Stability and Variability in Extinction

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Some studies have found that extinction leaves response structures unaltered; others have found that response variability is increased. Responding by Long-Evans rats was extinguished after 3 schedules. In one, reinforcement depended on repetitions of a particular response sequence across 3 operanda. In another, sequences were reinforced only if they varied. In the third, reinforcement was yoked: not contingent upon repetitions or variations. In all cases, rare sequences increased during extinction—variability increased—but the ordering of sequence probabilities was generally unchanged, the most common sequences during reinforcement continuing to be most frequent in extinction. The rats' combination of generally doing what worked before but occasionally doing something very different may maximize the possibility of reinforcement from a previously bountiful source while providing necessary variations for new learning.

The main goal of the present study is to reconcile two competing accounts of extinction. One is that variability increases during extinction of operant responses. Another is that operant structures, manifest in response topographies, sequences, and distributions, are unaffected by extinction and remain intact. How can structures be maintained if variability is increased? We review the evidence for each.

Antonitis (1951) performed one of the earliest studies to show increased variability. Rats were reinforced for poking their noses anywhere along a 50-cm opening. The exact location did not matter, but pokes during training nevertheless became increasingly predictable with respect to location. When reinforcement was then withheld, variability increased, with responses now occurring all along the strip (see also Eckerman & Lanson, 1969). Variability induced by extinction has been observed with many other response dimensions, including response force (Notterman & Mintz, 1965), response number (Mechner, 1958), response topography (Stokes, 1995), and response sequences (Balsam, Paterniti, Zechowy, & Stokes, 2000; Mechner, Hyten, Field, & Madden, 1997), and across species, from bacteria to humans. In summary, the evidence is clear that extinction increases response variability.

The other body of literature shows that extinction leaves previously reinforced responses unchanged. For example, Schwartz (1981) reinforced pigeons for sequences of eight responses across left and right keys, the only constraint being that the sequence contain four left and four right responses. During the reinforcement phase, each bird developed a dominant, or most frequent, pattern, such as RRRRLLLL (R = right peck, L = left peck). The dominant patterns were retained throughout extinction. Schwartz (1981) concluded, "in well trained animals, extinction disrupts

neither the particular sequence of responses that has developed nor the temporal patterning of those responses" (p. 39). Myerson and Hale (1988) showed that reinforced distributions of choices were also maintained during extinction. Under a concurrent variable-interval schedule, pigeons' choices approximately matched relative frequencies of reinforcement. The same distributions were maintained throughout extinction as response rates slowed. Under common schedules of reinforcement as well, what is learned during reinforcement is manifest during extinction. A notable demonstration was offered by Machado and Cevik (1998). Pigeons were reinforced under fixed-interval 40-s schedules or, for different birds, under 80-s schedules. When reinforcement was later withheld, cycles of responding and pausing continued relatively unchanged. Other support comes from Nevin's (1967) discrimination-learning studies, in which pigeons were intermittently reinforced for pecking the brighter of two response disks, generating 70%–80% accuracies. During 10 sessions of extinction, response rates decreased markedly, but response accuracies were maintained at their previous levels. Similar results were reported when pigeons learned to match colored stimuli (Cumming, Berryman, Cohen, & Lanson, 1967).

Also supporting the apparently stable nature of responding during extinction are demonstrations of the resurgence of previously learned responses and response sequences, despite a long period of absence during extinction (Epstein, 1985; Mechner et al., 1997). Also consistent are studies by Rescorla (1993, 1998) showing that stimulus–response, stimulus–reinforcer, and response–reinforcer relationships learned during instrumental conditioning are retained intact after extinction of responding (see also Colwill, 1994). Rescorla's work parallels a wealth of findings from the literature on Pavlovian conditioning, showing that extinction leaves previously conditioned associations intact (reviewed by Bouton, 1994; Bouton & Nelson, 1998; Falls, 1998). Thus, there are two sets of findings, one indicating that extinction increases variability and the other, that previously conditioned responses and response structures remain unchanged. This apparent inconsistency has rarely been discussed and, to the best of our knowledge, has never been resolved.

A second and related goal of the present research is to document effects of extinction after reinforcement of variable behaviors, or extinction of operant variability. Experimental studies documenting operant variability include the following: Pryor, Haag, and O'Reilly (1969) reinforced porpoises for novel movements and observed never-before-seen behaviors; Blough (1966) reinforced least frequent interresponse times in pigeons and observed distributions expected from a random process; a number of studies reinforced low-probability response sequences and observed highly variable sequences in rats and pigeons (Machado, 1989, 1992; Page & Neuringer, 1985) and, in human subjects apparently random or chaotic performances (Neuringer, 1986; Neuringer & Voss, 1993). In each of these cases, response variability was found to be higher when explicitly reinforced than when not, supporting the conclusion that variability is similar to other operant dimensions, such as response rate, force, and topography. Further support for this conclusion comes from findings that levels of variability are precisely controlled by schedules of reinforcement (Neuringer, 1992) and by discriminative stimuli (Denney & Neuringer, 1998). It is not known, however, what happens when reinforcement is withheld. Extinction after reinforced variability is especially interesting because extinction generally results in decreased frequencies of the previously reinforced response. After variability is itself reinforced, would extinction result in its decrease? The first experiment was undertaken to fill this gap in our knowledge.

