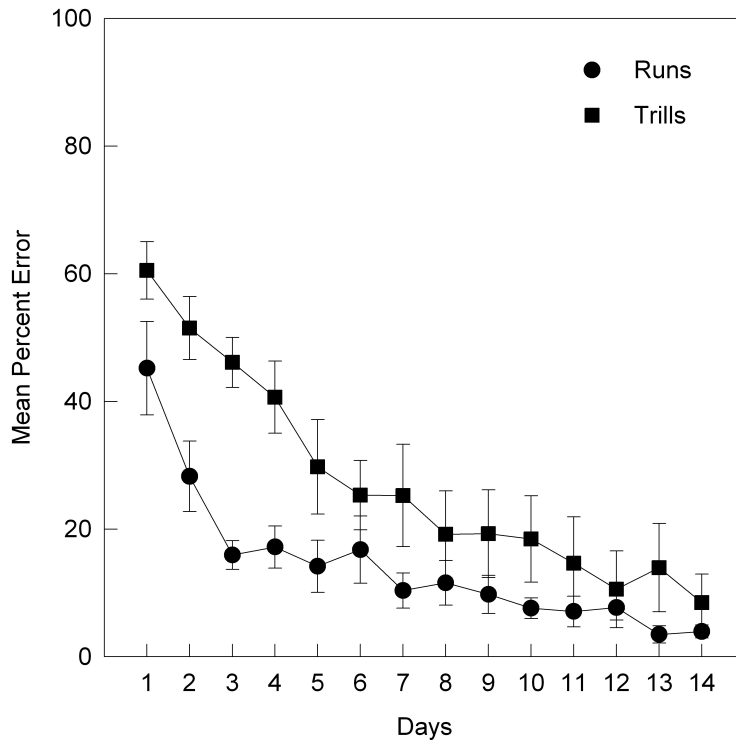


Figure 1. Acquisition curves for the Runs and Trills groups over the 14 days of the experiment. Percentages of daily mean errors were averaged across all elements of the patterns. Error bars: \pm SEM.

Data analyses employing a factorial ANOVA evaluated the rats' trial-by-trial error rates for the two weeks of training revealed various differences in pattern acquisition. Trial-by-trial results revealed that the rats' performance improved from the first to the second week of training, that the Trills pattern overall (26.82% mean error) was more difficult than the Runs pattern (13.90%), and that some elements within the patterns were more difficult than others, as discussed in greater detail below. The ANOVA revealed significant main effects for week, $F(1,10)=66.960$, pattern, $F(1,10)=5.657$, and element $F(3,30)=8.959$. Analyses also revealed significant interactions for Pattern x Week, $F(1,10)=5.439$, Pattern x Element, $F(3,30)=4.144$, Week x Element, $F(3,30)=3.158$, and Pattern x Week x

Element, $F(3,30)=3.481$. The analysis found no significant main effect for Chunks of the pattern or any significant interaction involving Chunks ($p>.05$).

When error profiles were collapsed across chunks of the pattern, as indicated by no significant Chunks effects in the ANOVA, planned comparisons showed that the Runs pattern group made more errors on the first element (26.54%) of chunks (e.g., on the “1” element of the first chunk, 1234, and likewise in other chunks) than on the second (8.96%), third (9.32%), and fourth (10.78%) elements within chunks; whereas the Trills pattern group made more errors on the first (36.48%) and third (39.88%) elements (e.g., on the “1” elements of the first chunk, 1212, and likewise in other chunks) than on the second (20.50%) and fourth (10.42%) elements of chunks.

An examination of the total proportion of responses on each lever suggests that the type of errors rats made was dependent on pattern structure. Errors were classified as anticipation and perseveration errors, rule-overextension errors, and other errors. An anticipation error was a response made in "anticipation" of the next correct response relative to the currently correct response of the pattern, for example, 3466 instead of 3456. A perseveration error was a lever press on the correct lever of the preceding trial, for example, 5578 rather than 5678. For some elements of the pattern, perseveration and anticipation errors were indistinguishable, that is, they are the same error. For this reason, anticipation and perseveration errors are presented combined in the figures. Rule-overextension errors could occur in the form of either a run-overextension (e.g., 1234 5456, rather than 1234 3456) or a trill-overextension error (e.g., 1212 1434 rather than 1212 3434). “Other” errors were incorrect responses on all other levers not defined by the above error types.

