PERSISTENCE AND RELAPSE OF REINFORCED BEHAVIORAL VARIABILITY

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The present study examined persistence and relapse of reinforced behavioral variability in pigeons. Pigeons emitted four-response sequences across two keys. Sequences produced food according to a lag schedule, in which a response sequence was followed by food if it differed from a certain number of previous sequences. In Experiment 1, food was delivered for sequences that satisfied a lag schedule in both components of a multiple schedule. When reinforcement was removed for one component (i.e., extinction), levels of behavioral variability decreased for only that component. In Experiment 2, food was delivered for sequences satisfying a lag schedule in one component of a multiple schedule. In the other component, food was delivered at the same rate, but without the lag variability requirement (i.e., yoked). Following extinction, levels of behavioral variability returned to baseline for both components after response-independent food delivery (i.e., reinstatement). In Experiment 3, one group of pigeons responded on a lag variability schedule, and the other group responded on a lag repetition schedule. For both groups, levels of behavioral variability increased when alternative reinforcement was suspended (i.e., resurgence). In each experiment, we observed some evidence for extinction-induced response variability and for variability as an operant dimension of behavior.

Key words: operant variability, reinforced behavioral variability, extinction, relapse, pigeon

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Variability may be an operant dimension of behavior (for reviews, see Neuringer, 2002, 2009, 2012, 2016). Like other operant behavior, behavioral variability is controlled by its antecedents and consequences (e.g., de Souza Barba, 2012, 2014). Behavioral variability arises and is maintained as a result of reinforcement. A lag schedule of reinforcement is a variability contingency in which a response produces a reinforcer only if it differs from a certain number of previous responses (Page & Neuringer, 1985). Under a lag 5 schedule, for instance, the current response must be different than the previous five responses for a reinforcer to occur. Page and Neuringer (1985) demonstrated that high levels of behavioral variability could be sustained using lag schedules. Reinforced behavioral variability has been observed in pigeons (e.g., Abreu-Rodrigues, Lattal, dos Santos, & Matos, 2005; Doughty & Galizio, 2015; Doughty, Giorno, & Miller, 2013; Machado, 1997; Odum, Ward, Barnes, & Burke, 2006; Ward, Bailey, & Odum, 2006; Ward, Kynaston, Bailey, & Odum, 2008), rats (e.g., Cohen, Neuringer, & Rhodes, 1990; Neuringer, 1991), and humans (e.g., Abreu-Rodrigues, Souza, & Moreira, 2007; Neuringer, 1986; Paeye & Madelain, 2011; Ross & Neuringer, 2002).

Operant behavior is characterized by control by antecedents and consequences. Behavioral variability is sensitive to reinforcing consequences. Several studies have shown that the stringency of the variability contingency determines the degree of behavioral variability (e.g., Doughty, Giorno, & Miller, 2013; Page & Neuringer, 1985). For example, a lag 10 schedule results in higher levels of behavioral variability than a lag 5 schedule. Behavioral variability can also be brought under discriminative stimulus control. Several studies have shown that organisms may learn to emit variable behavior in the presence of one stimulus and emit repetitive behavior in the presence of another stimulus (e.g., Denney & Neuringer, 1998; Ward, Kynaston, Bailey, &

Odum, 2008). Taken together, these findings support the notion of behavioral variability as an operant, although other theoretical interpretations have been proposed as well (de Souza Barba, 2014; Holth, 2012; Machado, 1997; Machado & Tonneau, 2012).

Operant behaviors can also be systematically affected by disruptors, such as extinction (for a review, see Craig, Nevin, & Odum, 2014). For example, if reinforcers are removed for responding at a high rate, then the overall rate of responding will decrease. Such disruption demonstrates the sensitivity of the behavior to its consequences, or lack thereof. According to behavioral momentum theory, the degree of persistence of responding in the presence of disruptors is an indicator of response strength (e.g., Nevin, 1974).

Although behaviors accompanied by equal reinforcer rates typically have equal response strength and therefore are equally resistant to change (e.g., Nevin, 1974), some behaviors are still more persistent than others. For example, behavioral variability tends to be more persistent than behavioral repetition, even with matched reinforcement rates (e.g., Odum, Ward, Barnes, & Burke, 2006). Results from a number of studies have supported this exception to behavioral momentum. Several drugs have been shown to disrupt performance under repetition contingencies while having little effect on performance under variability contingencies; for example, this effect has been demonstrated with ethanol (Cohen et al., 1990; Ward et al., 2006), *d*-amphetamine (Pesek-Cotton, Johnson, & Newland, 2011; Ward et al., 2006), other stimulants, and benzodiazepines (Abreu-Rodrigues, Hanna, de Mello Cruz, Matos, & Delabrida, 2004). Similar results have been found for delay of reinforcement (Odum et al., 2006; Stahlman & Blaisdell, 2011; Wagner & Neuringer, 2006), prefeeding, and other response-independent food presentations (Doughty & Lattal, 2001). Even though other dimensions of behavior, such as rate of responding, are altered by these disruptors, behavioral variability per se does not seem to be affected.

Another prediction of behavioral momentum theory is that more persistent behaviors will be more susceptible to relapse (Craig et al., 2014). In the laboratory, relapse is often studied using reinstatement or resurgence preparations. Reinstatement is the reoccurrence of a previously reinforced behavior after extinction as a result of the delivery of response-independent reinforcers (e.g., de Wit & Stewart, 1981, 1983). Resurgence is the reoccurrence of a previously reinforced behavior following extinction of a more recently reinforced behavior (e.g., Epstein, 1985). Given the clinical implications of behavioral variability, discussed later, it is important to determine whether it is susceptible to relapse. Evidence of the relapse of behavioral variability is sparse (Bishop, 2008), and more research is needed in this area to better test whether behavioral variability has typical operant characteristics.

One difficulty posed by studying relapse of behavioral variability is that relapse procedures frequently rely on extinction as a disruptor (e.g., de Wit & Stewart, 1981, 1983; Epstein, 1985). In the context of behavioral variability, the use of extinction creates complications because of the difficulty in distinguishing between reinforced behavioral variability and extinction-induced behavioral variability. This distinction is important to consider, given that extinction can result in high levels of behavioral variability even with no history of reinforcement for specifically behaving variably (e.g., Antonitis, 1951; Eckerman & Lanson, 1969; Jensen, Stokes, Paterniti, & Balsam, 2014; Mechner, 1958; Mechner, Hyten, Field, & Madden, 1997; Mintz & Notterman, 1965).

Few studies have examined the effects of extinction on behavior under the control of a variability contingency (Arantes, Berg, Le, & Grace, 2012; Neuringer, Kornell, & Olufs, 2001). Neuringer et al. (2001) studied extinction of variable behavior in rats. Three groups of rats emitted sequences of lever- and key-presses. One group earned food for emitting variable sequences (Experiments 1, 2, & 3), another group received yoked reinforcement rates, matched to other groups, but no specific responses were required to produce reinforcement (Experiment 2), and a final group earned food for repeating a single target sequence (Experiment 3). When responding was extinguished, molar, statistical measures of behavioral variability increased slightly, indicative of extinction-induced behavioral variability. Neuringer and colleagues also conducted molecular, response-specific analyses.

In baseline, rats in all groups emitted particular sequences more often than others. In extinction, those specific sequences continued to be emitted more often than others, but the probability of emitting a particular sequence tended to decrease if it had been produced more frequently in baseline, and increased if it had been produced less frequently in baseline. Overall, rats behaved similarly in baseline and extinction, but occasionally emitted less frequent sequences when extinction was in place. It is important to further examine the potentially confounding effects of extinction on behavioral variability, especially in the context of relapse.

The purpose of the present study was to determine the effects of extinction on reinforced behavioral variability and to determine if behavioral variability is susceptible to relapse. Experiment 1 was designed to examine extinction and reacquisition of reinforced behavioral variability in pigeons. Pigeons responded on a lag schedule in both components of a multiple schedule. Reinforcement was removed for behavior in one component to differentiate between reinforced and extinction-induced behavioral variability. In Experiments 2 and 3, we examined whether behavioral variability would relapse under reinstatement and resurgence procedures, respectively.

Experiment 1: Extinction and Reacquisition

The aim of the present experiment was to examine the effects of extinction on reinforced behavioral variability in pigeons using a multiple schedule to directly compare behavioral variability under reinforcement and extinction within subjects. In this experiment, four-peck sequences produced food on a lag

Table 1

Recent behavioral histories and identifying symbols for each individual subject

Subject	Symbol used	Immediate prior history	Experiment 2	Experiment 3	Experiment 1
55	●○	Relapse of key pecking	X	X	X
220	■□	Relapse of key pecking	X	X	X
223	▲△	Relapse of key pecking	X	X	X
237	▼▽	Relapse of key pecking	X	X	X
373	◆◇	Delay discounting	-	-	X
381	⊗⬡	Relapse of key pecking	X	-	-
927	⬖⬗	Relapse of key pecking	X	-	-
936	⬢⬡	Relapse of key pecking	X	X	X
956	★✳	Relapse of key pecking	X	-	X
957	◐⊙	Relapse of key pecking	X	X	X
966	▶▷	Relapse of key pecking	X	X	X
1158	◀◁	Delay discounting	-	X	X
1499	▣▣	Delay discounting	-	X	X
17556	◆◇	Delay discounting	-	X	X

Note. An X indicates that the pigeon participated in that experiment, and a - signifies that the pigeon did not. The first column shows the subject number, the second column shows the symbol used in all graphs, the third column shows the immediate behavioral history prior to the three reported experiments, and the next three columns show which pigeons participated in each experiment. Experiments are listed in chronological order from left to right.

schedule. Then, responding in one component was maintained on the same lag schedule, whereas responding in the other component was extinguished. Finally, the lag schedule of food delivery was restored for both components.

Method

Subjects. Twelve adult pigeons with prior experimental histories served as the subjects for this experiment. Although presented first, Experiment 1 was conducted after Experiments 2 and 3. Table 1 shows the chronological order of the experiments, as well as recent experimental histories for each subject. Subjects were maintained at 80% of their ad libitum body weight by supplemental feeding when necessary. Pigeons received Purina pigeon chow in the home cage and also in a food hopper during experimental sessions. When not in experimental sessions, the subjects were housed in a temperature-controlled vivarium with a 12-h light/dark cycle, and had continuous access to water. Sessions were conducted 5 days per week at approximately the same time each day.

Apparatus. Four experimental chambers were used in this study. Each operant chamber was 29 cm x 26 cm x 29 cm and made of clear plastic and aluminum. Each chamber contained two 2.5-cm diameter response keys, each requiring a force of about 0.1 N to operate. One of the response keys was 6 cm left of center and 16 cm above the floor, and the second response key was 6 cm right of center and 16 cm above the floor. The keys could be illuminated white and blue from behind by 28-V DC bulbs. The chamber included a 28-V DC shielded houselight centered on the wall, 33 cm from the floor of the chamber. A 6-cm x 5-cm aperture, located 5 cm from the chamber floor and directly below the houselight, allowed the pigeon to access chow from a raised solenoid-operated hopper during food deliveries. During food deliveries, the houselight and keylights were extinguished and a 28-V DC bulb in the hopper aperture was illuminated. A ventilation fan was used to mask extraneous sounds. Control of experimental events and data recording were conducted on a PC using Med Associates® interfacing and software.

Procedure. In this and all subsequent experiments, pigeons made sequences of responses across two keys. A response sequence consisted of four key pecks across left and right response keys (e.g., RLRL). With four-peck sequences and two possible responses, there were 16 possible response sequences. Each trial began with the illumination of the houselight and the left and right keylights. After a response to either key, the keylights were extinguished for a 0.5-s resetting interresponse interval (IRI). After the fourth key peck, the houselight and keylights were extinguished. Each four-response sequence resulted in either activation of the hopper and hopper light for 1.5 s (reinforcement) or flashing of the houselight for 1.5 s with a 0.25-s on/off cycle (nonreinforcement). The next trial began immediately after reinforcement or nonreinforcement.

A two-component multiple schedule of reinforcement was in place throughout the experiment. Each component of the multiple schedule was active for 5 min and each component was presented three times per session, with the two components alternating and a 30-s intercomponent interval (ICI) between each component. One component was designated by blue keylights and the other component was designated by white keylights (colors were counterbalanced across subjects).

