Effects of runway shift and stay rules on rats' serial pattern learning in the T-maze

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Rats received three-trial series on a T-maze consisting of extended visually distinct left-black and right-striped side runways. During the first phase of training, when allowed to select baited runways within these series, they predominantly alternated their choices. During the second phase, rats received forced-choice serial pattern training of series consisting of two rewarded (R) trials and one nonrewarded (N) trial in two fixed orders, RRN and RNR. In Experiment 1, the rats in the runway shift rule group always received the second R trial when forced down a runway opposite that on the preceding trial in the series and the N trial when forced down the same runway. The rats in the runway stay rule group always received the second R trial when forced down the same runway and the N trial when forced down the opposite runway. In Experiment 2, each rat was conditionally trained with both runway outcome rules as determined by the central alley lighting and the type of food in the side alleys. The rats took longer to reduce their running speed on the N trial within each sequence under the runway stay rule than under the runway shift rule. They also took longer to acquire serial pattern responding for the RNR than for the RRN series only under the runway stay rule condition. When subsequently reexposed to series of free-choice trials on the final phase, rats maintained spontaneous alternating choice patterns under the runway shift rule conditions but either seldom alternated their choices (Experiment 1) or greatly reduced choice alternations (Experiment 2) under the runway stay rule condition. We discussed these effects in terms of rats' natural foraging strategies and as a factor that interacts with other within- and between-series variables that affect serial pattern behavior.

When repeatedly exposed to a series of rewarded (R) and nonrewarded (N) trials in a fixed order on a runway, rats eventually run slower on N trials (Capaldi, Verry, Nawrocki, & Miller, 1984; Hulse, 1978). Rats acquire such serial pattern behavior more easily when each series of trials is separated by long intervals or when each alternates over visually distinct runways (Fountain, Henne, & Hulse, 1984). Although Hulse (1978, 1980) considered that serial pattern performance reflects a unitary formal rule, Capaldi and Molina (1979) maintained that it is based on sequential, interitem associations. That is, repeated exposures to a specific outcome sequence cause each event within a series to activate memories of prior events that signal the outcome in a current trial. Hence, this idea is referred to as the sequential memory model.

Capaldi (1992) extended the sequential memory model to include a hierarchical chunking notion. According to this idea, rats initially form a "trial" chunk by learning to

associate a sequence of events when trained to run down the runway for a reward. Then they learn to integrate or sequentially associate different trials into a "series" chunk as already described. At an even higher level, the rat may further integrate different series chunks into a "list" chunk to differentiate between different fixed outcome sequences. There are two types of list chunks: One type occurs when each outcome sequence repeatedly occurs on separate sessions. Thus, the outcome sequence of the first series of trials in a session signals which of the possible sequences will only repeatedly occur in that session. For example, Capaldi, D. J. Miller, Alptekin, and Barry (1990) found that rats anticipate (run more slowly on) each N trial within RN or RRN sequences when each sequence repeatedly occurs on separate sessions but not when the sequences are intermixed within each session. Rats in the intermixed presentations group, however, run more slowly only on the last trial within the RRN sequence. Thus, they learned that the outcome of the second trial signals the possibility of a third N trial, a lower order rule. For the other type of list chunk, rats can acquire different serial patterns for different sequences that occur in a fixed order within every session (e.g., RNN and RNR) (Capaldi, Nawrocki, & Verry, 1983).

In recent investigations of the hierarchical chunking model in our laboratory (Cohen, Simpson, Westlake, & Hamelin, 2002; Cohen, Westlake, & Pepin, 2001), we attempted to determine whether rats could "chunk" RRN and RNR outcome sequences into a higher order RRR *super*

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chunk. In those studies, rats experienced both sequences in a T-maze consisting of a black runway on the left and a striped runway on the right. Some rats received each sequence on a different runway (the “associated-runways” group), and other rats received each sequence equally on both runways (the “nonassociated-runways” group). As expected, rats in both groups evidenced list chunking by developing slower speeds on the N trial in each sequence when each repeatedly occurred on separate sessions. However, only the associated-runways rats continued to run more slowly on N trials when each sequence was later intermixed within each session. Thus, the associated-runways rats had learned to associate each runway with a different sequence. The nonassociated-runways rats ran more slowly on the N trial within the RRN sequence. Consequently, they had only learned to associate the outcome of the second trial with the outcome of the final trial in the sequence.

The main question in our recent research, however, was whether the associated-runways rats could further combine RRN and RNR sequences into a single, higher order RRR super chunk. That is, when allowed to choose a runway on each trial in a series, would they always select a baited runway after having acquired forced-choice serial pattern behavior? We reasoned that to do this, they would have to learn which runway would be baited on each trial within any series during forced-choice training. That is, they would have to associate each trial’s ordinal position with its outcome, as suggested by the ordinal position model of serial pattern learning (Burns, Dunkman, & Detloff, 1999; Burns, Wiley, & Payne, 1986). For example, if a rat can associate the RRN sequence with the left runway and the RNR sequence with the right runway, it should learn that either runway is baited on the first trial, but only the left runway is baited on the second trial, and only the right runway is baited on the last trial. Consequently, it should select a baited runway on any trial by making either left-left-right or right-left-right choices during free-choice testing. The sequential memory model (Capaldi & Molina, 1979) predicts that rats in both groups should at least be able to select the baited runway correctly on the last free-choice trial by remembering the outcome from the runway selected on the second free-choice trial.