Experiment 1

Response sequence variability was reinforced in Experiment 1, after which reinforcement was withdrawn. One problem with studying extinction of operant variability is the need to distinguish between variability generated for unknown reasons, or *noise*, and variability explained by known aspects of the environment. To help us distinguish between baseline noise and learned variability, we used operanda that generated unequal baseline levels of responding: two levers and a key. The two levers were close to the reinforcer dispenser, and the key was distant, located on the rear wall of the chamber; in addition, the response topographies differed. We expected that these differences would result in some sequences being "easier," or more probable, than others. Reinforcement of variations was expected to flatten the distribution, thereby enabling us to compare variability during reinforcement and extinction phases.

Method

Subjects. Fifty male Long-Evans rats, approximately 32 weeks old at the start of the experiment, were housed in pairs and maintained on a 12-hr light–dark cycle with water continuously available. The feeding cycle included 21.5 hr of deprivation and 2 hr of free food available after experimental sessions. Sessions were generally conducted 5 days per week, with 24 hr of free access to food after the 5th session. The rats had previously experienced reinforcement of sequence variability across left and right levers.

Apparatus. Ten Apple Macintosh Classic II computers were connected to 10 modified Gerbrands (Cambridge, MA) operant chambers via Meta-Research (Portland, OR) Benchtop interfaces. The chambers measured 27 cm deep × 30.5 cm wide × 29 cm high, with front, back, and ceiling made of Plexiglas, side walls of aluminum, and a floor of stainless steel rods.

Each chamber was equipped with two levers, each 5.1 cm wide, designated right (R) and left (L), situated side-by-side, 8.9 cm apart. Between the two levers, on the same side wall, was a pellet tray into which 45-mg Noyes (Lancaster, NH) pellets were presented as reinforcers. On the opposite wall were three response keys, each 2 cm in diameter, only the center one (K) of which was lighted and active during the experiments. Above each lever was a 28-V DC light bulb recessed behind an opaque plastic lens that was flush with the chamber wall. There was also a 28-V DC bulb behind the key, which was itself an opaque plastic lens. An overhead 28-V DC bulb served as the houselight. A speaker was located outside of the chamber but within the sound- and light-attenuating outer box that surrounded the chamber. Controlling computer programs were written in True Basic.

Procedure. To gain food reinforcement, the rats were required to generate variable sequences across the three operanda. Each trial consisted of three responses, for example, KLL (keypress, left leverpress, left leverpress), RLR (right leverpress, left leverpress, right leverpress), or KKK (three keypresses in a row). The variability contingency was met if the relative frequency of the current sequence was less than or equal to .05, the value of the threshold for reinforcement. If the sequence's relative frequency was greater than .05, the trial terminated with a 1-s time-out. Determining whether the variability contingency was met required 28 computational variables: one for each of the 27 possible response sequences plus one for the sum of all sequences. Whenever a sequence occurred, that sequence's variable and the sum were both increased by one. The variability contingency was met if the just-emitted sequence's variable, divided by the sum, was less than or equal to .05. To differentially weight recent trials, after every reinforcement, all 28 computational variables were multiplied by a weighting coefficient of .97, resulting in an exponential decrease in the contributions of sequences that had occurred earlier in the session: The further back a particular sequence had occurred, the more often the weighting coefficient had been applied to it, and the less it contributed to the current value. The values of the 28 computational counters were retained from one session to the next. In brief, only sequences that had been emitted less than 5% of the time (weighted for recency) met the variability contingency (see Denney & Neuringer, 1998).

Additional details are as follows: Effective right leverpresses were followed by a 0.15-s, 1300-Hz tone; left leverpresses, by a 0.15-s, 1600-Hz tone; and keypresses, by a 0.15-s, 2000-Hz tone. In addition, all effective responses caused the lights illuminating all three operanda to be darkened for 0.33 s. Additional responses during the 0.33-s dark period caused the 0.33 interval to reset until 0.33 s had elapsed without a response. When the variability contingency had been met, a food pellet was dispensed, accompanied by a 3100-Hz tone of 0.1 s duration. After the pellet, there was a 0.5-s pause during which any response reset the pause to 0.5 s and after which the lever and key lights were illuminated. If the variability contingency had not been met, the chamber was completely dark for a 1-s time-out. Responses during the time-out interval reset the interval until 1 s had elapsed without a response. Each session was 30 min in duration.

Because the rats had previously been trained to press the levers, at the beginning of the current experiment, they were shaped to press the center key in the rear of the chamber. The variability contingencies just described were put into effect for 15 sessions. Four sessions of extinction followed. During the extinction phase, all aspects of the procedure were identical to those just described except that every trial ended with the time-out period.

The main datum was the proportion of trials in which the subject met the variability criterion, or MetVar, calculated by dividing the number of trials in which the variability contingency was satisfied by the total trials in a session. MetVar continued to be computed during the extinction period, despite the fact that the subjects were not reinforced. Performances during the last four sessions of the reinforcement phase were compared with those during the four sessions of extinction. For purposes of unbiased analysis, MetVar calculations were initialized at the beginning of each phase.

Results and Discussion

Response rates were approximately constant during the reinforcement phase and decreased across the four extinction sessions, as shown by a significant phase by session interaction, $F(3, 147) = 63.586, p < .0001$ (Figure 1, bottom). Overall response rates were lower during extinction than during the reinforcement phase, $F(1, 49) = 581.626, p < .0001$.