Experiment 1 consisted of three phases: Baseline, Extinction, and Reacquisition. In Phase 1, Baseline, both components of the multiple schedule were identical, except for the key colors. A separate lag 8 schedule of reinforcement was in place for each component; that is, a sequence produced access to pigeon chow if it were different than the previous eight sequences in that component. The lag was continuous across sessions and component presentations. We used a lag 8 schedule because this requirement is relatively strict, ensuring high levels of behavioral variability, but not so strict that we would not be able to observe either an increase or decrease in behavioral variability. For each phase of each experiment, we used fixed-time stability criteria to determine when to progress from one phase to another (Perone, 1991). Phase 1 was in effect for 20 sessions.

There were two additional phases. Phase 2, Extinction, was similar to Baseline, except that reinforcers were suspended for one of the components (Vary Ext). The other component

remained active on a lag 8 schedule (Vary). Phase 2 was in effect for 10 sessions. Phase 3, Reacquisition, was identical to Baseline. Both components were once again active on a lag 8 schedule of food delivery. Phase 3 was in effect for 10 sessions.

Data analysis. The primary dependent measures used in this study were response rate, reinforcer rate, proportion of sequences meeting the lag schedule, and U-value. Response rates were calculated as trials per min for each component, with all time in that component included. Reinforcer rates were calculated as reinforcer deliveries per min, with all component time included. Proportion of sequences meeting the lag schedule was calculated as all sequences that satisfied the lag 8 contingency divided by the total number of sequences emitted for each component. Even if a sequence was not followed by food (i.e., during Extinction), it counted towards this measure if it would have satisfied the lag schedule. A higher proportion of sequences meeting the lag schedule indicates higher levels of behavioral variability.

U-value is a common measure of behavioral variability that ranges from 0 to 1 (Miller & Frick, 1949; Page & Neuringer, 1985). A U-value of 0 would indicate absolute repetition (i.e., only a single sequence occurred throughout the session). A U-value of 1 would indicate an even distribution of response sequences (i.e., every possible sequence occurred an equal number of times throughout the session). U-value is calculated using Equation (1),

$$U = -\sum_{i=1}^{n} \frac{Rf_i * log_2(Rf_i)}{log_2(n)} \qquad (1)$$

where Rf is the relative frequency of a given sequence and n is the total number of possible sequences, in this case 16. Higher U-values indicate higher levels of behavioral variability.

Although U-value can be a useful molar measure of behavioral variability, it has limitations (Kong, McEwan, Bizo, & Foster, 2017; Neuringer et al., 2001). Namely, U-value is dependent on the number of sequences included in the calculation, that is, the number of trials completed in a session. We used a random number generator to simulate U-values for hypothetical sessions with 1 to
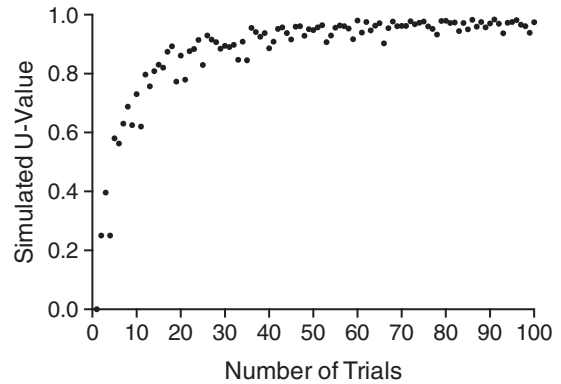

Fig. 1. Simulated U-value as a function of number of trials.

100 trials completed (see Fig. 1). Because we used a random number generator, levels of variability should have been high; however, with fewer trials, simulated U-values were low. Only with approximately more than 25 trials were U-values relatively unaffected by the number of trials included. This ceiling effect is especially problematic because we used extinction as a disruptor, which results in greatly reduced response rates.

To minimize the impact of the ceiling effect on U-value, we calculated a pooled U-value for each component using all trials across five sessions instead of a single session. In this way, each data point is based on a greater number of trials, leading to a more accurate measure of behavioral variability (e.g., Neuringer et al., 2001). In the rare event that a five-session block consisted of 25 trials or fewer, those data were excluded.

Group and individual subject data are displayed graphically for response rate, pooled U-value, and proportion of sequences meeting the lag schedule. In each figure, the top two panels show individual subject data, and the bottom panel shows group data. Symbols used in the graphs depicting individual subject data are consistent across experiments, such that the same symbol is used for the same pigeon across all experiments.

Relevant inferential statistical analyses were conducted on all primary dependent measures. All statistical tests were conducted using an alpha level of 0.05. Analyses were conducted using the final five sessions of Phase 1, the first five sessions of Phase 2, the final five sessions of Phase 2, and the first five

sessions of Phase 3. A two-way analysis of variance (ANOVA) was conducted, using a Greenhouse–Geisser correction for violations of the sphericity assumption. Planned comparisons were then evaluated with *t*-tests. Corrections for multiple comparisons were not used to reduce the likelihood of a Type II error (Rothman, 1990). Tables depicting the details of these planned pairwise comparisons are shown in the Supplemental Material. Each table contains, for each comparison, descriptive statistics (mean and standard error of the mean) and details of the statistical test (degrees of freedom, obtained *t*-statistic, *p*-value, and effect size, *d*).

In addition to the molar measures described, we also plotted relative frequency distributions for individual subjects across phases. Graphs showing the relative frequencies for each sequence across phases and subjects are included in the Supplemental Material. Additionally we analyzed specific aspects of the relative frequency distributions, including the most frequently and least frequently emitted sequences, average number of switches per sequence, the proportion of sequences beginning with the left key, and the total number of distinct sequences emitted. These data are depicted in tables.

Results

Response rates were relatively high when the lag reinforcement schedule was active but decreased when extinction was in place. Figure 2 shows that, for some individual subjects, response rates increased from the last five sessions of Baseline to the first five sessions of Extinction, but otherwise did not change across phases in the unchanged Vary component (top panel). Figure 2 also shows that response rates decreased during the Extinction phase and increased during Reacquisition for nearly all individual subjects in the Vary Ext component (middle panel).

The bottom panel of Figure 2 shows response rates averaged across all subjects across phases and components. Response rates significantly changed across phases: $F(3, 33) = 16.338$, $p < .001$, $\eta^2 = .735$; and components: $F(1, 11) = 49.797$, $p < .001$, $\eta^2 = .819$; with a significant interaction: $F(1.115, 12.265) = 30.487$, $p < .001$, $\eta^2 = .735$. As supported by planned pairwise comparisons
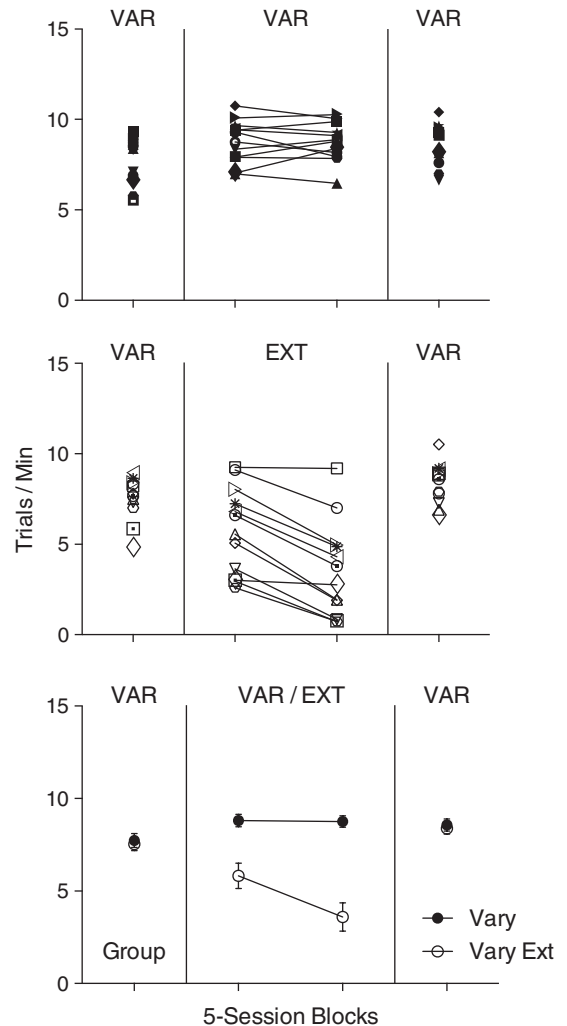

Fig. 2. Response rate (trials/min) across phases for both components in Experiment 1. Each point represents a five-session block. The top panel shows individual subject data for the Vary component. The middle panel shows individual subject data for the Vary Ext component. The bottom panel shows group data. Symbols for individual subjects are consistent across components and phases. Filled symbols show response rates for the Vary component, and open symbols show response rates for the Vary Ext component. For all graphs, the first phase is Baseline and is labeled with the contingency in place, the second phase is Extinction and is labeled with the contingency in place, and the third phase is Reacquisition and is labeled with the contingency in place. Error bars in the bottom panel show standard error of the mean.

(shown in Table 1 in the Supplemental Material), in Baseline, response rates were similar across components. In the first five sessions of Extinction, response rates slightly increased

from Baseline for the Vary component, and response rates decreased throughout Extinction for the Vary Ext component. Response rates returned to levels similar to Baseline during Reacquisition.

Reinforcer rates were similar across components when the lag schedule was in place. Planned comparisons confirmed that reinforcers per min were not significantly different across the Vary (M = 2.823, *SEM* = .0239) and Vary Ext (M = 2.798, *SEM* = 0.310) components in Baseline [$t(11)$ = 0.126, p = .902, d = 0.076]. Similarly, reinforcers per min during the Vary (M = 3.408, *SEM* = 0.245) and Vary Ext (M = 3.183, *SEM* = 0.279) components were not significantly different during Reacquisition [$t(11)$ = 0.965, p = .355, d = 0.582]. Reinforcer rates throughout Extinction were similar to the other phases for the Vary component, but were zero for the Vary Ext component and thus not formally compared to those in the Vary component.

The proportion of sequences meeting the lag contingency did not change systematically across phases in the Vary component but decreased during Extinction and increased during Reacquisition for the Vary Ext component. Figure 3 shows no change in the proportion of sequences meeting the lag contingency across phases for individual subjects in the Vary component (top panel). Figure 3 also shows a decrease in proportion of sequences meeting the lag contingency from the last five sessions of Baseline to the first five sessions of Extinction and an increase from the last five sessions of Extinction to Reacquisition for individual subjects in the Vary Ext component (middle panel).

Group data for the proportion of sequences meeting the lag contingency across components and phases are shown in the bottom panel of Figure 3. There was no significant main effect of phase: $F(3, 33)$ = 1.928, p = .144, η^2 = .149; or component: $F(1, 11)$ = .424, p = .528, η^2 = .037; but a trend towards a significant interaction: $F(3, 33)$ = 2.663, p = .064, η^2 = .195. As supported by planned pairwise comparisons (shown in Table 2 in the Supplemental Material), the proportion of sequences meeting the lag contingency was similar across components during Baseline, and remained similar during Extinction for the Vary component. The proportion of sequences meeting the lag
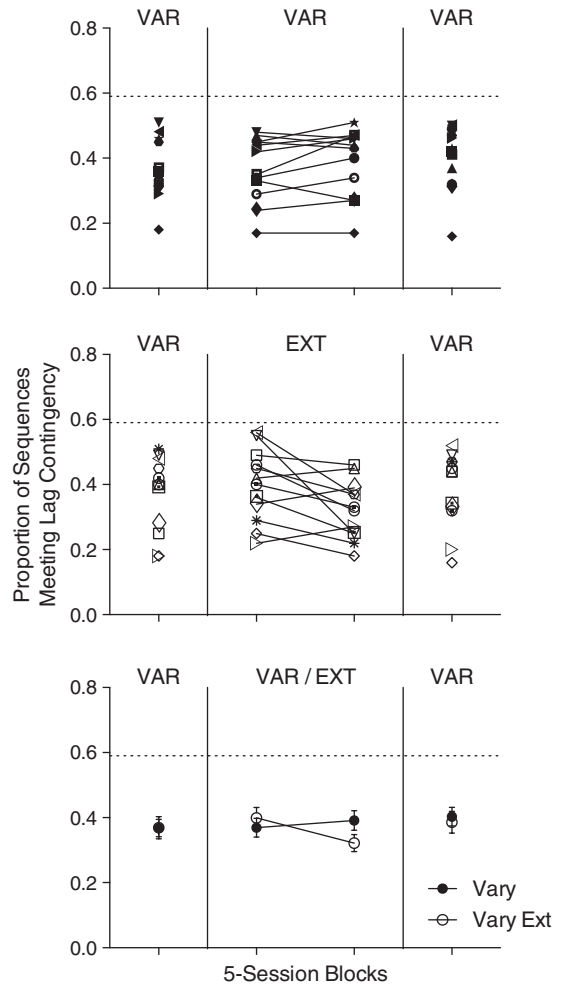
Fig. 3. Proportion of sequences meeting the lag contingency in Experiment 1. In all panels, the horizontal dashed line represents the expected proportion of sequences meeting the lag contingency given random responding, determined through simulations.

contingency decreased slightly from Baseline and the first five sessions of Extinction to the final five sessions of Extinction. During Reacquisition, the proportion of sequences meeting the lag contingency was similar across components and similar to Baseline levels.