The top panel of Figure 2 shows the proportions of errors of each type that Runs rats made in learning their pattern. Anticipation and perseveration errors occurred most frequently relative to other error types and “other” errors occurred least frequently. Run overextension errors were consistently made on the first element of chunks whereas trill overextension errors were found at low rates on the third element of chunks.

The bottom panel of Figure 2 shows the proportions of errors of each type that Trills rats made in learning their pattern. As for the Runs group, anticipation and perseveration errors occurred most frequently relative to other error types and “other” errors occurred least frequently. Similarly, run overextension errors were consistently made on the first element of chunks whereas trill overextension errors were found on the third element of chunks. Error rates for the trills group for all error types were generally inflated compared to those of corresponding error types for the Runs condition. High anticipation and perseveration rates were observed on the first and third element of each chunk of the pattern learned under the Trills phrasing condition. Notably, both runs overextension errors and trills overextension errors were inflated for the Trills group compared to the rates of the same errors in the Runs condition. An important feature of the results was that these inflated rates of both run overextension and trill overextension errors were observed in individual rats within individual days of training and over many days of the experiment. This result strongly supports the view that rats concurrently coded the pattern as composed of runs and trills.

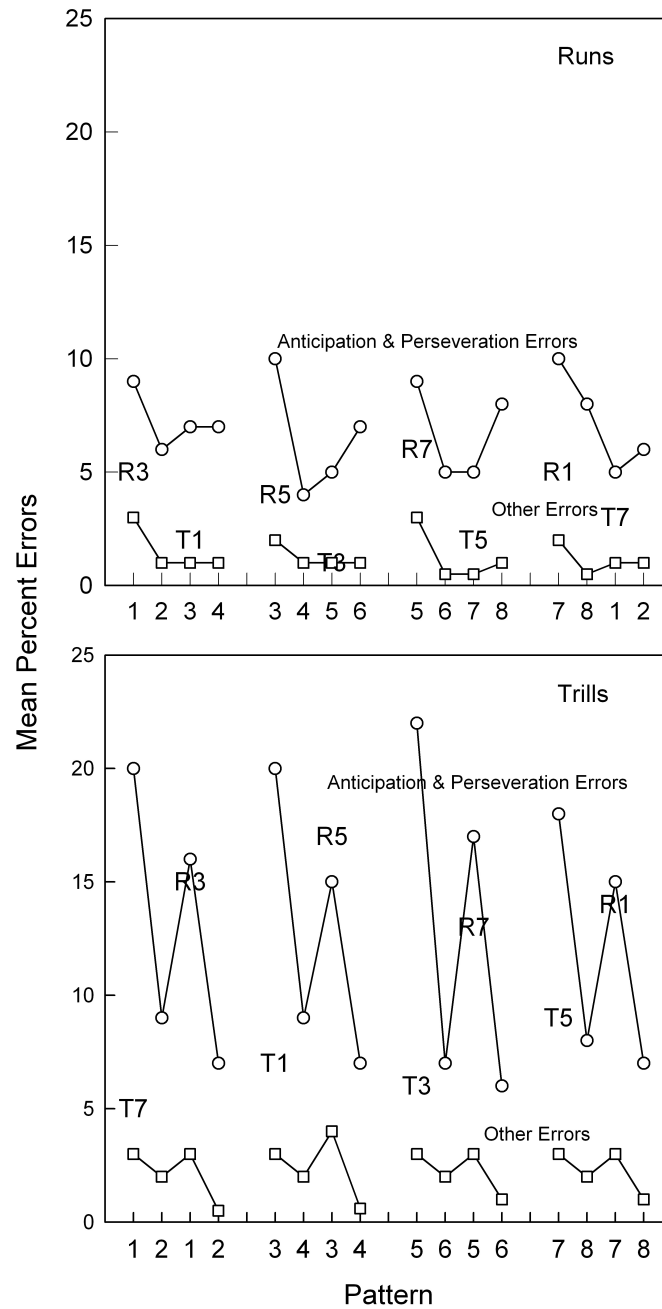


Figure 2. Rats' group mean element-by-element percent error rates collapsed across both weeks of the experiment for Runs and Trills groups (top and bottom panels, respectively). Both graphs show error rates for overextension errors consistent with a runs (R) or trills (T) interpretation of the structurally ambiguous pattern, rates of responses identified as anticipation and perseveration errors, and the rates of other errors that could not be classified into these categories.