Sequence variability, as assessed by the MetVar measure, changed in a direction opposite to response rate, increasing across

the four sessions of extinction, with the phase by session interaction again being significant, $F(3, 147) = 15.062, p < .0001$, and overall variability higher during extinction than reinforcement, $F(1, 49) = 64.701, p < .0001$ (Figure 1, top). Thus, extinction caused response rates to decrease and variability to increase.

Additional analyses show that despite this increased variability, response structures remained stable. Probabilities of the 27 sequences (total number of times that a particular sequence was emitted across the four sessions divided by total trials) are shown in Figure 2 (top) separately for the reinforcement and extinction phases. The sequences are ordered from most to least probable during the reinforcement phase. The distributions during the two phases were highly correlated ($r = .94$), with the most common sequences during reinforcement (RLR, LRL, RLL, and LRR) continuing to be emitted most frequently during extinction, the only exception being that KKK sequences increased markedly in extinction. The least common sequences during reinforcement (RRK, LRK, KRK, and KLK) continued to occur least frequently. During both phases, sequences composed exclusively of lever responses (L and R) were more likely than those containing keypresses (K), and sequences ending in K were especially improbable, except for KKK. This analysis indicates that the hierarchy of individual sequence probabilities established during the reinforcement phase was generally maintained during extinction. This was not a necessary outcome, of course, because the distribution could have flattened—all sequences becoming equally probable—or the most likely sequence(s) could have predominated.

The U-value statistic provides another way to characterize the distribution of sequence probabilities. It was computed as follows:

$$\frac{- \sum_{i=1}^{n} [\mathrm{RFi} \times [\log(\mathrm{RFi})/\log(2)]]}{[\log(n)/\log(2)]},$$

in which n equals the number of sequences possible (in this case, 27), and RF refers to the unweighted relative frequency (or probability) of each of the n sequences (see Denney & Neuringer, 1998 for details). U value evaluates the distribution of sequence probabilities, with equal probabilities—indicating high variability—yielding a high U value (1.0 being the highest) and unequal probabilities—indicating low variability—generating low U value (0.0 being the lowest value). Because the U statistic is sensitive to differences in numbers of trials and because fewer and fewer trials were generated during extinction, we calculated Us on the basis of the same number of trials across the two phases; in other words, number of trials in extinction determined the number used for the reinforcement phase. As expected from visual inspection of Figure 2, average U values across reinforcement and extinction phases were similar, .845 during reinforcement increasing to .867 during extinction, but the difference reached statistical significance, $t(49) = 5.385, p < .0001$.