Free-choice tests failed to confirm either model. Associated-runways rats did not predominantly choose baited runways on the second and third free-choice trials, nor were rats in either group always able to select the baited runway on the last trial. Rather, rats sometimes spontaneously alternated between runways regardless of outcome consequences, a well-known behavioral predisposition of rats in T-mazes (Douglas, 1966). Rats in a subsequent experiment (Cohen et al., 2002, Experiment 2), however, reliably selected the baited runway on the last free-choice trial after being trained on serial pattern learning in which the first runway sometimes differed from the runway on the next two trials. Varying runways during forced-choice serial pattern learning

may have improved free-choice test performance by reducing rats’ tendency to spontaneously alternate choices. Despite this possibility, rats continued to maintain some aspect of spontaneous alternation and thus developed slightly but reliably different serial pattern responding within the same outcome sequences as a function of this manipulation (see Cohen et al., 2002, Figure 3, p. 267). That is, rats in both groups ran equally fast on each of the first two trials within RRN sequences when forced to a different runway after the first trial, but they ran slower on the second trial when forced into the same runway on every trial. Rats in the nonassociated-runways group ran slower on the second trial than on the first trial within the RNR sequence only when exposed to the same runway, but they ran equally fast on every trial when exposed to different runways. Thus, rats may reduce their speed on a runway they have been forced down on a previous trial within a series simply as a manifestation of their inherent tendency to spontaneously alternate choices. Consequently, our previous experiments may have inadvertently uncovered a runway variation factor deserving of more systematic examination to determine its effect on serial pattern learning.

The present study represents the start of such an investigation. It was designed to answer two related questions: First, on the basis of findings in Cohen et al. (2002, Experiment 2), will rats acquire serial pattern responding for complementary RRN and RNR sequences more slowly when runway entries are made inconsistent with their spontaneous alternation tendencies? Second, given that rats can eventually acquire serial pattern behavior inconsistent with such a predisposition, can they suppress spontaneous alternations to select baited runways during subsequent free-choice test series?

To answer these questions, we initially presented rats with several series of free-choice trials in which spontaneous alternations were rewarded (Phase 1) and then trained them on forced-choice RRN and RNR series (Phase 2). During this serial pattern training, the rats received each outcome sequence for patterns of forced choices that were either inconsistent or consistent with their previously rewarded free-choice alternations. In Experiment 1 of this study, we trained rats under one or the other forced-choice runway condition (independent groups). In Experiment 2, we conditionally trained other rats on both forced-choice runway conditions (within-subjects factor). For inconsistent patterns of forced entries, the rats were rewarded on the next trial in any series when they were forced down the same runway they had gone down on the previous trial in the series, but they were not rewarded when forced down the opposite runway. Thus, rats were forced to make a left-left-right or a right-right-left pattern of entries for an RRN outcome sequence and a left-right-right or a right-left-left pattern of entries for an RNR outcome sequence. As seen in Table 1, these forced-choice patterns are designated as *a-a-b* for RRN and *a-b-b* for RNR, where *a* represents the runway entered on the first trial of a series,

Table 1
Outcome Sequences and Their Corresponding Runway
Entry Patterns for Each Phase in Experiment 1,
Between-Subjects Design

Between-Subjects Design									
Phase 1: Free Choice									
Outcome Sequence		RRR		RRN		RNR		RNN	
Entry Pattern		a-b-a		a-b-b		a-a-b		a-a-a	
		Runway Stay Rule Group				Runway Shift Rule Group			
Phase 2: Forced Choice									
Outcome Sequence		RRN		RNR		RRN		RNR	
Entry Pattern		a-a-b		a-b-b		a-b-b		a-a-b	
Phase 3: Free Choice									
Outcome Sequence		RRR	RRN	RNR	RNN	RRR	RRN	RNR	RNN
Entry Pattern		a-a-a	a-a-b	a-b-b	a-b-a	a-b-a	a-b-b	a-a-b	a-a-a

Note—Outcome sequences: R, rewarded trial; N, nonrewarded trial. Entry patterns: a, runway entered on the first trial of any series; b, other runway.

and *b*, the other runway. For ease of explication, we label these forced-choice patterns as the *runway stay rule* for a second rewarded trial in any sequence. For consistent patterns, rats were rewarded when they were forced into the runway different from the previous trial but not rewarded when they were forced into the same runway. Thus, they were forced to make a left-right-right or right-left-left pattern of entries (*a-b-b*) for an RRN sequence and a left-left-right or right-right-left pattern (*a-a-b*) for an RNR sequence. These patterns are labeled as the *runway shift rule* for a second rewarded trial in any sequence. Following extensive training to ensure that rats had acquired reliable serial pattern responding under each runway rule, rats were again exposed to free-choice trials (Phase 3). Runways were baited based on which forced-choice runway rule had been in effect during Phase 2. Although we expected rats to continue alternating their selection of runways (*a-b-a* patterns) following forced-choice serial pattern training with the runway shift rule, we were uncertain whether they could switch to selecting only the same runway initially chosen on their first free-choice trial (*a-a-a* patterns) following forced-choice serial pattern training with the runway stay rule.