Pooled U-values, a measure of sequence variability, were high when the lag schedule was in place but decreased with prolonged exposure to extinction. Figure 4 shows that pooled U-values did not change systematically for most individual subjects across phases for the Vary component (top panel). Figure 4 also shows that pooled U-values decreased for most

Table 2

Average switches per sequence and number of distinct sequences emitted per five-session block for individual subjects and on average (with standard error of the mean in parentheses) across phases and components in Experiment 1

| | Average switches per sequence | | | | | | | | Number of distinct sequences per five-session block | | | | | | | |
| | VAR | | | | VAR EXT | | | | VAR | | | | VAR EXT | | | |
Subject	BL	EXT 1	EXT 2	REAC	BL	EXT 1	EXT 2	REAC	BL	EXT 1	EXT 2	REAC	BL	EXT 1	EXT 2	REAC
55	1.05	1.17	1.33	1.37	1.02	1.03	0.63	1.07	16	16	16	16	16	16	16	16
220	1.76	1.61	1.29	1.58	0.99	1.29	1.28	1.63	16	13	13	16	15	16	16	15
223	0.83	0.94	1.00	0.82	0.99	0.96	0.88	0.99	15	16	16	15	15	15	14	15
237	1.14	1.04	1.29	1.20	1.10	1.43	1.06	1.13	16	16	16	16	16	16	13	16
373	1.53	1.39	1.40	1.17	1.57	0.86	0.46	1.24	16	16	16	15	16	16	16	16
936	0.85	0.96	0.92	1.25	0.88	1.01	1.20	1.02	15	16	16	16	16	16	14	16
956	1.24	0.51	0.47	0.55	0.46	0.39	0.23	0.52	16	5	9	5	10	12	10	6
957	0.87	0.73	0.84	0.97	1.09	0.80	0.63	0.95	13	14	13	11	11	15	15	11
966	0.74	1.01	1.15	1.03	0.55	0.52	0.39	0.51	14	16	16	16	7	14	14	14
1158	1.02	1.13	1.20	1.31	1.03	1.48	0.97	1.29	16	16	16	16	16	16	16	16
1499	1.47	1.15	1.18	1.30	1.32	0.91	0.56	1.49	16	16	16	16	16	16	10	15
17556	0.67	0.56	0.69	0.65	0.70	0.75	0.70	0.72	14	13	14	12	14	14	13	15
Mean	1.10	1.02	1.06	1.10	0.98	0.95	0.75	1.05	15.25	14.42	14.75	14.17	14.00	15.17	13.92	14.25
(SEM)	(0.10)	(0.09)	(0.08)	(0.09)	(0.09)	(0.10)	(0.10)	(0.10)	(0.30)	(0.92)	(0.63)	(0.97)	(0.87)	(0.37)	(0.62)	(0.85)

Note. VAR represents the Vary component and VAR EXT represents the Vary Ext component. BL represents the last five sessions of the Baseline phase, EXT 1 represents the first five sessions of Extinction, EXT 2 represents the last five sessions of Extinction, and REAC represents the first five sessions of the Reacquisition phase.
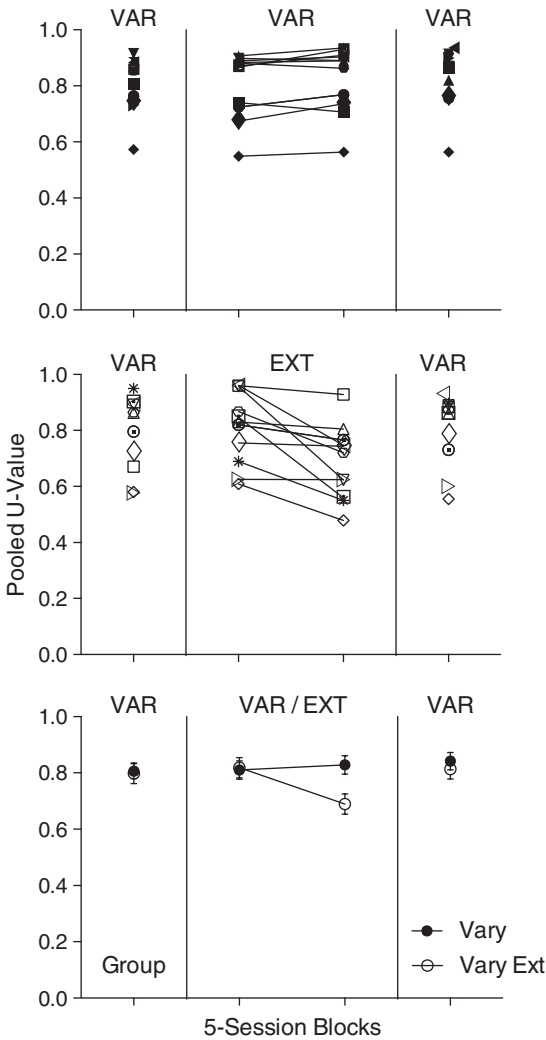
Fig. 4. Pooled U-value across phases for both components in Experiment 1.

values were similar across components. From the first five sessions of Extinction to the last five sessions of Extinction, pooled U-values remained high for the Vary component but decreased slightly for the Vary Ext component. Pooled U-values returned to Baseline levels during Reacquisition.

Relative frequency distributions for each subject across components and phases are shown in the Supplemental Material. Table 2 shows, for each individual subject across phases and components, the average number of switches and the number of distinct sequences emitted. The average number of switches per sequence was similar across components for all phases except the last five sessions of Extinction, as well as across phases for the Vary component. There was an average of one switch per sequence across phases for the Vary Ext component, except in the last five sessions of Extinction, in which the average number of switches decreased. The number of distinct sequences emitted did not change systematically with component or phase. Table 3 shows the sequences emitted most and least frequently, as well as the proportion of sequences emitted beginning with a left key peck, for each individual subject across phases and components. For most subjects, the dominant sequences in the last five sessions of Baseline were also dominant during other phases. For the Vary Ext component, the proportion of sequences beginning with a left key peck frequently changed during Extinction. Despite these few general findings, the results of these analyses appear largely idiosyncratic across subjects.

Discussion

The results of Experiment 1 provide evidence for disruption of reinforced behavioral variability by extinction. Disruption was observed in terms of response rate, as well as levels of behavioral variability. We observed changes in response rate; specifically, response rates decreased during Extinction for the Vary Ext component. Additionally, for the Vary component, response rates increased from the last five sessions of Baseline to the first five sessions of Extinction. This effect resembles behavioral contrast (Reynolds, 1961): the reduction in reinforcement rate (and response rate) in the Vary Ext component was accompanied by an increase in response rate for the Vary

subjects from the first five sessions of Extinction to the final five sessions of Extinction for the Vary Ext component (middle panel).

The bottom panel of Figure 4 shows average pooled U-values across phases for both components. Pooled U-values changed significantly across phases: $F(3, 33) = 5.620$, $p = .003$, $\eta^2 = .338$; but were similar across components: $F(1, 11) = 2.897$, $p = .117$, $\eta^2 = .208$, overall. The interaction between phase and component was significant: $F(1.472, 16.190) = 5.252$, $p = .025$, $\eta^2 = .323$. As supported by planned pairwise comparisons (shown in Table 3 in the Supplemental Material), in Baseline and the first five sessions of Extinction, pooled U-

Table 3

Specific sequences emitted for individual subjects across phases and components in Experiment 1

Most frequently emitted sequence (proportion) / Least frequently emitted sequence (proportion) / Proportion of sequences starting with a left keypeck

Subject	VAR				VAR EXT			
	BL	EXT 1	EXT 2	REAC	BL	EXT 1	EXT 2	REAC
55	LLRR (0.19) RLRL (0.00) L 0.77	RLLL (0.18) LLRL (0.00) L 0.32	RLLL (0.19) LLRL (0.00) L 0.38	RLLL (0.13) LLRL (0.01) L 0.39	LLLL (0.21) RLRL (0.00) L 0.70	LLLL (0.20) RLRL (0.01) L 0.57	LLLL (0.43) RLRL (0.00) L 0.68	RRLL (0.18) RLRL (0.00) L 0.41
220	RLRR (0.29) LLRL (0.00) L 0.50	RLRR (0.25) LLRL (0.00) L 0.31	RRRR (0.27) LLLL (0.00) L 0.22	RLRR (0.17) LLRL (0.00) L 0.60	RRRR (0.37) LLLL (0.00) L 0.36	LRLR (0.10) RRRR (0.03) L 0.61	RLRR (0.06) RLRL (0.02) L 0.64	RLRR (0.17) LLRL (0.00) L 0.45
223	RRRR (0.20) LRLR (0.00) L 0.29	RRRR (0.15) LRLR (0.00) L 0.47	LLLL (0.16) LRLR (0.01) L 0.56	RRLL (0.18) RLRL (0.00) L 0.40	LLLL (0.16) LRLR (0.00) L 0.55	RRLL (0.19) LRLR (0.00) L 0.35	RRRR (0.18) RLRL (0.00) L 0.55	LLLL (0.17) LRLR (0.00) L 0.55
237	RRRR (0.14) RLRL (0.00) L 0.56	RRRR (0.19) RLRL (0.00) L 0.55	LLRR (0.17) RLLL (0.00) L 0.62	LLRR (0.13) RLLL (0.00) L 0.62	RRRR (0.17) RLRL (0.00) L 0.53	RRRR (0.08) RLLR (0.04) L 0.51	LLLL (0.39) RRRL (0.00) L 0.82	RRRR (0.17) RLLL (0.01) L 0.56
373	RRRL (0.17) LLLL (0.01) L 0.40	RRRL (0.15) RLLR (0.01) L 0.40	RRRL (0.13) RLLR (0.01) L 0.49	RRRL (0.18) RLLR (0.00) L 0.52	RRRL (0.11) RLLR (0.02) L 0.52	RRRR (0.51) RLRR (0.00) L 0.30	RRRR (0.65) LRLL (0.01) L 0.18	RRRL (0.13) RLLR (0.00) L 0.58
936	LLLL (0.19) LRLR (0.00) L 0.44	LLRR (0.17) RLRL (0.00) L 0.57	RRRR (0.15) LRLR (0.00) L 0.51	LLLL (0.15) RLRL (0.01) L 0.52	LLLL (0.17) RLRL (0.00) L 0.54	LLLL (0.20) LRLR (0.01) L 0.61	RRRR (0.23) RRRL (0.00) L 0.45	RRRR (0.14) LRLR (0.00) L 0.40
956	RRRL (0.13) RLLR (0.00) L 0.58	LRRR (0.28) RLLL (0.00) L 0.78	LLLL (0.32) RRLL (0.00) L 0.78	LLLL (0.26) RLLL (0.00) L 0.81	LLLL (0.34) LRLL (0.00) L 0.78	LLLL (0.34) RLRR (0.00) L 0.65	LLLL (0.55) LRLL (0.00) L 0.67	LLLL (0.30) RRLL (0.00) L 0.82
957	LRRR (0.20) RRLR (0.00) L 0.60	RRLL (0.21) RRLR (0.00) L 0.34	LRRR (0.18) RLLR (0.00) L 0.52	LRRR (0.23) RLRR (0.00) L 0.72	LRRR (0.16) RLRR (0.00) L 0.76	LLLL (0.19) LRLR (0.00) L 0.57	LLLL (0.30) RLRR (0.00) L 0.60	LRRR (0.24) RLRR (0.00) L 0.79
966	RLLL (0.21) LLRL (0.00) L 0.26	LLLL (0.19) LRLR (0.01) L 0.41	RLLL (0.16) LRLR (0.01) L 0.34	RRRR (0.15) LRLR (0.01) L 0.31	RRRR (0.24) LLRR (0.00) L 0.22	LLLL (0.35) LRLR (0.00) L 0.40	LLLL (0.40) LRLR (0.00) L 0.50	RRRR (0.27) LRLR (0.00) L 0.25
1158	LRRR (0.14) LRLR (0.00) L 0.56	RRLL (0.15) LLRL (0.00) L 0.41	LRRR (0.15) RLRL (0.01) L 0.58	RRLL (0.13) RRRL (0.02) L 0.48	LLLL (0.13) RLRL (0.00) L 0.44	LRLL (0.12) RLLL (0.03) L 0.53	RRRR (0.41) LLLL (0.01) L 0.22	LRRR (0.12) LLLL (0.01) L 0.50
1499	RLLL (0.14) LLRL (0.00) L 0.19	RRRL (0.17) LLRR (0.01) L 0.21	RLLL (0.13) LLRR (0.02) L 0.39	LRRR (0.15) LLLR (0.00) L 0.61	RLLL (0.18) LLLR (0.01) L 0.48	RRRR (0.22) LRRL (0.01) L 0.36	LLLL (0.31) RLLL (0.00) L 0.44	LRLL (0.21) LLLR (0.00) L 0.62
17556	LLLL (0.25) RRLR (0.00) L 0.70	LLLL (0.26) RRLL (0.00) L 0.71	LLLL (0.21) LRLR (0.00) L 0.70	LLLL (0.20) RLRR (0.00) L 0.60	LLLL (0.24) RRLR (0.00) L 0.78	LLLL (0.20) RLRR (0.00) L 0.64	LLLL (0.25) RLRR (0.00) L 0.66	RRRR (0.21) RLRL (0.00) L 0.56

Note. Each cell contains the sequence emitted most frequently for that five-session block, with the relative frequency of that sequence in parentheses, the sequence emitted least frequently for that five-session block, with the relative frequency of that sequence in parentheses, and the proportion of sequences emitted starting with a left keypeck (L).

component, even though there was no change in reinforcement rate in that component.