The bottom of Figure 2 helps to explain why it was possible that measures of variability increased while response structures were approximately unchanged; in other words, how those could occur simultaneously. Shown are the ratios of each sequence's probabilities in the two phases (extinction phase divided by reinforcement phase), with a ratio of 1.0 (dotted horizontal line) indicating no
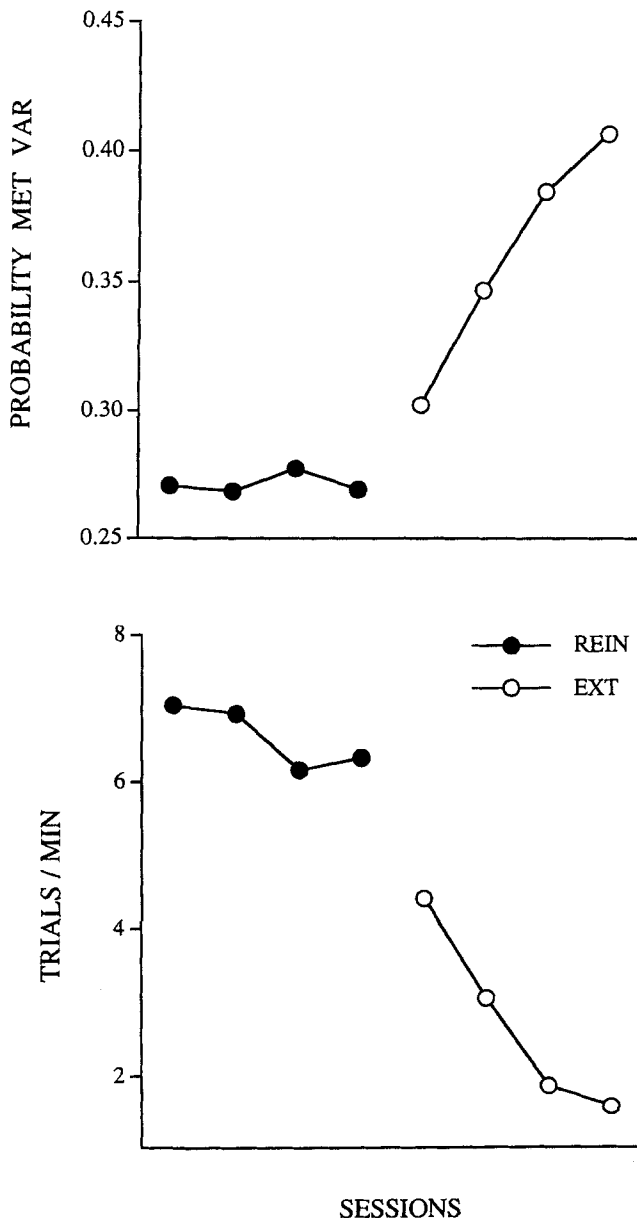
Figure 1. The top graph shows probability of varying, in other words, of meeting the variability criterion (MetVar contingency), during four sessions of reinforcement (REIN; solid circles) and four sessions of extinction (EXT; open circles). The bottom graph shows rates of responding (trials per minute) during the same sessions.
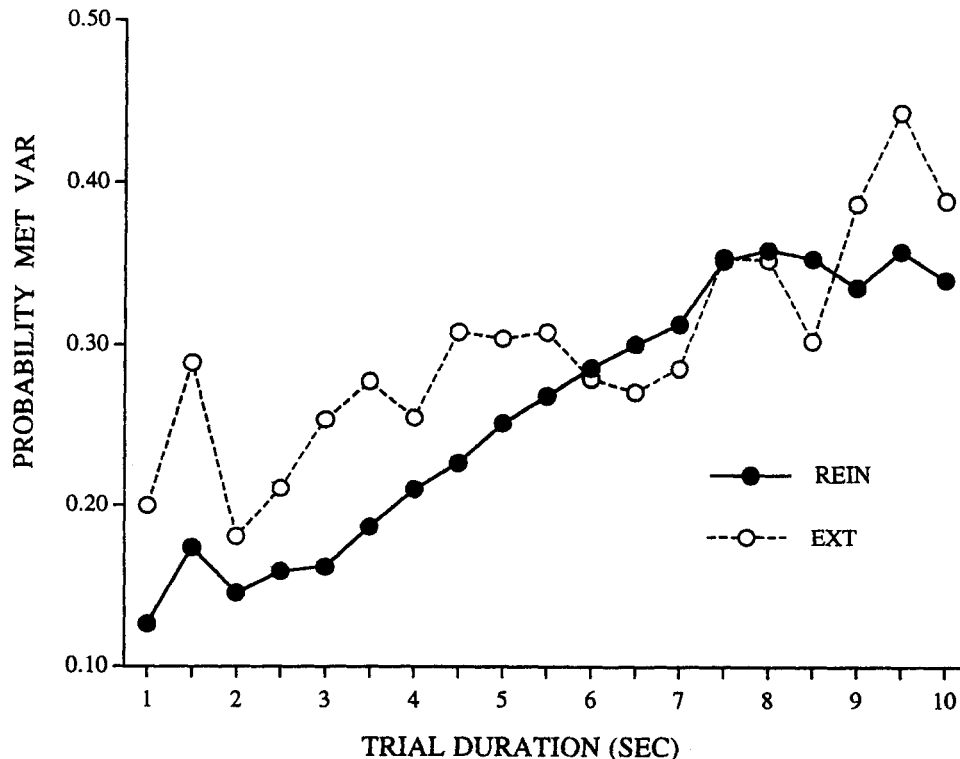
Figure 2. The top graph shows the probabilities of each of the 27 possible response sequences during reinforcement (REIN; solid circles) and extinction (EXT; open circles) phases. The bottom graph shows the ratios of these probabilities, in other words, extinction probabilities divided by reinforcement probabilities.

change from reinforcement to extinction, ratios greater than 1.0 indicating higher probabilities during extinction, and ratios less than 1.0 indicating the opposite. The largest changes are seen for the least probable sequences (those to the right of the graph), with 13 of the 14 least probable sequences increasing relative to their baseline levels. In relative terms, the increases seen on the right side of the bottom figure were large, which explains the significant increase in the MetVar statistic: Whenever a low-probability sequence occurred, the MetVar criterion was satisfied. However, in absolute terms, these increases were small (see top of Figure 2), which helps to explain the stability of the hierarchy. Although 11 of the 13 most probable sequences decreased relative to their baseline levels, both absolute and relative changes were small, consistent with a stable hierarchy. In summary, extinction resulted in large increases in low-probability sequences relative to their baseline levels but left approximately unchanged the overall hierarchy of sequences.

Stable response structures were also observed in another possibly important dimension, namely, response speed. Previous research with both human and nonhuman animal subjects showed that variability increases when time-outs are interposed between consecutive responses or between responses otherwise paced

(Baddeley, 1966; Neuringer, 1991). In the present case, both speed and variability were controlled by the subjects, and our question concerned the relationship between the two. Figure 3 shows that probability of meeting the variability contingency increased with trial duration—the time between the beginning of a trial (lights on) and the last response in that trial—for both reinforcement and extinction phases, the functions in the two phases being highly correlated, $r(17) = .82$, $p < .0001$. At the shorter durations, variability was higher during extinction, but both functions increased in approximately linear fashion. One possible explanation of these correlations is that low-probability sequences—and therefore those most likely to meet the variability contingency—consisted of multiple crossings of the experimental chamber. For example, RLK, LRK, KRK, and KLK, among the least likely of the sequence patterns, involved running between the key and a lever at least once, and this may have taken a relatively long time. However, in many trials, sequences with one and two switches were emitted within a 1- to 2-s period, and as will be shown in Experiment 3 below, an LKR sequence, which required the maximum number of chamber crossings, was emitted with high probability in approximately 3 s. (Note that the trial duration data differed from the response rates shown in Figure 1 [bottom] in that

Figure 3. Probabilities of meeting the variability contingency (MetVar) as a function of trial duration during reinforcement (REIN; solid circles) and extinction (EXT; open circles) phases.

trial durations excluded the pause before the first response in each trial.) Thus, the linear relationship between MetVar and trial duration appears not to be solely a function of the physical distances among operanda, and the similarity in reinforcement and extinction phase functions therefore lends further support to the stability of responses during extinction.