EXPERIMENT 1

The present experiment consisted of three phases as shown in Table 1. In Phase 1, all rats were trained to choose a baited runway on three massed trials in the T-maze, an RRR outcome sequence, by spontaneously alternating their choices—that is, by making left-right-left or right-left-right choices (*a-b-a* patterns). Any other pattern led to fewer trials being rewarded. In Phase 2, rats received forced-choice serial pattern training either based on the runway stay rule or on the runway shift rule (independent groups) for RRN and RNR outcome sequences, as already described. In Phase 3, rats received series of free-choice trials during which they could select a baited runway on the second and third trials of a series based on their respective Phase 2 forced-choice rules. Thus, rats in the runway stay rule group could only experience

an RRR sequence by making *a-a-a* runway choices, whereas those in the runway shift group continued to experience this outcome sequence when they made *a-b-a* choices.

Method

Subjects

Ten experimentally naive male Long-Evans hooded rats from the Charles River Breeding Farms, St. Constant, Quebec, served in this experiment. They were approximately 75 days old and weighed at or over 350 g at the start of the experiment. They were housed and maintained under the same conditions as reported in Cohen et al. (2001) and were randomly assigned into equal runway shift rule and runway stay rule groups before the experiment began. One rat in the runway shift rule group was later removed due to illness. Therefore, we report data from all five runway stay rule rats and from the remaining four runway shift rule rats.

Apparatus

We used the T-maze described in Cohen et al. (2001, see Figure 1) throughout this study. It consisted of an enclosed black wooden T-maze with a 7.5-cm wide and 160-cm long metal runway extending from each 20-cm long side arm. A return alley, located 20 cm from the beginning of each attached runway, curved back to a standard stainless steel holding cage that served as a start chamber to the 20-cm long center arm. The interior of the left runway was black, and the right runway was painted with black and white stripes from the return alley to the goal area. A moveable food tray containing eight food wells could be slid in and out of the goal area from the side of the runway. Each food tray was baited with eight shelled, unsalted, roasted sunflower seeds. A 40-W incandescent light over each runway and behind a translucent plastic panel at the end of the center arm illuminated the maze.

Procedure

Rats were shaped to run down each runway for sunflower seeds by procedures slightly modified from those reported in Cohen et al. (2001). The experimenter began a session by placing the rat backward into the start chamber and lifting the clear center-arm door when the rat turned around and faced the center arm of the T-maze. Lifting the door activated a silent digital clock that stopped when the rat crossed a photo beam 190 cm away and 10 cm from the end of a runway, its goal area. The experimenter lowered the start chamber's door as soon as the rat entered the center arm and lowered the side arm's guillotine door when it entered its side runway. When the rat broke the photo beam at the end of the runway, the experimenter

Figure 1. Mean percentage of times rats in the runway shift rule (left) and runway stay rule (right) groups made each type of free-choice serial pattern during Phases 1 and 3 in Experiment 1. Vertical error lines show $\pm$ SEMs.

either slid the baited food into the goal area or removed it from outside the runway area, depending upon the trial's programmed outcome. The experimenter then opened the side door to the start chamber from the return alley, and closed it when the rat reentered the start chamber. The rat could also reenter the start chamber without first running down to the end of an arm, a *bypass* response, if it either ran into the return alley and stayed there for 10 sec or refused to enter a side arm from the center arm within 60 sec. The experimenter then reset the clock and prepared the maze for the next trial by baiting both food trays outside the runways and lifting the appropriate side-arm door while a rat waited in the start chamber for 10 sec (the intertrial interval). Upon returning to the start chamber after its last trial of a series, the rat was removed and placed into its individual holding cage, where it waited approximately 15–20 min until all other rats had completed the current series. Then it was returned to the start chamber for its next series of trials. The experimenter recorded each rat's running time (to the nearest 0.1 sec) from when the start chamber door into the center alley was raised to when the rat intersected the photo beam at the end of a runway. Running times were transformed into speed scores (cm/sec) for statistical analysis. A runway bypass was recorded as a default speed of 2 cm/sec. Specific procedures for each of the three phases were as follows.

Phase 1: Free-choice series. All rats received 12 sessions, each containing 4 free-choice three-trial series, for a total of 48 series. As previously described and shown in Table 1, both runways were baited for the first free-choice trial, but only the runway opposite from that chosen on the first trial was baited for the second trial, and only the runway opposite from that chosen on the second trial was baited for the final trial of the series.

Phase 2: Forced-choice series. Rats in each group were trained on RRN and RNR outcome sequences over 48 sessions. Rats received two RRN and two RNR outcome sequences in a random order within each session, with the constraint that the same order could not occur for more than 2 sessions in a row. Rats received each exemplar of the *a-a-b* (left-left-right; right-right-left) and *a-b-b* (left-right-right; right-left-left) patterns of forced choices in each session.

Phase 3: Free-choice series. Rats received another 12 sessions, each containing 4 free-choice three-trial series, for a total of 48 se-

ries. Rats in the runway shift rule group received the same baiting contingencies as those in Phase 1. Rats in the runway stay rule group received the opposite baiting contingencies; that is, the runway baited on the second and third trials was always the same as the runway chosen on the first and second trials, respectively, in the series, as shown in Table 1.

Results and Discussion

Phase 1: Free-Choice Series

Figure 1 shows the mean percentage choices made by each group for each of the four free-choice patterns over the 48 series. As expected, every rat predominantly alternated runway choices ($>80\%$). These data were statistically compared with those in Phase 3, as subsequently reported. The latencies for all of the rats on all free-choice trials were less than 5 sec.