We also observed disruption of levels of behavioral variability by extinction. Levels of behavioral variability decreased with increased exposure to extinction. The use of a multiple schedule with identical components allowed for the direct comparison between reinforcement-maintained behavioral variability and extinction-induced behavioral variability. When we removed reinforcement in one component but continued to provide food for variable sequences in the other, we observed a systematic decrease in levels of behavioral variability only in the component in which extinction was implemented. We also observed an increase in levels of behavioral variability when the lag contingency was implemented again. These results provide some support for behavioral variability as an operant, because the removal of the reinforcement contingency resulted in a decrease in levels of behavioral variability, demonstrating the sensitivity of behavioral variability to consequences.

Experiment 2: Reinstatement

The results from Experiment 1 suggest that reinforced behavioral variability may be decreased by extinction, providing additional evidence that behavioral variability is an operant. In addition to disruption by extinction, operant behaviors also tend to be susceptible to relapse under certain conditions. Experiment 2 was designed to examine whether behavioral variability would relapse under reinstatement conditions. A typical laboratory preparation consists of studying reinstatement across three phases. In Phase 1, Baseline, a target response produces reinforcers. In Phase 2, Extinction, reinforcement is suspended, and the target response decreases in frequency. In Phase 3, Reinstatement, extinction is still in place, but reinforcers are occasionally delivered response-independently (de Wit & Stewart, 1981, 1983). Reinstatement of reinforced behavioral variability has yet to be investigated. Therefore, the goal of this experiment was to determine if behavioral variability would relapse under typical reinstatement conditions.

Method

Subjects and apparatus. Twelve adult pigeons with prior experimental histories served as the subjects for this experiment. Although reported second, Experiment 2 was the first experiment conducted in this study (see Table 1). Two pigeons' data were excluded due to problems with data collection. Details of subject maintenance, general procedures, and apparatus were the same as in Experiment 1.

Procedure. A multiple schedule was used to compare responding on a lag contingency and responding with yoked reinforcer delivery (i.e., in the yoked component, pigeons earned food at the same rate as in the variability component, but behavioral variability was not required) and to investigate reinstatement of behavioral variability. As in Experiment 1, pigeons emitted four-peck sequences across two keys in a two-component multiple schedule. The two components alternated, with each being presented for 4 min at a time, four times per session. One component was designated by blue keylights and the other component was designated by white keylights (colors were counterbalanced across subjects). There was a 10-s intertrial interval (ITI) and a 30-s ICI. Because this experiment was conducted first, the 10-s ITI was used for this experiment but was later removed for Experiments 1 and 3. Recent research has shown that the duration of the ITI does not affect overall levels of behavioral variability (Doughty & Galizio, 2015).

Experiment 2 consisted of three phases: Baseline, Extinction, and Reinstatement. In Phase 1, Baseline, a lag 10 schedule of reinforcement was in place for one component (Vary), and the other component (Yoke) served as a control. We used a lag 10 schedule to produce high levels of variability while allowing for a clear comparison between Vary and Yoke. When the Yoke component was active, food delivery was probabilistic and the emission of any specific response sequence had no effect on food delivery. The probability that food was delivered after a given response sequence was matched to the overall rate of reinforcement in the immediately preceding Vary component. For example, if a pigeon earned food for 75% of sequences emitted in the preceding Vary component, food was delivered after each sequence with a probability of .75 for the current Yoke component. For each session, the initial component of the multiple schedule was always a Vary component. Phase 1 was in effect for 30 sessions.

There were two additional phases. Phase 2, Extinction, was similar to Baseline, except that reinforcement was suspended for both components. Phase 2 was in effect for 15 sessions. Phase 3, Reinstatement, was similar to Phase 2, except that food was delivered response- independently 1.5 and 10 s after the start of each component. These food deliveries were 1.5 s in duration. Phase 3 was in effect for five sessions. Only two food deliveries occurred per component and these events occurred independent of any responding.

Data Analysis. As in Experiment 1, the primary dependent measures for Experiment 2 were response rate, reinforcer rate, proportion of sequences meeting the lag contingency, and pooled U-value. Each of these measures was calculated as in Experiment 1, except that ITI time was excluded from all rate measures. Statistical analyses were conducted as in Experiment 1. Relative frequency distribution analyses were conducted as in Experiment 1.

Results

Response rates were high during Baseline and Reinstatement but decreased during Extinction for the Vary and Yoke components. Figure 5 shows that, for most subjects, response rates decreased from Baseline to the first five sessions of Extinction and from the first five sessions of Extinction to the last five sessions of Extinction for the Vary (top panel) and Yoke (middle panel) components. Additionally, response rates increased for all subjects during Reinstatement for both components.

The bottom panel of Figure 5 shows average response rates across phases for both components. Response rates changed significantly across phases: $F(3,27) = 87.043$, $p < .001$, $\eta^2 = .906$; but did not change significantly across components: $F(1,9) = 3.268$, $p = .104$, $\eta^2 = .266$. The interaction between phase and component was significant: $F(3,27) = 5.819$, $p = .003$, $\eta^2 = .393$. As supported by planned pairwise comparisons (shown in Table 4 in the Supplemental Material), response rates decreased from Baseline to the first sessions of Extinction and to the last sessions of Extinction for both components. Response rates for both components increased to near-Baseline levels during Reinstatement.
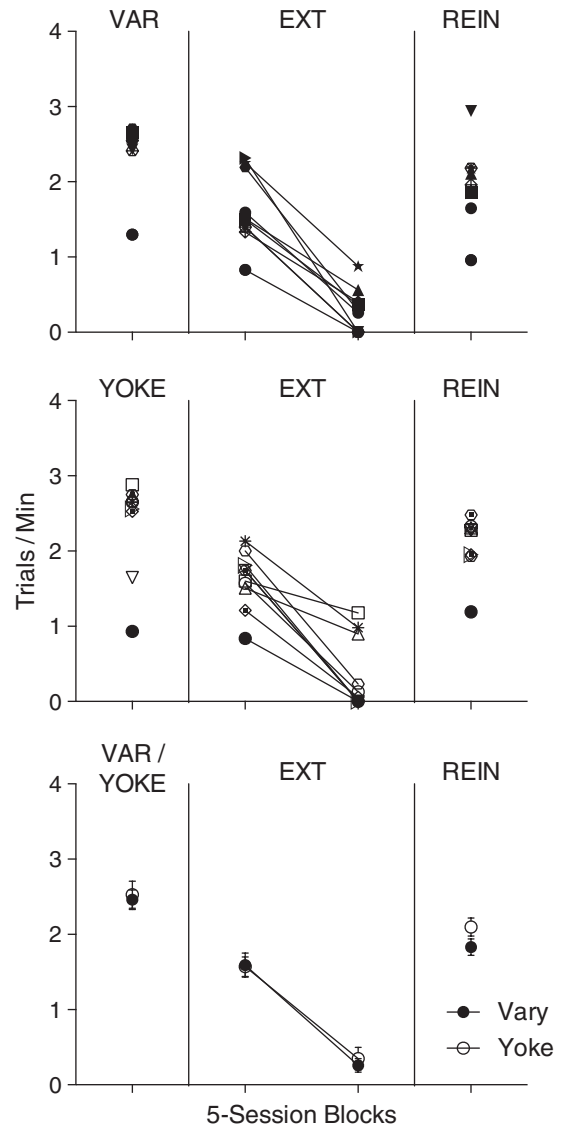

Fig. 5. Response rate (trials/min) across phases for both components in Experiment 2. The top panel shows individual subject data for the Vary component. The middle panel shows individual subject data for the Yoke component. The bottom panel shows group data. Symbols for individual subjects are consistent across components and phases. Filled symbols show response rates for the Vary component, and open symbols show response rates for the Yoke component. For all graphs, the first phase is Baseline and is labeled with the contingency in place, the second phase is Extinction and is labeled with the contingency in place, and the third phase is Reinstatement. Error bars in the bottom panel show standard error of the mean.

There was no significant difference between reinforcers per min for the Vary ($M = 0.878$, $SEM = 0.248$) and Yoke ($M = 0.944$, $SEM =$

Table 4

Average switches per sequence and number of distinct sequences emitted per five-session block for individual subjects and on average (with standard error of the mean in parentheses) across phases and components in Experiment 2

| | Average switches per sequence | | | | | | | | Number of distinct sequences per five-session block | | | | | | | |
| | VAR | | | | YOKE | | | | VAR | | | | YOKE | | | |
Subject	BL	EXT 1	EXT 2	REIN	BL	EXT 1	EXT 2	REIN	BL	EXT 1	EXT 2	REIN	BL	EXT 1	EXT 2	REIN
55	0.99	0.66	0.80	0.03	0.00	0.00	0.08	0.16	14	14	5	6	2	1	2	9
220	1.23	0.85	0.48	1.21	0.05	0.09	0.03	0.08	16	16	8	16	4	8	5	6
223	0.81	0.89	0.36	1.06	0.40	0.32	0.18	0.54	13	15	9	15	12	11	7	14
237	1.26	1.29	-	1.13	0.03	0.74	-	0.58	16	16	-	16	7	15	-	15
381	1.18	1.29	-	0.94	0.00	0.74	-	0.04	16	16	-	16	2	15	-	5
927	0.64	0.75	0.41	0.90	0.02	0.16	0.00	0.22	11	13	8	14	6	8	1	11
936	0.97	0.96	0.45	0.78	0.15	0.20	0.22	0.25	14	16	9	16	7	9	5	10
956	1.20	1.12	0.47	0.94	0.27	0.26	0.14	0.23	14	16	14	15	9	10	7	12
957	0.75	0.73	-	0.70	0.14	0.04	-	0.11	12	10	-	11	6	4	-	7
966	0.88	1.26	-	0.79	0.07	0.19	-	0.16	15	16	-	15	8	9	-	9
Mean (SEM)	0.99	0.98	0.50	0.85	0.11	0.28	0.11	0.24	14.10	14.80	8.83	14.00	6.30	9.00	4.50	9.80
	(0.07)	(0.08)	(0.07)	(0.10)	(0.04)	(0.08)	(0.04)	(0.06)	(0.55)	(0.63)	(1.19)	(1.01)	(0.98)	(1.37)	(1.02)	(1.04)

Note. VAR represents the Vary component and YOKE represents the Yoke component. BL represents the Baseline phase, EXT 1 represents the first five sessions of Extinction, EXT 2 represents the last five sessions of Extinction, and REIN represents the first five sessions of the Reinstatement phase. Dashes represent five-session blocks in which fewer than 25 trials were emitted.
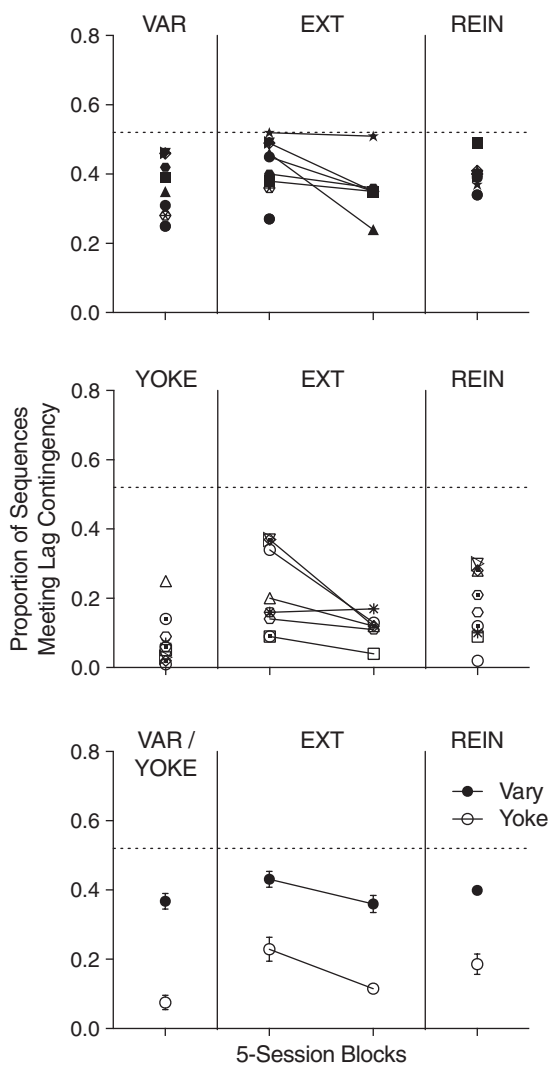
Fig. 6. Proportion of sequences meeting the lag contingency in Experiment 2. In all panels, the horizontal dashed line represents the expected proportion of sequences meeting the lag contingency given random responding, determined through simulations. Missing data points represent five-session blocks in which fewer than 25 trials were emitted.