In summary, withholding reinforcement slowed responding and increased the likelihood of meeting a variability criterion. At the same time, response structures established during reinforcement were little affected by extinction: Probability distributions in the two phases were highly correlated, as were the functions relating variability to trial durations. This is the first experiment to document simultaneously both increased variability and maintained response structures during extinction and to show that the increased variability resulted from relative increases in the least likely response sequences.

Experiment 2

The next experiment assessed the generality of these findings by asking whether increased variability and maintained structure would be found after more permissive reinforcement contingencies. Reinforcement was provided without regard to sequence variability under a yoking procedure. The same subjects as in Experiment 1 were divided into two groups, Var and Yoke, with each rat in the Yoke group paired with a Var rat. The Var animals were returned to the same reinforcement contingencies as in Experiment 1. Reinforcement for a Yoke animal did not depend on its

own response patterns; rather, the animal was reinforced for completing a trial whenever its paired Var partner had been reinforced for the parallel trial. Thus, for example, if the Var animal had been reinforced (for meeting the variability contingency) on Trials 3, 4, 7, 8, 9, 11, and so on within a given session, then the Yoke partner would be reinforced on those same trials, whether or not the variability contingency had been met. The benefits of this pairing were that Yoke and Var animals received identical frequencies and distributions of reinforcement but that Yoke group contingencies did not require, although they permitted, response variability. Reinforcement and extinction phases were repeated twice.

Method

Subjects and apparatus. The subjects and apparatus were the same as those used in Experiment 1.

Procedure. Twenty-five subjects continued to be reinforced for variable responding exactly as in Experiment 1 (the Var group). The other 25 had their reinforcement yoked to Var partners. If, in a given session, the Var animal generated fewer trials than did its yoked partner, the yoked schedule of reinforcement cycled back to the beginning of the session. Thus, the Var animal was required to vary its sequences, as in Experiment 1, and the Yoke animal was permitted to vary but was not required to do so.

Partners were assigned such that each pair had responded at similar rates and with similar levels of variability in Experiment 1. Within each pair, one animal was randomly assigned to the Yoke group, the other to Var. An ABAB design was employed, with a reinforcement phase (13 sessions), an

extinction phase (4 sessions), another reinforcement (15 sessions), and a final extinction (4 sessions). Because of equipment problems with one of the operant chambers, 5 rats were excluded from the analyses, 2 Var and 3 Yoke animals, leaving a total of 23 Var and 22 Yoke animals. As in Experiment 1, analyses were based on the last four sessions of reinforcement phases and the four sessions of extinction. On the basis of previous work, we expected variability to be higher in the reinforcement phases for the Var group as compared with the Yoke group. The main question was whether variability would increase in extinction in both of these groups and whether response structures, whatever they happened to be, would be maintained.

Results and Discussion

As expected, response rates decreased in both groups during the extinction phases, $F(1, 43) = 314.678$, $p < .0001$ (Figure 4, bottom). The group by phase interaction was significant, $F(1, 43) = 4.742$, $p < .05$, because Yoke group response rates were higher than those for the Var group during the reinforcement phases but not during extinction. A possible reason for this was that during the reinforcement phase, the Yoke animals responded almost exclusively on the levers and tended to repeat responses on

Figure 4. The top graph shows probability of varying, in other words, of meeting the variability criterion (MetVar contingency), during reinforcement (REIN; solid points) and extinction (EXT; open points) phases. Circles represent the Var group (reinforced for variations), and squares represent the Yoke group (reinforced independently of variations). The bottom graph shows rates of responding (trials per minute) during the same sessions. Note that there were four sessions per phase and that each phase was repeated twice.

a single operandum. The time required to emit such sequences was less than that for those containing both lever and key responses, which required traversing of the chamber.

Variability increased during extinction for both groups, $F(1, 43) = 86.768, p < .0001$ (Figure 4, top), and the group by phase interaction also was significant, $F(1, 43) = 13.219, p < .001$. Post hoc analyses showed that MetVar increased during extinction for both Var, $F(1, 43) = 8.247, p < .01$, and Yoke, $F(1, 43) = 41.019, p < .001$, and that the Var group maintained a higher level of variability than did the Yoke group, during both reinforcement, $F(1, 66) = 107.696, p < .001$, and extinction $F(1, 66) = 47.633, p < .001$. Thus, significant differences in variability were engendered by Var versus Yoke contingencies, as well as by the presence versus absence of reinforcement. The main conclusion is the same as that reached in Experiment 1: Extinction increased variability, this now being demonstrated after noncontingent reinforcement as well as after reinforcement of variations.