Phase 2: Forced-Choice Series

Each rat's running speed (cm/sec) on each trial within each outcome sequence (RRN, RNR) was averaged for each block of six sessions. Thus, a rat's mean speed on each trial within an outcome sequence was derived from 12 speed scores for each block. We analyzed the speed scores for each outcome sequence with a 2 (group) $\times$ 3 (trial) $\times$ 8 (block) analysis of variance (ANOVA) with repeated measures on the last two factors. On the basis of the findings from these two ANOVAs, we conducted separate 2 (group) $\times$ 8 (block) ANOVAs on each trial within each outcome sequence. The large degrees of freedom generated by the number of levels for within-subjects factors were reduced by the Greenhouse–Geisser method to decrease the likelihood of Type 1 errors. Individual comparisons between groups' trial speeds for each

Figure 2. Mean speeds on each forced-choice trial within each outcome sequence (Graph A, RRN; Graph B, RNR) for each block of six sessions (24 three-trial series) for each group in Experiment 1.

block within each outcome sequence were carried out by Newman-Keuls tests when appropriate. Effects were considered significant at $p \leq .05$.

Figures 2A and 2B show each group's mean speed for each trial within the RRN and the RNR outcome sequences, respectively, over the eight blocks. We did not depict standard errors of the mean (*SEMs*) in these figures to preserve their visual integrity, but *SEMs* varied between ± 1.7 and ± 11.3 cm/sec. As seen in Figures 2A and 2B, the runway shift rule rats ran consistently more slowly on N than on R trials within each outcome sequence on every block. The runway stay rule rats developed similar slower speeds on the N trials after the second block within the RRN sequence and after the fourth

block within the RNR sequence. Groups did not appear to differ in their speeds on the R trials within either sequence. The three-way interaction (groups $\times$ trials $\times$ blocks) just missed significance for both the RRN [$F(1,7) = 5.02, p = .06$] and RNR [$F(1,7) = 5.41, p = .053$] sequences. A significant group $\times$ trial interaction was found for the RNR sequence [$F(1,7) = 7.52$], however, reflecting differences between groups over the first five blocks. Subsequent group $\times$ block ANOVAs for each trial for each outcome sequence revealed only a significant interaction involving N-trial speeds for each sequence [$F_s(1,7) = 7.77, 5.96$]. Individual comparisons between groups at each block for the RRN ANOVA revealed that the runway shift rule rats ran significantly slower than the runway stay

Table 2
Outcome Sequences and Their Corresponding Runway Entry Patterns
for Each Phase in Experiment 2, Within-Subjects Design

Phase 1: Free Choice								
Center Arm/Food Cues	2 (lit/unlit center arm) × 2 (seeds/pellets), counterbalanced across rats							
Outcome Sequence	RRR		RRR		RRR		RRR	
Entry Pattern	a-b-a		a-b-b		a-a-b		a-a-a	
	Runway Stay Rule				Runway Shift Rule			
Phase 2: Forced Choice								
Center Arm/Food Cues	Illumination A / Food Y				Illumination B / Food Z			
Outcome Sequence	RRN		RNR		RRN		RNR	
Entry Pattern	a-a-b		a-b-b		a-b-b		a-a-b	
Phase 3: Free Choice								
Center Arm/Food Cues	Same as in Phase 2				Same as in Phase 2			
Outcome Sequence	RRR	RRN	RNR	RNN	RRR	RRN	RNR	RNN
Entry Pattern	a-a-a	a-a-b	a-b-b	a-b-a	a-b-a	a-b-b	a-a-b	a-a-a

Note—Outcome sequences: R, rewarded trial; N, nonrewarded trial. Entry patterns: a, runway entered on the first trial of any series; b, other runway. Center arm/food cues: A, lit (unlit); B, unlit (lit); Y, seeds (pellets); Z, pellets (seeds).

rule rats on N trials over the first two blocks. Individual comparisons between groups at each block for the RNR ANOVA revealed that the runway shift rule rats ran significantly slower than the runway stay rule rats on N trials over the first four blocks.

Phase 3: Free-Choice Test Series

Figure 1 shows that the runway shift rule rats continued to predominantly alternate their runway choices (*a-b-a* pattern), whereas the runway stay rule rats predominantly selected the same runway on the last two trials as that chosen on the first trial (*a-a-a* pattern). Rats in both groups seldom displayed choice patterns that yielded either just one (the first) or two rewarded trials. Indeed, no rat selected a baited runway on every trial in a series less than 79% of the time (38 of the 48 free-choice series). The only other obvious effect was that the percentage of times a baited arm was selected on both the second and third trials increased slightly in the runway shift rule group but decreased slightly in the runway stay rule group from the percentages in Phase 1. Every runway shift rule rat made more *a-b-a* choices in Phase 3 than in Phase 1, but 4 of the 5 runway stay rule rats made fewer *a-a-a* choices during the final phase than they made *a-b-a* choices in Phase 1. The remaining rat in the runway stay rule group made 45 *a-b-a* choices in Phase 1 and 46 *a-a-a* choices in Phase 3. These changes were significant for each group [$F(1,3) = 21.235, 7.86$].

To summarize the results from Experiment 1, the runway stay rule rats developed serial pattern responding to RRN and RNR sequences more slowly than did the runway shift rule rats. This difference was greater within the RNR sequence. The runway stay rule rats were able to overcome their reinforced alternating choice patterns in Phase 1, however, to predominantly choose a baited runway on every trial in Phase 3. These rats, however, were slightly less likely to choose an *a-a-a* pattern in Phase 3 than to choose an *a-b-a* pattern in Phase 1. Although this differ-

ence was statistically reliable, it was not large enough to justify an explanation based on possible intrusions of spontaneous alternations.