0.317) components in Baseline: $t(9)$ = -1.917, p = .087. This finding confirmed that reinforcer rates in both components were matched. Because the remainder of the experiment was conducted under extinction, reinforcement rates were always zero and were not formally analyzed.

Figure 6 shows that the proportion of sequences meeting the lag contingency for individual subjects across phases in the Vary

component (top panel) was higher than the proportion in the Yoke component (middle panel). Figure 6 also shows group data across components and phases. The proportion of sequences meeting the lag contingency was generally high for the Vary component and lower for the Yoke component: F $(1,9)$ = 79.204, p < .001, η^2 = .898; and changed across phases: $F(1.493, 13.437)$ = 10.312, p = .003, η^2 = .534. The interaction between phase and component was also significant: F $(3,27)$ = 3.319, p = .035, η^2 = .269. As supported by planned pairwise comparisons (shown in Table 5 in the Supplemental Material), the proportion of sequences meeting the lag contingency was higher for the Vary component than the Yoke component, and both components showed a slight increase from the last five sessions of Baseline to the first five sessions of Extinction.

Pooled U-values were higher for the Vary component than the Yoke component throughout the experiment, and generally decreased throughout Extinction and increased during Reinstatement. Figure 7 shows that pooled U-values decreased for nearly all subjects during Extinction and increased during Reinstatement in the Vary component (top panel). Figure 7 also shows that pooled U-values were not systematically affected during Extinction for the Yoke component, although an increase was observed for several subjects during the first five sessions of Extinction (middle panel). Pooled U-values were generally not affected during Reinstatement during the Yoke component, although there was an increase for some subjects.

The bottom panel of Figure 7 shows average pooled U-values across phases for the Vary and Yoke components. Pooled U-values changed significantly across phases: $F(1.761, 15.846)$ = 6.706, p = .009, η^2 = .427; and components: $F(1, 9)$ = 104.689, p < .001, η^2 = .921; with a significant interaction: $F(3, 27)$ = 9.023, p < .001, η^2 = .501. As supported by planned pairwise comparisons (shown in Table 6 in the Supplemental Material), in Baseline, pooled U-values were higher for the Vary component than in the Yoke component. From the last five sessions of Baseline to the first five sessions of Extinction, pooled U-values did not change for the Vary component but increased for the Yoke component. Pooled U-values decreased from the first five sessions of

Table 5

Specific sequences emitted for individual subjects across phases and components in Experiment 2

Most frequently emitted sequence (proportion) / Least frequently emitted sequence (proportion) / Proportion of sequences starting with a left keypeck

Subject	VAR BL	VAR EXT 1	VAR EXT 2	VAR REIN	YOKE BL	YOKE EXT 1	YOKE EXT 2	YOKE REIN
55	LLLL (0.19) RLRR (0.00) L 0.65	LLLL (0.44) RLLR (0.00) L 0.75	LLLR (0.40) RRRR (0.00) L 0.80	RRRR (0.97) RLLL (0.00) L 0.02	RRRR (1.00) LLLL (0.00) L 0.00	RRRR (1.00) LLLL (0.00) L 0.00	RRRR (0.92) LLLL (0.00) L 0.08	LLLL (0.47) LRLL (0.00) L 0.56
220	RRRR (0.20) RLRR (0.00) L 0.25	LLLL (0.38) LRRL (0.02) L 0.69	LLLL (0.52) LRRR (0.00) L 0.76	RRRR (0.17) RLRL (0.01) L 0.43	LLLL (0.83) LRRR (0.00) L 0.83	LLLL (0.83) LRRR (0.00) L 0.85	LLLL (0.95) LRRR (0.00) L 0.96	LLLL (0.79) LRRR (0.00) L 0.80
223	LLLL (0.20) RLRR (0.00) L 0.59	LLLL (0.17) RLRL (0.00) L 0.48	LLLL (0.60) LRLL (0.00) L 0.82	LLLL (0.17) LRLR (0.00) L 0.60	LLLL (0.51) RLRR (0.00) L 0.75	LLLL (0.55) LLRR (0.00) L 0.70	LLLL (0.64) LRRR (0.00) L 0.74	LLLL (0.38) LRLR (0.00) L 0.54
237	RRRR (0.19) RLLL (0.02) L 0.43	LLLL (0.19) RLRR (0.01) L 0.54	-	LLLL (0.30) LRRL (0.01) L 0.69	LLLL (0.96) LRLL (0.00) L 0.97	RRRR (0.29) LLLL (0.00) L 0.44	-	LLLL (0.58) RLLR (0.00) L 0.82
381	LLLL (0.13) LRLL (0.01) L 0.46	LLLL (0.19) RLRR (0.01) L 0.54	-	LLLL (0.28) RRRL (0.01) L 0.57	RRRR (0.98) LRRR (0.00) L 0.02	RRRR (0.29) LRLL (0.00) L 0.44	-	RRRR (0.95) RLLL (0.00) L 0.04
927	LLLL (0.22) LRLL (0.00) L 0.55	RRRR (0.25) LRRL (0.00) L 0.48	RRRR (0.53) RLLL (0.00) L 0.22	RRRR (0.21) LRLR (0.00) L 0.45	RRRR (0.78) RRLL (0.00) L 0.21	RRRR (0.74) RLLL (0.00) L 0.16	RRRR (1.00) LLLL (0.00) L 0.00	RRRR (0.67) LRLL (0.00) L 0.23
936	RRRR (0.17) RLLR (0.00) L 0.54	RRRR (0.15) LRLR (0.00) L 0.47	LLLL (0.59) LLLR (0.00) L 0.73	LLLL (0.38) RLLR (0.01) L 0.63	RRRR (0.48) RLLL (0.00) L 0.48	RRRR (0.46) RLLL (0.00) L 0.46	LLLL (0.61) LLRR (0.00) L 0.78	LLLL (0.42) RLRR (0.00) L 0.49
956	LLLL (0.19) RRLL (0.00) L 0.75	LLLL (0.25) RLLL (0.01) L 0.70	LLLL (0.59) RRRL (0.00) L 0.79	LLLL (0.36) LRLL (0.00) L 0.77	RRRR (0.80) LLLL (0.00) L 0.15	RRRR (0.79) RLLL (0.00) L 0.18	RRRR (0.59) RRLL (0.00) L 0.36	RRRR (0.66) RLLR (0.00) L 030
957	LLLL (0.19) LRLL (0.00) L 0.33	LLLL (0.26) LRRR (0.00) L 0.33	-	LLLL (0.27) LRLL (0.00) L 0.45	RRRR (0.50) LRLL (0.00) L 0.38	RRRR (0.70) LRRL (0.00) L 0.25	-	LLLL (0.47) RRRL (0.00) L 0.52
966	LLLL (0.21) RLRL (0.00) L 0.71	RRRR (0.14) RRLR (0.01) L 0.61	-	LLLL (0.22) RLRL (0.00) L 0.61	RRRR (0.56) LRLL (0.00) L 0.41	RRRR (0.45) LLLR (0.00) L 0.45	-	LLLL (0.47) LRLL (0.00) L 0.56

Note. Each cell contains the sequence emitted most frequently for that five-session block, with the relative frequency of that sequence in parentheses, the sequence emitted least frequently for that five-session block, with the relative frequency of that sequence in parentheses, and the proportion of sequences emitted starting with a left keypeck (L). Dashes represent five-session blocks in which fewer than 25 trials were emitted.
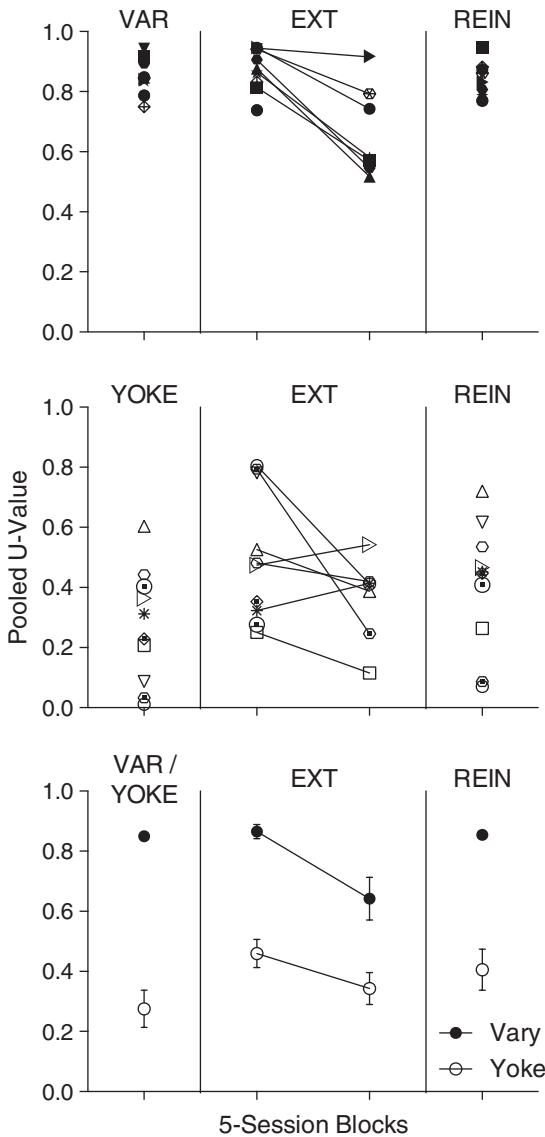
Fig. 7. Pooled U-value across phases for both components in Experiment 2. Missing data points represent five-session blocks in which fewer than 25 trials were emitted.

Extinction to the last five sessions of Extinction for both components. From the last five sessions of Extinction to Reinstatement, pooled U-values did not change for the Yoke component but increased for the Vary component.

Relative frequency distributions for each subject across components and phases are shown in the Supplemental Material. Table 4 shows, for each individual subject across phases and components, the average number

of switches and the number of distinct sequences emitted. Across all phases, subjects typically emitted sequences with more switches in the Vary component than in the Yoke component. From the last five sessions of Baseline to the first five sessions of Extinction, the average number of switches per sequence did not change for the Vary component but increased for the Yoke component. From the first five sessions to the last five sessions of Extinction, the average number of switches decreased for both components. Finally, from the last five sessions of Extinction to the first five sessions of Reinstatement, the number of switches increased for both components. The number of distinct sequences emitted per five-block session changed in the same way as the average number of switches across phases and components. Table 5 shows the sequences emitted most and least frequently, as well as the proportion of sequences emitted starting with a left key peck, for each individual subject across phases and components. For most subjects, the dominant sequence in Baseline was the same as in other phases for both components. For some subjects, however, another sequence became dominant in the first or last sessions of Extinction. Similarly, the proportion of sequences beginning with a left key peck was similar across phases for both components, except during Extinction, when some subjects showed an increase or decrease from Baseline.