Probabilities of the 27 response sequences (averaged across the two replications) are shown at the top of Figure 5, with the Var group to the left and the Yoke to the right and the extinction-to-reinforcement ratios below. The ordering along the x-axis for the Var group was based on its hierarchy during the reinforcement phase (as in Experiment 1) and for the Yoke group, on that group's hierarchy during the reinforcement phase. The main results were as follows: (a) The Var group's distributions were flatter than those of the Yoke group (compare solid circles in the upper-left graph with those in the upper-right graph), corresponding to the Var group's higher sequence variability. (b) The distributions during extinction were similar to those during reinforcement, this being true for both groups, the Var correlation between reinforcement and extinction phases, $r[25] = .95, p < .0001$, and Yoke, $r(25) = .97$. (c) The most frequent sequences for the Yoke group (LLL, RRR, LRR, RLL, LRL, RLR, LLR, and RRL) were also most frequent for the Var group, although the exact ordering differed. (d) As in Experiment 1, the low-probability sequences increased most during extinction relative to the reinforcement phase, this again being true for both Var and Yoke groups. More low-probability sequences increased for Yoke than Var, possibly be-
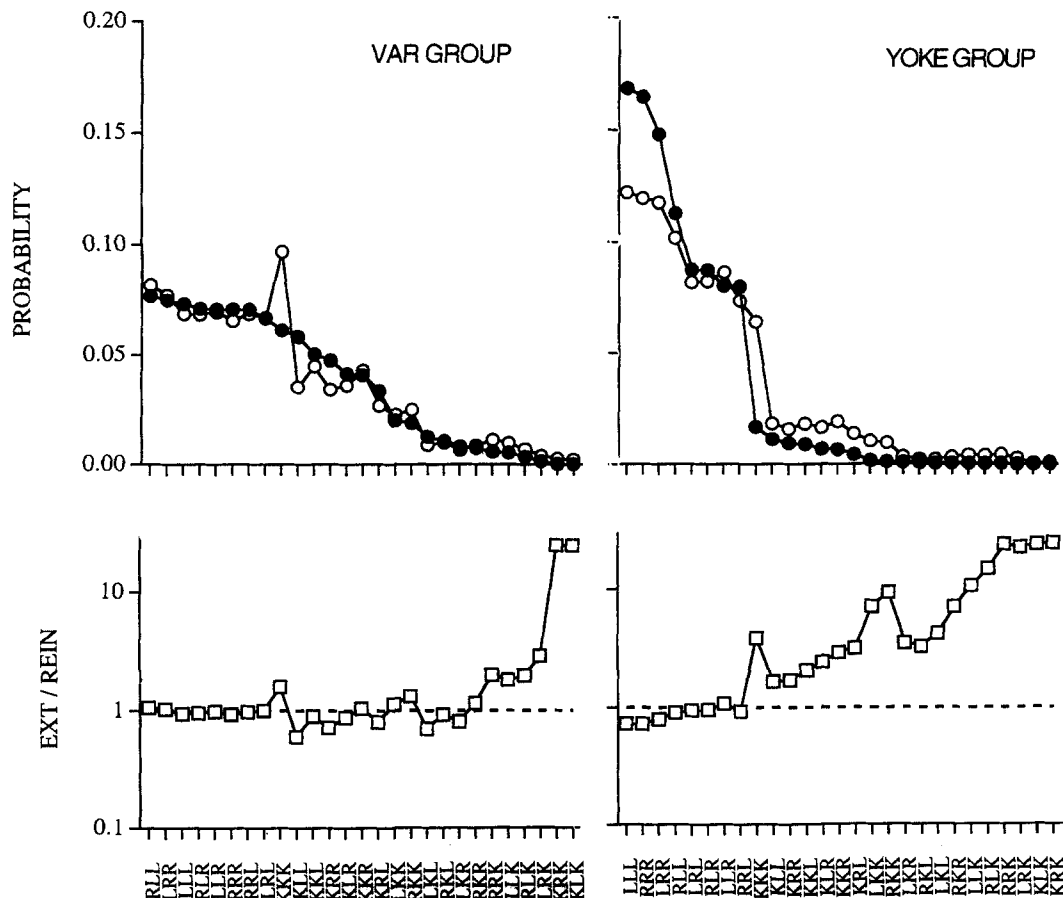

Figure 5. The top graphs show the probabilities of each of the 27 possible response sequences during reinforcement (REIN; solid circles) and extinction (EXT; open circles) phases. The Var group (reinforced for variations) is on the left, and the Yoke group (reinforced independently of variations) is on the right. The order of sequences was based on each group's hierarchy during the reinforcement phase and is given along the x-axis. The bottom graph shows the ratios of these probabilities; in other words, extinction probabilities divided by reinforcement probabilities.

cause there were more of them. (e) As in Experiment 1, but now for both groups, KKK was more probable during extinction than during reinforcement, with an associated decrease in KLL and KRR. That is, subjects tended to stay in the rear of the chamber during extinction and to respond repetitively on the key. In summary, the Yoke group's probability distributions were much steeper than were the Var group's during the reinforcement phase, and the changes during extinction were correspondingly greater for the Yoke group. For both, however, distributions characteristic of the reinforcement phases were maintained during extinction.

Differences in U values across the two phases were small for the Var group (an increase from .853 to .863 in the first replication and from .848 to .850 in the second), as was the case in Experiment 1, and were larger for the Yoke group (.644 to .759 in the first replication and .592 to .730 in the second). For the Var group, the differences approached significance in the first replication, $t(22) = 1.815$, $p = .08$, but not the second, $t(22) = 0.370$, ns. For the Yoke group, the differences were significant in both, $t(21) = 7.602$, $p < .0001$, and $t(21) = 8.716$, $p < .0001$, respectively. With respect to the Var group, the MetVar statistic showed larger changes than did U value, in part because relative increases in low-probability sequences satisfied the MetVar criterion (see Figure 5, bottom), whereas U value was mainly governed by the overall distribution (see Figure 5, top). In general, these data are consistent with those from Experiment 1, but here, for both stringent variability contingencies (Var) as well as permissive ones (Yoke).