EXPERIMENT 2

Rats in Experiment 1 were able to apply a runway stay rule acquired during forced-choice serial pattern learning almost as well as other rats were able to maintain the runway shift rule during the final free-choice series. Given no other alternative, rats might simply have to switch from alternating to not alternating their choices of runways during free-choice series. The question remains whether rats could acquire and apply the runway stay rule if they were also trained on the forced-choice runway shift rule. In other words, in Experiment 2 we asked whether rats could develop flexible, conditional serial pattern responding and, if so, whether they would be able to apply either rule under free-choice conditions. In this experiment, rats were exposed to both rules in Phase 2. The rule that was in effect during a series of trials was signaled by the brightness of the center arm and the type of food (seeds or pellets) at the end of the side runways on R trials. Following this conditional forced-choice serial pattern training, the rats received several series of free-choice trials to determine whether they could similarly choose baited runways under each signaled condition.

Table 2 shows the general design of Experiment 2. In Phase 1, rats experienced free-choice trials in which any choice was rewarded. Some rats always received seeds in the chosen runway when the center alley was lit and pellets when it was unlit; other rats received the opposite pairings. Unlike Phase 1 in Experiment 1, the rats in this phase were always rewarded on every free-choice trial, regardless of their choice patterns. We also gave rats half as many free-choice series as in Experiment 1 to limit any effect their reinforced free-choice patterns might have on acquisition of forced-choice serial patterns and

Figure 3. Mean speeds on each forced-choice trial within each outcome sequence (Graph A, RRN; Graph B, RNR) for each block of 48 three-trial series for each signaled forced-choice rule during Phase 2, second training segment. Neither the food nor the center-arm brightness cues referenced in Table 2 (Experiment 2) are labeled in this figure.

subsequent free-choice patterns. We expected that, as in Experiment 1, rats would predominantly alternate spontaneously between runways, even though they were reinforced for any pattern of choices.

The rats received extensive signaled serial pattern training under both the runway shift and stay rules for RRN and RNR outcome sequences in Phase 2. Food type on R trials and the lighting condition of the center alley signaled which rule was in effect for each series. This phase was divided into two training segments. In the first segment, for several sessions, some rats were exposed to the outcome sequences on odd-numbered sessions under their redundantly signaled runway shift rule, and on even-

numbered sessions under their redundantly signaled runway stay rule. The other rats were exposed to the outcome sequences on even-numbered sessions under their signaled runway shift rule and in odd-numbered sessions under their signaled runway stay rule. This final training segment determined whether the rats had learned to associate both rules with their specific center-arm brightness and R-trial food type during the first training segment. These specific training segments of Phase 2 are not depicted in Table 2.

In Phase 3, the rats received modified free-choice test series training. Here they were forced to one of the baited side runways on the first trial and then were allowed to

choose between baited and nonbaited runways on each of the two remaining trials within each series. We conducted forced entries on the first trial of these test series to ensure that the rats experienced each runway equally at the beginning of each test series under each signaled rule condition. Within each session, free-choices on half the series were reinforced according to the signaled runway shift rule, the other half, according to the signaled runway stay rule. We originally had planned to present rats with the same number of test series as in Phase 3 of Experiment 1. However, the rats were less accurate in selecting baited runways under the runway stay rule than under the runway shift rule over the first 12 sessions in Experiment 2. Therefore, we extended this phase to determine whether the rats would eventually reach levels of accuracy under the runway stay rule comparable to those achieved under the runway shift rule.

Method

Subjects and Apparatus

Five experimentally naive male Long-Evans hooded rats from the Charles River Breeding Farms, St. Constant, Quebec served in this experiment. They were approximately 150 days old and weighed at or over 450 g at the start of the experiment. One animal became ill during the course of the experiment and was removed. We report data only from the remaining four animals. We used the same apparatus used in Experiment 1, except that we varied the illumination of the center arm of the T-maze by means of a light behind a translucent plastic panel at end of the center arm. Runways were either baited with sunflower seeds or with dustless, lactose enriched 45-mg food pellets (Bio-Serv, Frenchtown, NJ).

Procedure

Phase 1: Free-choice series. The experiment began with shaping procedures in which rats were trained to run down each runway for seeds or food pellets under each center-arm lighting condition. All rats received 4 series of massed free-choice trials per session for six sessions, for a total of 24 series. In each session, runways were always baited with eight seeds on each trial for 2 of the series and with eight food pellets on each trial for the other 2 series. The order of these series was randomly determined and did not occur on more than two sessions in a row. Throughout the experiment, 2 rats always received seeds when the center arm was lit and pellets when it was unlit (condition seeds-lit). The other 3 rats always received seeds when the center arm was unlit and pellets when it was lit (condition seeds-unlit).

Phase 2: Forced-choice serial pattern training. For the 2 seeds-lit rats, 1 rat was trained with the runway shift rule when the center arm was lit and with the runway stay rule when it was unlit. These conditions were reversed for the other rat. For the 3 seeds-unlit rats, 2 were trained with the runway shift rule when the center arm was lit and with the runway stay rule when it was dark. For the remaining rat, these conditions were reversed; this last rat became ill during training in this phase and was dropped from the experiment.