Discussion

In Experiment 2, we found evidence for reinstatement of reinforced behavioral variability. In the Vary component, U-values and response rates decreased during Extinction and increased again in Reinstatement. In the Yoke component, response rates decreased during Extinction and increased during Reinstatement, but levels of variability did not change significantly throughout. These results further demonstrate the sensitivity of behavioral variability to consequences and support the notion that behavioral variability may be susceptible to relapse in a manner similar to that of operant behavior. As in Experiment 1, we observed disruption of behavioral variability as a result of extinction. In addition, we observed relapse of behavioral variability with reinstatement.

Table 6

Average switches per sequence and number of distinct sequences emitted per five-session block for individual subjects and on average (with standard error of the mean in parentheses) across phases and groups in Experiment 3

Group	Subject	Average switches per sequence				Number of distinct sequences per five-session block			
		BL	ALT 1	ALT 2	RES	BL	ALT 1	ALT 2	RES
VAR	220	1.71	1.61	0.63	1.08	15	15	6	15
	223	1.27	1.18	0.96	0.86	15	16	10	14
	237	1.68	1.46	0.71	0.56	16	16	11	14
	936	1.11	1.05	0.94	0.46	12	12	7	15
	1158	1.63	1.29	0.71	0.89	15	16	10	16
	Mean (SEM)	1.48	1.32	0.79	0.77	14.60	15.00	8.80	14.80
		(0.12)	(0.10)	(0.07)	(0.11)	(0.68)	(0.77)	(0.97)	(0.37)
REP	55	1.85	1.69	2.16	1.90	15	13	16	16
	957	0.77	0.82	0.96	0.62	7	6	6	14
	966	0.97	0.87	0.89	0.70	7	5	3	14
	1499	0.41	0.25	0.21	0.02	7	5	7	5
	17556	0.89	0.91	0.85	0.81	12	11	10	14
	Mean (SEM)	0.98	0.91	1.01	0.81	9.60	8.00	8.40	12.60
		(0.24)	(0.23)	(0.32)	(0.30)	(1.66)	(1.67)	(2.20)	(1.94)

Note. VAR represents the Vary group and REP represents the Repeat group. BL represents the last five sessions of the Baseline phase, ALT 1 represents the first five sessions of the Alternative phase, ALT 2 represents the last five sessions of the Alternative phase, and RES represents the first five sessions of the Resurgence phase.

Experiment 3: Resurgence

In this experiment, we determined whether reinforced behavioral variability is susceptible to another type of relapse: resurgence. Resurgence is the reoccurrence of a previously extinguished response after reinforcement is suspended for a newly trained alternative response (e.g., Epstein, 1985). Like reinstatement, resurgence is typically studied in three phases. In Phase 1, Baseline, a target response is reinforced. In Phase 2, Alternative, reinforcement for the target behavior is suspended and an alternative response is reinforced. In Phase 3, all responding is extinguished. Resurgence is said to have occurred if the target response returns when reinforcement of the alternative response is removed.

In an attempt to distinguish between resurgence of reinforced behavioral variability and extinction-induced behavioral variability, we divided pigeons into two groups. One group responded on a lag variability schedule and the other earned food on a lag repetition schedule. Because the repetition group only had a recent history of behaving repetitively, any increase in variation observed for that group during the final phase was likely extinction-induced as opposed to evidencing resurgence of reinforced behavioral variability.

Method

Subjects and apparatus. Twelve adult pigeons with prior experimental histories served as the subjects for this experiment. Although reported last, this experiment was conducted second (see Table 1). Data for one pigeon from the Vary group and one pigeon from the Repeat group were excluded due to failure to earn at least 25% of reinforcers after 15 sessions of Baseline. Details of subject maintenance, general procedures, and apparatus were the same as in Experiments 1 and 2.

Procedure. In this experiment, we used a group design to examine resurgence of behavioral variability. As in the previous experiments, pigeons emitted four-peck sequences across two keys. Experiment 3 consisted of three phases: Baseline, Alternative, and Resurgence. Pigeons were divided into Vary and Repeat groups. In Phase 1, Baseline, a lag 8 variability schedule of reinforcement was in place for the Vary group. We used a lag 8 variability schedule because it was strict enough to result in high levels of behavioral variability but would also allow relatively frequent reinforcers. For the Repeat group, a lag 3 repetition contingency was in place for Phase 1 (see Cherot, Jones, & Neuringer, 1996; Odum et al., 2006). A lag repetition contingency is similar to a lag variability contingency, except

that a sequence will only produce food if it is the same as any of a certain number of previous responses. In this way, a specific target sequence is not required; instead, the pigeon simply must repeat a sequence it has emitted recently. We used a lag 3 repetition contingency because this value has been used in previous research (Cherot et al., 1996; Odum et al., 2006). In addition, this contingency resulted in reinforcement rates that were similar to or higher than the Vary components in the previous experiments and the Vary group in the present experiment. For both groups, the sequences LLLL and RRRR were never eligible for reinforcement, because of the tendency to perseverate on these sequences (see Cherot et al., 1996; Odum et al., 2006). As in Experiment 1, there was a 0-s ITI between sequences for both groups. Phase 1 was in effect for 15 sessions.

There were two other phases. Phase 2, Alternative, was similar to Baseline, except that the lag 3 repetition contingency was now in place for both groups. For both groups, response sequences produced food if they were the same as any sequence emitted in the previous three trials. Phase 2 was in effect for 25 sessions. Phase 3, Resurgence, was similar to previous phases, except that there were no food deliveries. Phase 3 was in effect for five sessions.

Data analysis. As in Experiments 1 and 2, the primary dependent measures for Experiment 3 were response rate, reinforcement rate, proportion of sequences meeting the lag variability contingency, and pooled U-value. Each of these measures was calculated as in Experiments 1 and 2. Statistical analyses were conducted as in Experiments 1 and 2 except that a two-way mixed ANOVA was used with the group as a between-subjects factor and the phase as a within-subjects factor. Relative frequency distribution analyses were conducted as in previous experiments.

Results

Response rates did not systematically change across any phase of the experiment for either group. The top panel of Figure 8 shows similar response rates for individual subjects across phases in the Vary group, and the middle panel shows similar response rates for individual subjects across phases in the Repeat group.
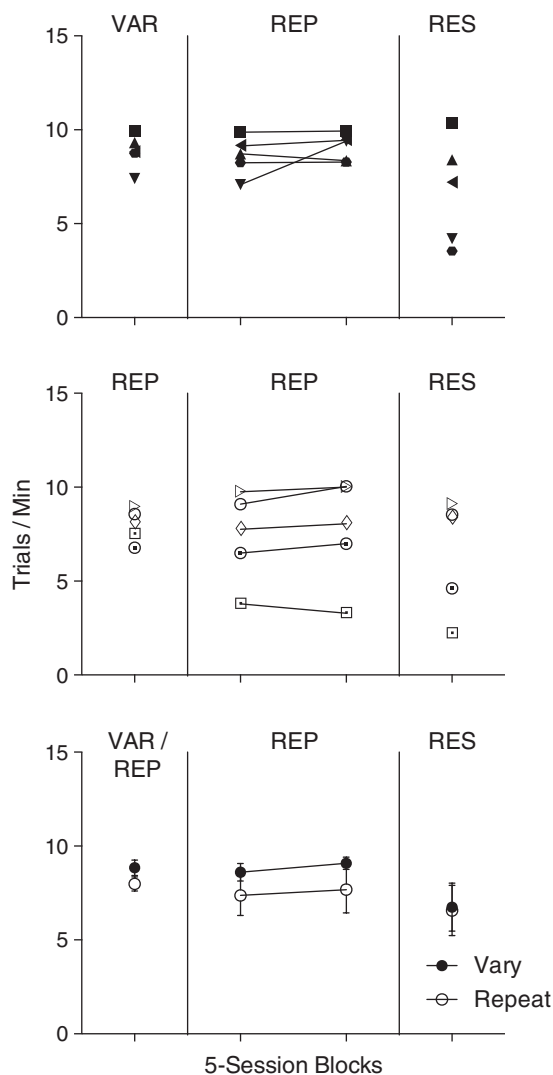

Fig. 8. Response rate (trials/min) across phases for both groups in Experiment 3. The top panel shows individual subject data for the Vary group. The middle panel shows individual subject data for the Repeat group. The bottom panel shows group data. Symbols for individual subjects are consistent across phases. Filled symbols show response rates for the Vary group, and open symbols show response rates for the Repeat group. For all graphs, the first phase is Baseline and is labeled with the contingency in place, the second phase is Alternative and is labeled with the contingency in place, and the third phase is Resurgence. Error bars in the bottom panel show standard error of the mean.

Although response rates did change slightly across phases for some individual pigeons, there were no systematic differences overall, except when extinction was in place during

Table 7

Specific sequences emitted for individual subjects across phases and groups in Experiment 3

		Most frequently emitted sequence (proportion) / Least frequently emitted sequence (proportion) / Proportion of sequences starting with a left keypeck			
Group	Subject	BL	ALT 1	ALT 2	RES
	220	LRRL (0.17)	RLRR (0.24)	LRRR (0.50)	LRRR (0.67)
		LLRL (0.00)	LLRL (0.00)	LLLL (0.00)	LLRL (0.00)
		L 0.55	L 0.45	L 0.50	L 0.85
	223	RRLL (0.26)	RRLL (0.21)	RRLL (0.55)	RRLL (0.40)
		LRLR (0.00)	LRLR (0.00)	LLRR (0.00)	LRLR (0.00)
		L 0.34	L 0.44	L 0.04	L 0.10
Vary	237	RRLR (0.13)	LLRR (0.27)	LRRR (0.54)	RRRR (0.54)
		RLLL (0.00)	RLLL (0.01)	RLLL (0.00)	LRLL (0.00)
		L 0.52	L 0.83	L 0.66	L 0.28
	936	RRLL (0.18)	RRLL (0.31)	RLLL (0.71)	RRRR (0.27)
		LRLL (0.00)	LRLL (0.00)	RRRR (0.00)	LRLR (0.00)
		L 0.39	L 0.29	L 0.07	L 0.21
	1158	RLRR (0.18)	RLLL (0.31)	RLLL (0.62)	RLLL (0.27)
		LRRL (0.00)	LLLR (0.00)	RRRR (0.00)	LLRL (0.01)
		L 0.57	L 0.29	L 0.37	L 0.29
	55	LRLL (0.25)	LRLL (0.25)	LRLR (0.27)	LRLR (0.22)
		RLRR (0.00)	LRRR (0.00)	RRRR (0.00)	RRRR (0.00)
		L 0.48	L 0.74	L 0.80	L 0.78
	957	LRRR (0.74)	LRRR (0.80)	LRRR (0.94)	LRRR (0.36)
		RRLL (0.00)	RLLL (0.00)	LLLL (0.00)	LRLL (0.00)
		L 0.76	L 0.82	L 0.95	L 0.73
Repeat	966	RLLL (0.76)	RLLL (0.83)	RLLL (0.85)	LLLL (0.25)
		RRRR (0.00)	RRRR (0.00)	RRRR (0.00)	RRLR (0.00)
		L 0.04	L 0.13	L 0.11	L 0.32
	1499	LLLL (0.59)	LLLL (0.34)	LLLL (0.26)	LLLL (0.26)
		LRRR (0.00)	RRRR (0.00)	LLLR (0.00)	LRRR (0.00)
		L 0.60	L 0.34	L 0.26	L 0.26
	17556	LRRR (0.41)	LRRR (0.38)	LRRR (0.85)	LRRR (0.29)
		LRRL (0.00)	LRLL (0.00)	RLLL (0.00)	LRLR (0.00)
		L 0.79	L 0.84	L 0.82	L 0.89

Note. Each cell contains the sequence emitted most frequently for that five-session block, with the relative frequency of that sequence in parentheses, the sequence emitted least frequently for that five-session block, with the relative frequency of that sequence in parentheses, and the proportion of sequences emitted starting with a left keypeck (L).

the Resurgence phase, in which response rates decreased.

The bottom panel of Figure 8 shows average response rate across each phase in Experiment 3. There was a significant main effect of phase: $F(3,24) = 4.726$, $p = .010$, $\eta^2 = .371$; but no significant main effect of group: $F(1,8) = .674$, $p = .435$, $\eta^2 = .078$; and the interaction between phase and group was not significant: $F(3,24) = 0.515$, $p = .676$, $\eta^2 = .061$. As supported by planned pairwise comparisons (shown in Table 7 in the Supplemental Material), at the group level, response rates did not change for either group throughout the experiment, except for a slight decrease from the last five sessions of Alternative to Resurgence.