Figure 6 shows variability as a function of trial duration. For both groups, probabilities of varying increased with trial duration and the extinction functions were similar to the reinforcement functions, Var: $r(17) = .86$; Yoke: $r(17) = .94$, both ps < .0001. Because Yoke animals varied less than Var animals in both phases, the Yoke functions fall below the Var. Again, for both groups, variability tended to be higher at the shortest intervals during extinction; all of these results were consistent with those of Experiment 1.

Experiment 2 replicated and extended the results of Experiment 1. Variability increased during extinction whether reinforcement had been contingent on the variability (Var group) or not (Yoke group); and response structures established during the reinforcement periods were maintained. The explanation was, as in Experiment 1, that extinction increased the least probable sequences while maintaining the overall hierarchy of sequence probabilities.

Experiment 3

To further test the generality of simultaneously increased variability plus maintained structure, we next studied responding at the opposite end of the variability continuum, namely, under conditions in which a single sequence was reinforced. Fifty experimentally naive rats were divided into two groups, one reinforced under the same Var group contingencies used in Experiments 1 and 2 and the other (Rep) reinforced exclusively for a single sequence, LKR.
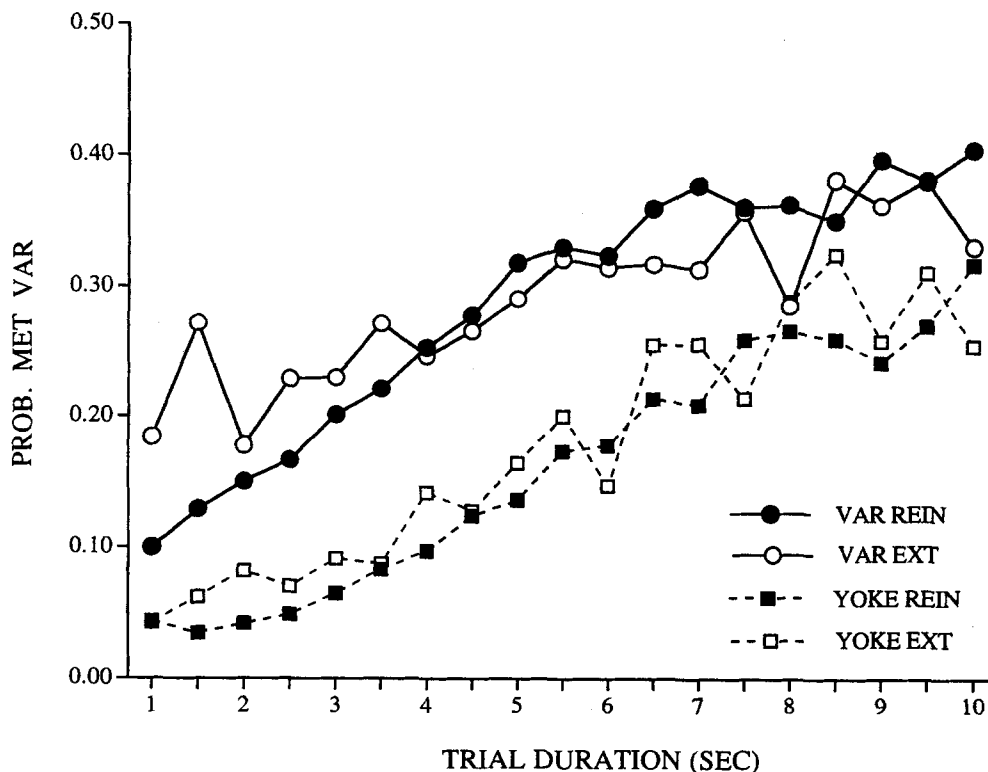

Figure 6. Probabilities of meeting the variability contingency (MetVar) as a function of trial duration during reinforcement (REIN; solid points) and extinction (EXT; open points) phases for the Var group (reinforced for variations; circles) and Yoke group (reinforced independently of variations; squares).

Naive animals enabled us to test the reliability of the Var group results in Experiments 1 and 2.

Method

Subjects. Fifty experimentally naive male Long-Evans rats, approximately 4 months old at the start of the experiment, were maintained as in Experiments 1 and 2.

Apparatus. The same apparatus used in Experiments 1 and 2 were used in Experiment 3.

Procedure. There were two minor changes in the basic procedure. Responses to the left lever, right lever, and key produced the same 0.1-s, 1300-Hz tone (it had been a 0.15-s tone with a different frequency for each operandum in Experiment 2). The time between reinforcement and the next trial was increased from 0.5 s to the same duration as time-out, 1 s. As in Experiment 2, an ABAB design was utilized, with two reinforcement and two extinction phases.