This phase consisted of 106 sessions. For the first 82 sessions, each runway rule alternated over sessions; for the final 24 sessions, the rules were intermixed within each session. During the first, 82-session training segment, two rats received serial pattern training under their specific signaled runway shift rule on odd-numbered sessions and under their specific signaled runway stay rule on even-numbered sessions. One of these rats was dropped from the experiment due to illness. The other three rats received serial pattern training under their specific signaled runway stay rule on odd-numbered sessions and under their specific signaled runway shift rule on even-numbered sessions. On each of the initial 20 sessions in this

segment, the rats were exposed to only four 3-trial series, as in Experiment 1. For the remaining 62 sessions, they were exposed to eight series per session. Each outcome sequence (i.e., RRN, RNR) was equally presented in random order within each of these sessions, with the constraint that the same sequence never occurred on more than two series in a row. Consequently, each outcome sequence occurred 144 times under each forced-choice runway rule during this part of training. Over the final 24 sessions, each session comprised eight series, with each outcome sequence occurring for each forced-choice runway rule within a session. Thus, every rat was exposed to each outcome sequence four times in a session, twice each under its specifically signaled runway shift and stay rules. Consequently, each outcome sequence occurred 48 times under each forced-choice runway rule during the final training segment. Each of the eight different types of series [$2(\text{RRN, RNR}) \times 2(\text{shift vs. stay rule}) \times 2(\text{left vs. right on first trial})$] occurred in a random order over sessions, constrained so that neither the same outcome sequence nor runway rule occurred on more than two series in a row.

Phase 3: Free-choice series. Rats received another 60 sessions like those at the end of Phase 2, except that both runways were open on the second and third trials within each series, and each session comprised only four series. One runway was always baited on each of these free-choice trials, depending upon which signaled runway rule was in effect on that series of trials. The free-choice outcome sequences, as depicted in Table 2, were generated by the same patterns of choices indicated by the specific redundant lighting and food cues.

Results and Discussion

Phase 1: Free-Choice Series

When rewarded for choosing either runway on each trial in a series, every rat alternated its choices (*a-b-a* pattern) on most series. One rat did so on 14 series (58%); another, on 16 series (67%); and each of the other two did so on 21 out of 24 series (88%). Every rat also occasionally made an *a-b-b* choice pattern. One rat did so on 7 series (29%); another, on 4 (17%); and each of the remaining 2 rats did so on 3 series (12%). Only 2 rats made an *a-a-b* pattern: One did so 4 times (17%), and the other, once (4%). Only 1 rat ever chose the same runway on all trials, an *a-a-a* pattern, which it did twice (8%).

Phase 2: Forced-Choice Serial Pattern Training

We carried out two separate analyses, one based on the first 82 sessions, in which runway variation rules alternated over sessions, and the other on the final 24 sessions, in which the runway variation rules were intermixed in each session. In the first training segment, we averaged a rat's running speed on trials for each outcome sequence under each signaled runway rule over six blocks of series. Each block contained 48 series presented under each runway variation rule. The first block comprised 11 sessions utilizing the signaled runway shift rule alternating with 11 sessions utilizing the signaled runway stay rule. As already described, the first 10 of those sessions for each runway rule comprised four series, and the last session comprised eight series. Each of the remaining five blocks consisted of 6 runway shift sessions alternating with 6 runway stay sessions, with eight series in each session. Therefore, within each block we averaged trial speeds for 24 series with each outcome

sequence (i.e., RRN, RNR) under each runway variation rule. In the second training segment (24 sessions), we analyzed the data in a similar way: Data were divided into four blocks of 6 sessions each, and rat speeds were averaged within each outcome sequence under each signaled runway rule. As each block contained 24 series under each signaled runway variation rule, we averaged trial speeds on 12 series for each outcome sequence and runway rule within a block.

In the interest of space and because the results from the first training segment of this phase did not differ substantially from those of Phase 2 in Experiment 1, we only graphically summarize results from the final segment of serial pattern training (Figure 3). The only difference in results in the first training segment from those of Phase 2 in Experiment 1 was that the rats in the present experiment did not immediately display reliably slower speeds on N trials under the runway shift rule on the first block. Such performance only developed on the third block of sessions. As in Experiment 1, however, for the RNR sequence the rats acquired reliable serial pattern behavior more slowly under the runway stay rule than under the runway shift rule. That is, the rats developed lower speeds on the second (N) trial from the fourth block of sessions on under the runway stay rule and from the third block of sessions on under the runway shift rule. Moreover, the rats did not run as slowly on this trial under the runway stay rule as under the runway shift rule until the final two blocks of sessions. A three-way interaction involving data from the RNR sequence [$F(10,30) = 3.30$], and individual comparisons confirmed these observations. The three-way interaction within the RRN sequence did not approach significance [$F(10,30) = 0.97$, $p = .50$].

Figures 3A and 3B show the mean running speeds for each trial within the RRN and RNR outcome sequences, respectively, over the four blocks of sessions in the second training segment. Each runway rule was intermixed within each session. SEMs are not depicted, to preserve the figures' visual integrity, but varied between ± 0.8 and ± 2.8 cm/sec. As seen in each figure and confirmed by a significant effect for trial within each outcome sequence [$F(2,6) = 110.82, 16.88$], the rats continued to run more slowly on N than on R trials. This effect occurred under each runway rule from the first block of sessions. Therefore, the rats had learned to associate the redundant central-arm brightness and R-trial food-type cues with the runway rules during the first training segment. However, the rats ran more slowly on N trials under the runway shift rule than under the runway stay rule, as seen in the figures and confirmed by a significant rules $\times$ trial interaction involving each outcome sequence [$F(2,6) = 18.37, 6.38$].