We also analyzed reinforcer rates across groups and phases. Reinforcers per min was

not significantly different across phases: $F(1.114, 8.911) = 4.167$, $p = .069$, $\eta^2 = .343$; or groups: $F(1, 8) = .497$, $p = .501$, $\eta^2 = .059$. The interaction between phase and group was also not significant: $F(2, 16) = 1.389$, $p = .278$, $\eta^2 = .148$. As supported by planned pairwise comparisons (shown in Table 8 in the Supplemental Material), reinforcer rates were not significantly different across groups or phases.

An analysis of the proportion of sequences meeting the lag variability contingency showed a decrease throughout the Alternative phase for the Vary group, no systematic change across Baseline and Alternative phase for the Repeat group, and an increase during Resurgence for every subject in both groups. Figure 9 shows individual subject data for the Vary group (top panel) and Repeat group (middle panel) across phases, as well as group
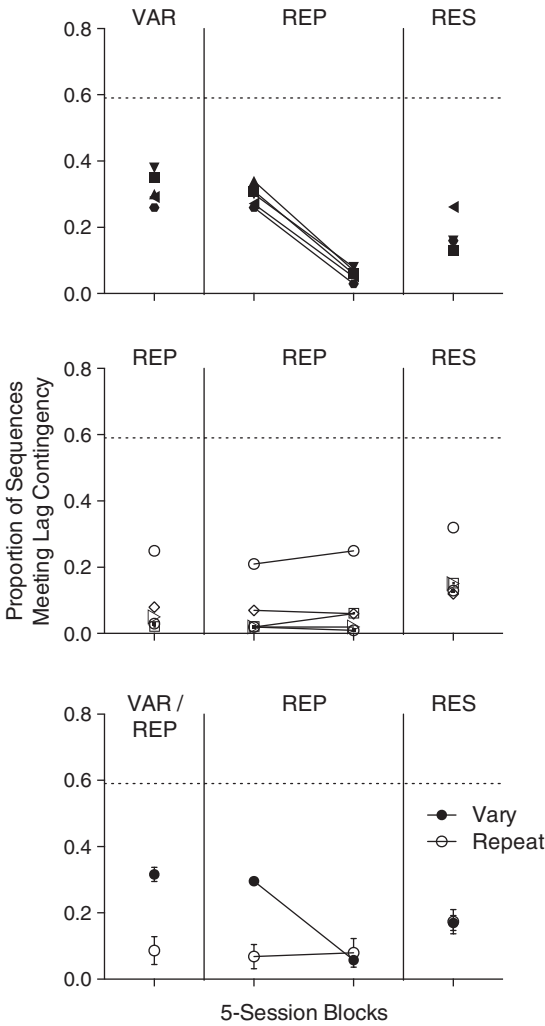
Fig. 9. Proportion of sequences meeting the lag contingency in Experiment 3. In all panels, the horizontal dashed line represents the expected proportion of sequences meeting the lag contingency given random responding, determined through simulations.

change from the last five sessions of Baseline to the first five sessions of Alternative for either group. From the first five sessions to the last five sessions of Alternative, the proportion of sequences meeting the lag variability contingency stayed low for the Repeat group and decreased to similar levels as the Repeat Group for the Vary group. The proportion of sequences meeting the lag variability contingency increased slightly from the last five sessions of Alternative to Resurgence for both groups.

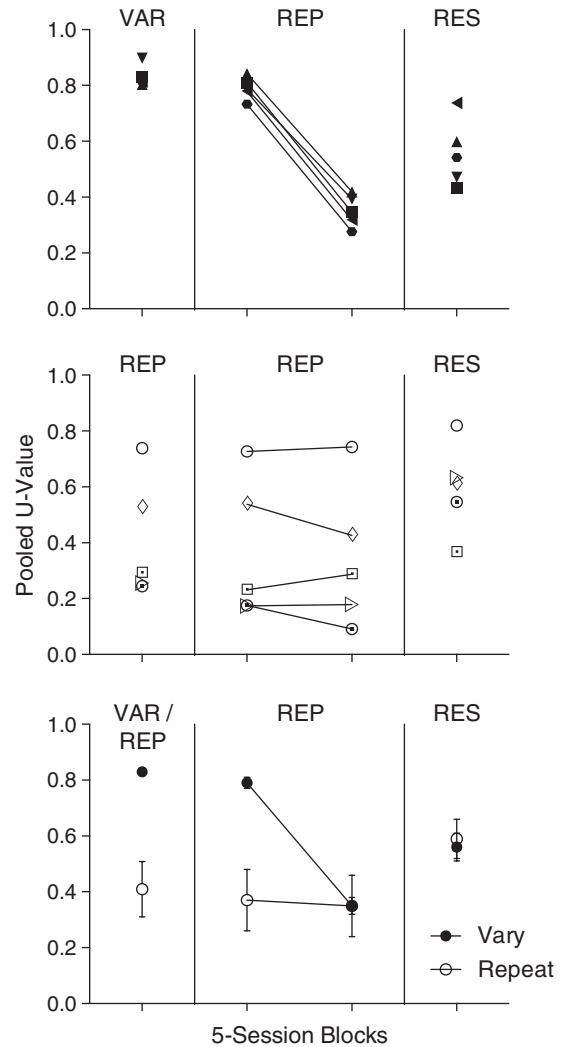Pooled U-values were higher for the Vary group than the Repeat group during Baseline,

Fig. 10. Pooled U-value across phases for both groups in Experiment 3.

data in the bottom panel. The proportion of sequences meeting the lag variability contingency changed significantly across phases: $F(3,24) = 34.343$, $p < .001$, $\eta^2 = .811$; and groups: $F(1,8) = 7.204$, $p < .028$, $\eta^2 = .474$; with a significant interaction: $F(3,24) = 47.902$, $p < .001$, $\eta^2 = .857$. As supported by planned pairwise comparisons (shown in Table 9 in the Supplemental Material), the proportion of sequences meeting the lag variability contingency was higher in Baseline for the Vary group than for the Repeat group and did not

but were low for both groups in Alternative and increased during Resurgence. Figure 10 shows that pooled U-values decreased in the final five sessions of the Alternative phase and increased during Resurgence for all individual subjects in the Vary group (top panel). Figure 10 also shows that pooled U-values were similar across Baseline and Alternative but increased during Resurgence for all individual subjects in the Repeat group.

The bottom panel of Figure 10 shows average pooled U-values across phases for the Vary and Repeat groups. Pooled U-values were significantly different across phases: $F(1.320, 10.562) = 22.454$, $p < .001$, $\eta^2 = .737$; but only trended towards significance across groups: $F(1, 8) = 4.509$, $p = .066$, $\eta^2 = .360$. There was a significant interaction between phase and group: $F(1.320, 10.562) = 23.391$, $p < .001$, $\eta^2 = .745$. As supported by planned pairwise comparisons (shown in Table 10 in the Supplemental Material), pooled U-values were higher for the Vary group than for the Repeat group in Baseline. From the last five sessions of Baseline to the first five sessions of Alternative, pooled U-values did not change for either group. From the first five sessions to the last five sessions of Alternative, pooled U-values did not change for the Repeat group but decreased to similar levels as that in the Repeat Group for the Vary group. From the last five sessions of Alternative to Resurgence, pooled U-values increased similarly for both groups.

Relative frequency distributions for each subject across components and phases are shown in the Supplemental Material. Table 6 shows, for each individual subject across phases and components, the average number of switches and the number of distinct sequences emitted. During Baseline, the Vary group emitted sequences with more switches than the Repeat group. From the last five sessions of Baseline to the first five sessions of Alternative, the number of switches stayed approximately the same for both groups. From the first five sessions to the last five sessions of Alternative, however, the average number of switches per sequence decreased for the Vary group and stayed relatively constant for the Repeat group. Finally, from the last five sessions of Alternative to Resurgence, the average number of switches stayed constant for the Vary group and decreased for the Repeat

group. The number of distinct sequences emitted per five-session block followed a similar pattern across phases and groups, except that both groups showed an increase from the last five sessions of Alternative to Resurgence. Table 7 shows the sequences emitted most and least frequently, as well as the proportion of sequences emitted starting with a left key peck, for each individual subject across phases and components. For the Vary group, the dominant sequence in Baseline was not necessarily the dominant sequence for other phases; however, the dominant sequences in Baseline and Resurgence were usually the same or started with the same key(s) (e.g., RRLR and RRRR in Baseline and Resurgence, respectively, for one subject). For the Repeat group, the dominant sequence in Baseline was usually the same as the dominant sequence in other phases.

Discussion

Overall, levels of behavioral variability for the Vary group were high with a lag variability schedule in place but decreased when a lag repetition schedule was implemented. Following the suspension of reinforcers for behaving repetitively, levels of behavioral variability increased, providing some evidence for resurgence, although levels of behavioral variability were not as high in Resurgence as they were in Baseline. However, levels of behavioral variability for the Repeat group were low during Baseline and Alternative, when a lag repetition schedule was in place, but increased following the suspension of reinforcers, highlighting the role of extinction-induced behavioral variability. That said, even though pooled U-values for the Repeat group increased during Resurgence, the average number of switches per sequence decreased. In other words, between-sequence variability increased while within-sequence variability decreased. Pigeons in the Repeat group made more distinct sequences but the makeup of those sequences became more repetitive.

Because the Repeat group did not have recent history of responding variably, it was likely that increases in levels of behavioral variability for this group during the Resurgence phase would be induced by extinction. Many of these subjects did participate in previous experiments on behavioral variability;

however, extinction-induced response variability is a more parsimonious explanation than resurgence of behavior learned in previous experiments. Because we saw similar increases in pooled U-value from the last five sessions of Alternative to Resurgence across groups, the increase for the Vary group may not be due to resurgence, but may instead be due to extinction-induced variability. These results, in combination with the results of the previous experiments, support the idea that behavioral variability can be disrupted by extinction and can relapse given certain conditions. However, with extinction as a disruptor, caution is warranted due to the potential confounding influence of extinction-induced response variability.

General Discussion

Our results show that behavioral variability can be disrupted and is susceptible to relapse under certain circumstances. In Experiment 1, levels of behavioral variability decreased during extinction and increased when the lag contingency was restored. In Experiment 2, levels of behavioral variability decreased during extinction and increased when food was delivered response-independently (i.e., reinstatement). In Experiment 3, levels of behavioral variability decreased when repetition was instead followed by food and then increased during extinction, although it is difficult to determine whether this finding was the result of resurgence or extinction-induced behavioral variability. These results demonstrate that behavioral variability is sensitive to consequences and that it may be susceptible to relapse in a manner similar to that of operant behavior.

This study had several limitations. First, pigeons were not experimentally naïve. When studying relapse with a subject that has an extensive behavioral history, the results must be interpreted cautiously, especially for Experiment 3. Additionally, in Experiment 2, we interpreted our findings as evidence for reinstatement, because of the delivery of response-independent food during reinstatement testing. However, those programmed food deliveries could have been experienced as response-independent or could have followed key pecks. If the latter, the results of Experiment 2 could actually illustrate reacquisition, similar to Experiment 1.

The present findings are consistent with previous research showing that behavioral

variability has similar characteristics to other dimensions of operant behavior. Variable behavior can be maintained by reinforcement, depends on the reinforcement contingency in place, and can be brought under discriminative control (e.g., Page & Neuringer, 1985). Although prior studies have shown that behavioral variability is more persistent than behavioral repetition, and that disruption only occurs in terms of rate of responding rather than levels of variability (e.g., Cohen et al., 1990; Doughty & Lattal, 2001; Odum et al., 2006; Wagner & Neuringer, 2006; Ward et al., 2006), our results demonstrate that variable behavior is not only disrupted in terms of response rate, but also in terms of overall levels of behavioral variability.

One major methodological difference between the present study and similar previous studies is the type of disruptor used. Most studies concerning the disruption of behavioral variability have used nonextinction disruptors, such as response-independent food delivery (e.g., Doughty & Lattal, 2001), drugs (e.g., Cohen et al., 1990; Ward et al., 2006), and delay to reinforcement (Odum et al., 2006; Wagner & Neuringer, 2006). Extinction is an important disruptor to study, because of the extent to which extinction is experienced in everyday life, across species and situations. However, the use of extinction poses a challenge in behavioral variability research because of the potential for observing extinction-induced response variability. This difficulty may explain why the effects of extinction on behavioral variability have not been extensively studied (Neuringer et al., 2001).