Discussion

The results reported above provide a basis for a rapprochement of seemingly contradictory conclusions from prior studies regarding the role of phrasing in serial pattern learning. Specifically, the results show that phrasing cues that are known to have properties of discriminative stimuli in this paradigm (Fountain et al., 2000; Stempowski et al., 1999) also bias the development of rats' memorial representation of pattern structure. The results thus contradict the view that earlier evidence that phrasing biases rule learning (cf. Fountain & Rowan, 1995b) might be accounted for by discrimination learning processes. Interestingly, the current results demonstrating that phrasing biases pattern learning also indicates that rats developed one or more cognitive representations that concurrently coded the same ambiguous sequence in terms of both "runs" and "trills". Taken together with earlier work, the results strengthen claims that serial pattern learning tasks of the type employed in the current study can recruit multiple psychological and neural processes concurrently (Fountain, 2006; Fountain & Benson, Jr., 2006; Fountain & Rowan, 2000).

Rats learned their structurally ambiguous runs- and trills-phrased patterns at different rates and with different error profiles. A pattern phrased as runs was easier to learn than when it was phrased as trills, a result that resembles a similar "runs bias" reported in the human sequential learning literature (e.g., Restle & Brown, 1970). Moreover, these results show that rats represented runs- and trills-phrased patterns somewhat differently. Whereas rats learning the runs-phrased pattern showed rapid learning and little tendency to make trills errors, rats learning the trills-phrased version of the pattern produced inflated rates of both trills and runs errors. Trills error rates were inflated at the beginning of trills chunks that were created by the trills phrasing cues. Runs error rates were inflated on the first and third element of each trill chunk, an effect reported earlier in both rat and human serial pattern learning studies in analogous tasks (cf. Fountain, 1990; Restle & Burnside, 1972). These latter results are consistent with the notion that in addition to coding the trills pattern as a series of trills, rats also concurrently coded trills chunks as segments of two runs. The latter idea explains why rats produced such high runs error rates on the third element of trills chunks—higher even than in the runs-phrased version of the pattern at runs chunk boundaries. According to this idea, these high run overextension rates occurred because there was no cue at this position in chunks of the trills-phrased pattern to terminate the concurrently perceived run chunk and, in so doing, prevent run overextensions (cf. Stempowski et al., 1999).

It should also be noted that anticipation and perseveration rates were inflated at boundaries of runs chunks in the runs-phrased pattern and on the first and third element of each trill chunk in the trills-phrased pattern. These errors appear to be related to uncertainty about which response to make, yet they indicate that rats anticipated a change in pattern structure at these serial positions in the pattern. This conclusion is justified by the fact that similar increases in these error types were not observed on other "within-chunk" trials of the pattern, that is, at positions where pattern structure did not change, and because a failure to anticipate a change in pattern structure would have produced overextension errors on these trials, not

anticipation or perseveration errors. These results also strengthen the argument that rats encoded different representations of runs- and trills-phrased versions of the pattern.

The results show that rats represented the runs- and trills-phrased versions of the pattern differently. These results add to the evidence that, in addition to serving as discriminative cues (Fountain et al., 2000; Stempowski et al., 1999), phrasing cues can bias pattern perception in rat serial pattern learning (cf. Fountain, 1990; Fountain & Rowan, 1995b). The results from the trills-phrased pattern group also fit with the idea that rats' cognitive representations of the same pattern elements could concurrently code them as consistent with both runs and trills interpretations of the ambiguous pattern. Whether or not this means that rats held multiple concurrent representations of the same pattern or simply integrated seemingly contradictory interpretations of the same pattern into a single memorial representation is still an open question. However, at a more general level the results fit with recent behavioral and neurobehavioral studies implicating multiple concurrent psychological and neural processes in rat serial pattern learning (Fountain, 2006; Fountain & Benson, Jr., 2006; Fountain & Rowan, 2000).

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