Phase 3: Free-Choice Series

We calculated the percentage of times each rat made each of the four possible free-choice patterns for each runway rule in each block of 12 sessions (48 series). Figure 4

shows the mean scores for each of the rules. We conducted a separate 2 (runway rule) $\times$ 5 (block) ANOVA for each possible outcome sequence (RRR, RRN, RNR, RNN).

Not surprisingly, as seen on the left half of this figure, when the runway shift rule was in effect, the rats were more likely to alternate choices of runways (*a-b-a*) than to use any other choice pattern. They were least likely to select the same runway on all trials (*a-a-a*). As seen in the right half of this figure, when the runway stay rule was in effect, the rats reduced their likelihood of alternating runway choices and increased the likelihood of selecting the same runway on each trial (*a-a-a*). Unlike the rats in the separate runway stay rule group in Phase 3 of Experiment 1, however, on the first block of sessions, the rats in the present experiment were much less likely to make *a-a-a* choices under the runway stay rule than to make *a-b-a* choices under the runway shift rule to achieve an RRR sequence. As seen in the figure and supported by a significant rule $\times$ block interaction [$F(4,12) = 3.90$], the rats increased their likelihood of making *a-a-a* choices over blocks under the runway stay rule to nearly equal that of making *a-b-a* choices under the runway shift rule. The rats seldom made *a-a-a* choices under the runway shift rule, a pattern that would have resulted in an RNN outcome sequence. However, rats persisted in making some *a-b-a* choices under the runway stay rule, resulting in an RNN outcome, although they did reduce this pattern of choices after the first block. Both a significant main effect for runway rule [$F(1,3) = 43.74$] and a two-way interaction [rule $\times$ block: $F(4,12) = 5.27$] supported these observations. For the RNR sequence, although the rats seemed more likely to make *a-b-b* choices under the runway stay rule than to make *a-a-b* choices under the runway shift rule, this difference was not statistically significant [$F(1,3) = 4.57$, $p = .12$]. For the RRN sequence, the rats also showed a slightly greater probability in the second and fifth blocks of making *a-b-b* choices under the runway shift rule than of making *a-a-b* choices under the runway stay rule. These differences might have accounted for the significant rule $\times$ block interaction [$F(4,12) = 3.83$].

GENERAL DISCUSSION

This study reveals that rats acquire serial pattern responding in a T-maze more slowly when their forced entries for RRN and RNR outcome sequences are inconsistent (the runway stay rule) rather than consistent (the runway shift rule) with their inherent spontaneous alternation tendency. Furthermore, only under the runway stay rule condition do they acquire serial pattern responding earlier for the RRN than for the RNR sequence. After acquiring serial pattern responding under the runway stay rule, however, rats can switch from alternating their selection of runways (*a-b-a* pattern) to mainly selecting the same runway (*a-a-a* pattern) during the final, free-choice phase. This effect was stronger in Experiment 1, in which rats acquired serial pattern responding under one or the

Figure 4. Mean percentage of times rats made each type of free-choice serial pattern under each signaled choice rule during Phase 3 in Experiment 2. Vertical error lines show $\pm$ SEMs. Legend shows outcome sequence for each set of free-choice serial patterns in parentheses; the first pattern occurred for the runway shift rule and the second for the runway stay rule. Neither the food nor the center-arm brightness cues referenced in Table 2 (Experiment 2) are labeled in this figure.

other rule, than in Experiment 2, in which they each acquired serial pattern responding conditionally under both rules.

In terms of rats' behavioral ecology, spontaneous alternation may be an example of a general inherent foraging tendency for animals to vary their location in searching for resources (Charnov, 1976; Kamil, Yoerg, & Clements, 1988; Krebs & McCleery, 1984; Olton, Walker, Gage, & Johnson, 1977). From this perspective, it comes as no surprise that rats would find it more difficult to learn forced-choice serial pattern responding that is inconsistent with their natural foraging tendency. Even though the runway shift rule rats in Experiment 1 displayed accurate serial responding within the first block of sessions in Phase 3, the rats in Experiment 2 developed serial pattern responding more gradually under that rule. Consequently, forced-choice serial pattern performance under the shift rule is not merely an automatic default option for these animals. Also noteworthy is the fact that rats in Experiment 2 did not always apply the runway stay rule immediately during free-choice testing (see first block, Figure 4) as did the runway stay rule rats in Experiment 1. In Experiment 2, the rats only gradually, over continued free-choice testing, reduced tendencies to make complete (*a-b-a*) and partial (*a-b-b*) alternations when the runway stay rule was in effect. Thus, rats will initially persist in making choice patterns consistent with their natural foraging tendencies in a T-maze when they are not under constraint.

In terms of the sequential memory model (Capaldi & Molina, 1979), the runway entered on a prior trial may

serve as a more or less salient predictor of a current trial's outcome than other events. Under the runway shift rule, the previously entered runway may be more salient than other events. Thus, rats may acquire serial pattern responding easily for both RNR and RRN sequences under the runway shift rule by recalling only the runway from the prior trial to determine a current trial's outcome. However, under the runway stay rule, the outcome on the prior trial may be more salient than the location and features of the runway. Thus, rats might initially learn to predict the outcome of the last trial of a series by recalling the second trial's outcome before they learn to predict the second trial's outcome by recalling the first trial's runway. This sequence for acquiring these two types of associations might account for why rats learn serial pattern responding earlier for RRN than for RNR sequences under the runway stay rule.