Neuringer et al. (2001) examined the impact of extinction on reinforced behavioral variability. Overall levels of behavioral variability increased, and the specific sequences emitted were different with extinction in place, highlighting the importance of distinguishing between reinforced and extinction-induced behavioral variability. There are several differences between this study and the present experiments. For example, Neuringer and colleagues used a group design, whereas in our Experiments 1 and 2, we used a multiple schedule to directly compare levels of behavioral variability in the context of reinforcement and extinction. Additionally, Neuringer and colleagues exposed subjects to only four sessions of extinction and observed an

increase in behavioral variability, attributed to extinction-induced variability. In our Experiments 1 and 2, subjects were exposed to extinction contingencies for 10 and 15 sessions, respectively. Although some subjects showed an initial increase in behavioral variability within the first several sessions of extinction, our most reliable finding was an overall decrease in behavioral variability. It is possible that such a decrease can only be observed after longer exposure to extinction. Additional evidence for this interpretation is that we observed extinction-induced increases in behavioral variability in Experiment 3 in which subjects experienced extinction for only five sessions in the Resurgence test.

The field of research concerned with behavioral variability is limited by the current analytic techniques (Kong et al., 2017). U-value is the measure most commonly used in behavioral variability studies (for reviews, see Neuringer, 2002, 2009, 2012, 2016, among others). U-value has many advantages: It provides a summary measure of the distribution of responding across all possible alternatives, it is relatively simple to compute, and it easily detects differences in behavioral variability based on whether or not a variability contingency is in place (i.e., U-values are high with a variability contingency in place and low with a control contingency in place).

However, U-value has limitations as a measure of behavioral variability. First, U-value is dependent on the total number of response sequences used in the calculation of the measure (see Fig. 1). When few trials are emitted (i.e., when the sample size is small), U-value is constrained. This limitation is a particularly important consideration for the present study, because extinction was used in each experiment. In extinction, the number of sequences decreased substantially, which necessarily impacts U-value. In the present study, we used a pooled U-value, calculated using five-session blocks, which prevented U-value analyses from being conducted with too few trials. By including more sessions in the analysis, we increased the number of response sequences that were used in the calculation of the measure and were more likely to have a representative U-value.

Another limitation of U-value is that it is a molar measure that only summarizes the total distribution of response sequences. Therefore,

U-value is insensitive to the order of sequences or which particular sequences are emitted (Kong et al., 2017). When U-value alone is examined, more molecular patterns of repetitive responding may be overlooked because the molar level distribution of response sequences is similar. Examining relative frequency distributions may provide a more complete measure of behavioral variability than U-value alone. Relative frequency distribution analyses involve examining the incidence of every possible response alternative (e.g., Doughty & Galizio, 2015; Doughty et al., 2013; Machado, 1997; Neuringer et al., 2001; Odum et al., 2006). Relative frequency distributions reveal whether any response options have been systematically omitted, which would affect U-value calculation. Relative frequency distributions may also uncover differences in responding that are not reflected in U-value; the same U-value may be obtained with different patterns of responding (e.g., changes in the average number of switches, number of distinct sequences, proportion of sequences emitted beginning with one key, etc.). For example, Doughty et al. (2013) found that U-values were lower when the magnitude of reinforcement was higher, and this decrease was largely due to an increase in the occurrence of sequences ending in repetitions (e.g., LRRR as opposed to LLLR). In another study, Odum et al. (2006) found under a multiple schedule that delay to reinforcement did not decrease U-values under a lag variability schedule, but that sequences from a component requiring repetition of a target sequence became more common in the variability component.

Given the importance of using these more molecular measures, we have provided relative frequency distributions for individual subjects across phases in each experiment in Tables 2–7 and in the Supplemental Materials. Although the results of these analyses were idiosyncratic across subjects, there were a few general findings. In all experiments, there tended to be a more even distribution of responding across sequences when a lag variability contingency was in place than when a control contingency was in place. In Experiment 1, responding became more restricted during Extinction for some subjects but even more evenly distributed for others. In Experiment 2, fewer sequences were emitted during Extinction, but responding became more

evenly distributed across many sequences during Reinstatement. In Experiment 3, responding was distributed across many sequences when the lag variability contingency was in place, and only a few sequences were usually emitted with a lag repetition contingency in place. During Resurgence, more sequences were emitted for all subjects, with and without a recent history of varying. A more detailed analysis of these relative frequency distributions can be found in the Supplemental Material.

The present results have important theoretical implications for understanding behavioral variability. Although Neuringer (2002, 2009, 2012, 2016) has conceptualized variability as an operant dimension of behavior, other explanations have been proposed to explain how behavioral variability can arise from reinforcement (i.e., lag schedules). Specifically, Machado (1997), Machado & Tonneau (2012), and Holth (2012) have suggested that variability itself is not reinforced when a lag schedule is in place; instead, some other aspect of behavior is reinforced inadvertently, resulting in high levels of behavioral variability as a byproduct.

Machado (1997) found that pigeons behaved with similar levels of behavioral variability when a lag schedule was in place and when switches between keys, or changeovers, were reinforced instead. In the lag schedule, pigeons would only earn food for sequences that had not been emitted recently. When switches were reinforced, pigeons would earn food anytime a sequence with a certain number of switches between keys was emitted (e.g., LLLL has no switches, LRRR has one switch, and LRLL has two switches), but the pigeon need not emit sequences variably. A pigeon could emit the same sequence repeatedly, as long as it had the required number of switches. However, high levels of behavioral variability were instead observed with both contingencies. Machado concluded that behavioral variability may arise as a result of generalization and limitations of stimulus control. In other words, reinforcers delivered following left key pecking may also strengthen right key pecking, and it may be difficult for a pigeon to exactly replicate a previous sequence, especially when longer sequences are used. However, when Doughty and Galizio (2015) arranged for shorter sequences than used in the prior experiments, reinforcing switches was insufficient to produce variable responding. Additionally, the results of the present study provide evidence that at least in some cases, increased switching does not lead to an increase in behavioral variability (see Experiment 3). Together, these results suggest that the generality of the explanation that variability arises secondarily, from reinforced switching, may be limited.

Machado and Tonneau (2012) also proposed the balance hypothesis (see also de Souza Barba, 2014). This hypothesis assumes that, with a lag schedule in place, reinforcers delivered in variability contingencies act on the properties of a sequence. Specifically, a particular sequence may be emitted and followed by reinforcement. The probability of that sequence occurring again in the future may increase due to the reinforcer delivery. However, due to the nature of a lag contingency, that sequence may be emitted again but not followed by reinforcement. In this case, the likelihood of that sequence occurring again may decrease. This process may continue until each sequence is occurring some of the time, resulting in variable behavior. In a similar hypothesis, Holth (2012) has questioned the sequence as the relevant, reinforced behavioral unit. Instead he has suggested that a variety of response units may be reinforced, such as specific key pecks and switches between keys. As a result of the lag contingency, these discrete response units may be repeatedly reinforced and extinguished in a cyclical manner, producing variable behavior.

Each interpretation of behavioral variability— as an operant (e.g., Neuringer, 2002), as a byproduct of reinforcing switches (Machado, 1997), or as a byproduct of cyclical reinforcement and extinction of sequences (Machado & Tonneau, 2012) or more basic responses (Holth, 2012) —has merits. The results of the present study support the conceptualization of variability as an operant dimension of behavior, but also are not inconsistent with the hypotheses of behavioral variability as a byproduct. Although we observed some clear evidence for relapse of behavioral variability, it is also important to note that relapse is not unique to operant behavior. For example, classically conditioned behavior can also relapse (e.g., Bouton, 2002). Therefore, more research is

needed to further investigate the potential mechanisms of reinforced behavioral variability.

Another potential future direction would be to examine different variability schedules. For example, we used a lag schedule of reinforcement for all experiments, but there are other schedules of reinforcement that make reinforcer deliveries contingent on variable responding, such as a relative frequency threshold contingency (e.g., Denney & Neuringer, 1998). Whereas a lag contingency provides reinforcement for responses that have not been emitted recently, a relative frequency threshold contingency provides reinforcers for responses that have been emitted infrequently, and it may have some advantages over a lag schedule. Further, the present study used relatively stringent lag requirements. Future studies should examine different variability contingencies, as well as different variability requirements.

Reinforced behavioral variability has important clinical implications. Deficits in behavioral variability are characteristic of some psychological disorders and may be expressed in the form of behavioral rigidity and inflexibility (Kashdan & Rottenberg, 2010). For example, individuals with autism spectrum disorders (ASD) display stereotyped behavioral patterns and have difficulty engaging in novel actions (D'Cruz, Ragozzino, Mosconi, Shrestha, Cook, & Sweeney, 2013; Jiujias, Kelley, & Hall, 2017). Additionally, repetitive behavioral and thought patterns are characteristic of individuals with depression (Jacobson, Martell, & Dimidjian, 2001; Nolen-Hoeksema, Wisco, & Lyubomirsky, 2008). Rigid rule following is another manifestation of behavioral inflexibility, which can prevent individuals from contacting natural contingencies (Galizio, 1979; Hayes, Brownstein, Zettle, Rosenfarb, & Korn, 1986). Due to its possible etiological role within, and ubiquity across, psychological disorders, behavioral rigidity could be considered a transdiagnostic pathological process.

Implementing a treatment that provides reinforcers for behaving variably may help to expand an individual's behavioral repertoire in an adaptive direction. Interventions designed to modify behavioral variability have been tested in individuals with depression (e.g., Hopkinson & Neuringer, 2003) and ASD (e.g., Betz, Higbee, Kelley, Sellers, & Pollard, 2011; Wolfe, Slocum, & Kunnavatana, 2014), with promising results. Interventions with typically developing populations have yet to be widely applied but would be useful to investigate, as behavioral variability may promote problem solving, creativity, and learning (e.g., Grunow & Neuringer, 2002; Weiss & Neuringer, 2012).

Relapse of reinforced behavioral variability may also be of clinical importance. In clinical settings, the goal is usually to teach individuals to behave with appropriate levels of behavioral variability depending on the situation. Therefore, the susceptibility of behavioral variability to relapse is encouraging for these applications. If behavioral variability is prone to relapse, then protocols based on reinforcement of behavioral variability are potentially robust treatment options. For example, if errors were to occur during the delivery of a clinical protocol and reinforcers were not delivered, behavioral variability may be temporarily elicited (extinction-induced variability) or suppressed (extinction of reinforced variability), depending on the time frame of the lapse in treatment integrity. By improving adherence to the protocol, recovery of reinforced variable behavior may be possible. Such recovery would be an illustration of reacquisition. Our reinstatement findings also suggest that simply providing stimuli that were used as reinforcers during treatment may be enough, at least temporarily, to increase behavioral variability. These findings could potentially be usefully applied in response generalization if response-independent reinforcers are provided in a novel context. New behaviors would then have the opportunity to contact naturally occurring contingencies in the novel context, expanding the behavioral repertoire.

This line of research also suggests the potential of studying renewal and other forms of relapse of behavioral variability. Renewal is a form of relapse in which a behavior is reinforced in one context and extinguished in another context (e.g., Berry, Sweeney, & Odum, 2014; Bouton, 2002). The shift to the original context or a novel context may induce renewal of the behavior in question. As an example, behavioral variability may be reinforced in one context (e.g., the therapeutic context) and disrupted in another (e.g., the home context). A return to the therapeutic context or a transition to a novel context (e.g., a recreational or educational context) could result in renewal of behavioral

variability. As in the present experiments, we would expect to see relapse of behavioral variability under renewal conditions as well, based on the similarities in how these relapse phenomena are explained by behavioral momentum theory (Berry et al., 2014).

Another form of relapse that may be interesting to examine is spontaneous recovery. Spontaneous recovery occurs when a behavior is extinguished and then returns after a period of time without exposure to the contingencies (Rescorla, 2004). If behavioral variability can spontaneously recover after extinction, then the effects of treatment fidelity errors could be only temporary. Relapse of behavioral variability is an important consideration if increased levels of behavioral variability are a therapeutic goal.

The results of the present study provide evidence for extinction, reacquisition, reinstatement, and possibly resurgence of reinforced behavioral variability, as well as extinction-induced response variability. These results support the notion that variability is sensitive to consequences and may be prone to relapse in a similar manner as operant behavior. However, these findings also raise questions about how to distinguish between reinforced and extinction-induced behavioral variability, as well as the best way to measure variable behavior. Identifying the conditions under which behavioral variability is susceptible to relapse has important theoretical and clinical implications, and future research should be aimed at better understanding this phenomenon.

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