The outcome factor may also influence the acquisition of serial pattern responding when two noncomplementary sequences (e.g., RNN and RNR; Capaldi et al., 1983) always occur in a fixed order within each session. Such serial pattern list learning is greatly facilitated when some rats (experimental group) experience a change of runways (black to white or white to black) only on the last R trial than when other rats (control group) experience these runway changes on the last trial in both series (Capaldi, Birmingham, & Miller, 1999, Experiment 2). These results support the idea that valid within-series intertrial associations based on runway variations are more salient than interseries associations based on ordinal position of third

trial outcomes. However, the rats in the experimental group were exposed to a runway shift rule consistent with their natural foraging tendency; they always obtained a second R trial when forced to enter a runway different from the one they entered on the previous trial in a series, but they received an N trial when forced to return to the same runway. A more valid test of the greater salience of within-series associations would require that some experimental rats be trained on forced-choice patterns in which a change in runway on only the third trial signals no reward, the runway stay rule. According to our scheme, these rats should develop serial pattern responding more slowly than rats for which a change in runways signals a reward. Recent results from our laboratory (Cohen & Szelest, 2004) confirm this prediction.

As already noted, separating instances of the same outcome sequence by long intervals or alternating them between different runways provides phrasing or grouping cues that promote serial pattern performance (Fountain et al., 1984). Changing runways may introduce a runway shift rule between two otherwise similar trials and, therefore, between each series of trials. For example, Haggbloom (1993, Experiment 1) observed that rats did not reliably run slower on N trials for an RNRNR-RNRNR sequence that alternated on black-and-white runways over sessions. Imposing either a long 10- to 15-min interval or changing runways between every three trials (RNR sequence) produced immediate serial pattern learning on the first postacquisition session. Of further interest was the fact that rats initially trained with the runway grouping cue could easily transfer to the temporal phrasing cue, as Haggbloom had previously found (Haggbloom, Birmingham, & Scranton, 1992), but rats initially trained with the temporal phrasing cue were unable to transfer to runway grouping cues. In Experiment 2 of that study, however, rats trained with a temporal phrasing cue separating RNR sequences could immediately transfer to the runway grouping cues. Thus, under some conditions runway shift cues may be as salient as temporal phrasing cues.

Temporal phrasing between series of trials may also help rats acquire or maintain serial pattern behavior inconsistent with otherwise dominant response patterns in the task. For example, in an octagonal operant chamber, Fountain, Benson, and Wallace (2000) reinforced rats with brain stimulation for pressing levers in a clockwise direction, except after every third clockwise choice, when they had to lever press counterclockwise for the next reinforcement (e.g., 123/234/345/ 456/567/678/781/812, where levers 1–8 were arranged clockwise and “/” is a series boundary). The selection of levers within each series was an easy-to-learn “forward” location shift rule, but choosing the first lever in each series required a rat to return to a previously selected lever from the previous series, a response inconsistent with its otherwise “forward” search behavior. All eight levers were retracted after every choice and reemerged after a 2.0-sec interval, ex-

cept at some boundary locations where they might emerge after a *shorter* 0.5-sec interval. Rats were more likely to choose the correct lever at the beginning of a series following a shorter temporal phrasing cue than following a longer regular interval. In the absence of the shorter phrasing cue, however, rats were more likely to select the next lever clockwise from the one chosen at the end of the last series.

We have characterized the effects of runway shift and stay rules on serial pattern learning in terms of the sequential memory model (Capaldi & Molina, 1979) rather than in terms of the ordinal trial position model (Burns et al., 1999; Burns et al., 1986). However, our preference for analyzing the runway rule factor in such a way does not suggest that the ordinal trial position model should be abandoned. Nor do we claim that the runway rule factor is prepotent for determining how rats develop serial pattern behavior. Indeed, findings from recent studies conducted in Burns’s laboratory (Burns et al., 1999; Burns, Kinney, & Criddle, 2000) are more in line with the ordinal trial position model than with the sequential memory model. Rats in the first of these studies were exposed to RNN and RNR sequences that were redundantly indicated by runway floor cues and by the type of food on the first trial of a series. Rats continued to display serial running patterns based on runway floor cues even when the type of food on the first trial signaled the opposite outcome on subsequent trials in the series or when the runway remained nonbaited on all trials during the posttraining test series. In addition, in Experiment 1 of the more recent study, rats learned to run slowly on a final nonrewarded trial more quickly when exposed to a consistent than to a random change in food type over first two trials in each series. This difference in acquisition is in accordance with the sequential memory model and replicates earlier findings (Capaldi, Alptekin, Miller, & Birmingham, 1997). However, when exposed to postacquisition NNN test sequences, all the rats continued to run more slowly on the third trial, as predicted by the ordinal trial position hypothesis. In Experiment 2 of that study, a second nonrewarded trial always preceded a third trial in which twice as much food as had been given on the first trial was provided as a reward. As predicted by the ordinal trial position model, and contrary to the sequential memory model, the rats continued to run more slowly on the second trial within postacquisition NNN or RRR sequences. An interesting replication and extension of that study might include redundant runway variations to further determine the extent to which rats’ serial pattern performance is controlled by intratrial (ordinal position) or intertrial (sequential memory) associations. Finally, we note that rats have been shown to require only training on separated RN and NR sequences or on a combined RNRNR sequence to be able to immediately transfer to an RNRNRNR sequence (Capaldi & R. M. Miller, 2003). Neither the ordinal trial position model nor our proposed runway rules factor can account for these findings.

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