The rats were shaped to press the right lever, the key, and the left lever and then were divided into two groups of 25 each, which were randomly designated: one, Var and the other, Rep. The Rep group was trained to emit the single target sequence (LKR). Reinforcement was first contingent only on right lever presses (R). As soon as a subject was pressing R consistently, the requirement became KR and then LKR. Stimulus lights associated with the operanda provided discriminative cues for the correct response; incorrect responses were ignored. For example, when KR was being reinforced, the keylight would remain on until the key was pressed, at which point the right-lever light came on, and the keylight went dark. At this point, responses to the key and left lever were ignored, and as soon as the animal pressed the right lever, reinforcement was given. A similar procedure was used for the Var animals, except that instead of a single sequence, the computer chose randomly on each trial, again starting with a trial length of one, for example, just K, and increasing to trial lengths of two, for example, RR, then of three, for example, LKL. The last five sessions of this training period consisted of fixed three-response trials. Thus, the two groups were trained with equivalent methods either to repeat the LKR sequence or to vary.

The Var animals were then put directly onto the experimental procedure, which was identical to that in Experiments 1 and 2. To recapitulate, sequences were reinforced only if their current relative frequencies were less than or equal to .05, the threshold value. Stimulus lights associated with the three operanda were illuminated until a response occurred and then darkened for 0.33 s, this being done identically for both Var and Rep subjects. For the Rep animals, there was one intervening phase to facilitate learning of the LKR sequence. If a Rep subject made an error at any point in the sequence, the trial immediately terminated with a time-out. For example, if the animal pressed L and then L again, an error, time-out immediately followed. This continued for four sessions, at which point the Rep subjects were given the final procedure: As for the Var rats, all Rep group trials included three responses, ending in time-out if the contingency was not met and with reinforcement if LKR had been emitted.

As training proceeded, one additional change was required. The Rep subjects became highly proficient, and their reinforcement frequencies therefore increased. Because the variability contingencies did not permit Var animals to be reinforced as frequently, the Rep subjects were reinforced probabilistically for the LKR sequence. After 28 sessions of LKR always being reinforced, that sequence was reinforced with a .75 probability, the other correct trials resulting in the same time-out as an incorrect trial. (Note that this procedure did not differ from the Var contingencies because a true random generator would sometimes not meet the Var contingencies, by chance, and therefore, for Var as well as Rep, correct sequences were occasionally not reinforced.) After 23 additional sessions, 4 sessions of extinction were provided, then 10 additional sessions of reinforcement were provided, followed by a second extinction, again of 4 sessions. During the second reinforcement phase, probability of reinforcement for correct Rep sequences was reduced to .65 to maintain approxi-

mately equal reinforcement frequencies in the Var and Rep conditions. As in the previous two experiments, analyses are based on the last four sessions of the reinforcement phases and the four sessions of extinction.

Results and Discussion

The bottom of Figure 7 shows that response rates again decreased during extinction, $F(1, 48) = 205.013$, $p < .0001$, with a significant group by phase interaction, $F(1, 48) = 27.154$, $p < .0001$, the groups differing only during the reinforcement phases, as was the case in Experiment 2. An explanation for why the Var group's response rates were higher than those of the Rep group's during reinforcement is analogous to that given in Experiment 2. The LKR sequence for the Rep group required the chamber to be traversed twice during each trial (from left lever to key then from key to right lever), whereas Var contingencies permitted some sequences to be repetitions or to contain only leverpresses.

As in the previous two experiments, subjects in both groups were more likely to meet the variability criterion during extinction than during reinforcement, $F(1, 48) = 100.392$, $p < .0001$ (Figure 7, top left). The group by phase interaction was again significant, $F(1, 48) = 30.654$, $p < .0001$, with post hoc analyses showing that MetVar increased during extinction for both the Var group, $F(1, 48) = 10.049$, $p < .01$, and the Rep group, $F(1, 48) = 120.997$, $p < .001$, and that the Var group's level of variability was higher than that of the Rep group during the reinforcement phases, $F(1, 96) = 71.035$, $p < .001$, but not during extinction, $F(1, 96) = .300$, ns.

For comparison, the upper righthand portion of Figure 7 shows the Rep group's probability of meeting its LKR contingency, which was approximately 0.50 during the reinforcement phases, a value considerably higher than chance, or .037. Extinction caused a marked and significant decrease in probability of LKR, $F(1, 24) = 94.499$, $p < .0001$, a finding consistent with the increased variability just reported. Whenever the Rep subjects did not meet the Rep contingency, they were likely to meet the Var contingency, the upper-left and -right functions in Figure 7 mirroring one another for the Rep group.

The left side of Figure 8 replicates the Var findings from the two previous experiments, the distributions of the 27 patterns being similar during reinforcement and extinction phases, $r(25) = .92$, $p < .0001$, with uncommon sequences increasing proportionately more during extinction than common ones and with KKK also increasing. To permit direct comparison, the y-axes were the same for the Var and Rep groups, accounting for why the Var group's functions appear to be flatter than in Experiments 1 and 2.

The data from the Rep group, shown in the right side of Figure 8, were similar to those from the Yoke group in Experiment 2, except that now LKR, the only reinforced sequence, was most probable. As in all other cases, the Rep group's distributions were similar during extinction and reinforcement phases, $r(25) = .96$, $p < .0001$, with the lower probability sequences increased proportionately more than the higher probability ones and the latter decreasing slightly.

U value comparisons were similar to those in Experiment 2. During the reinforcement phase, U values for the Rep group were much lower than for Var. U values correspondingly increased more for the Rep group during extinction than for the Var group (Rep group: .534 to .707 in the first replication and .556 to .793 in
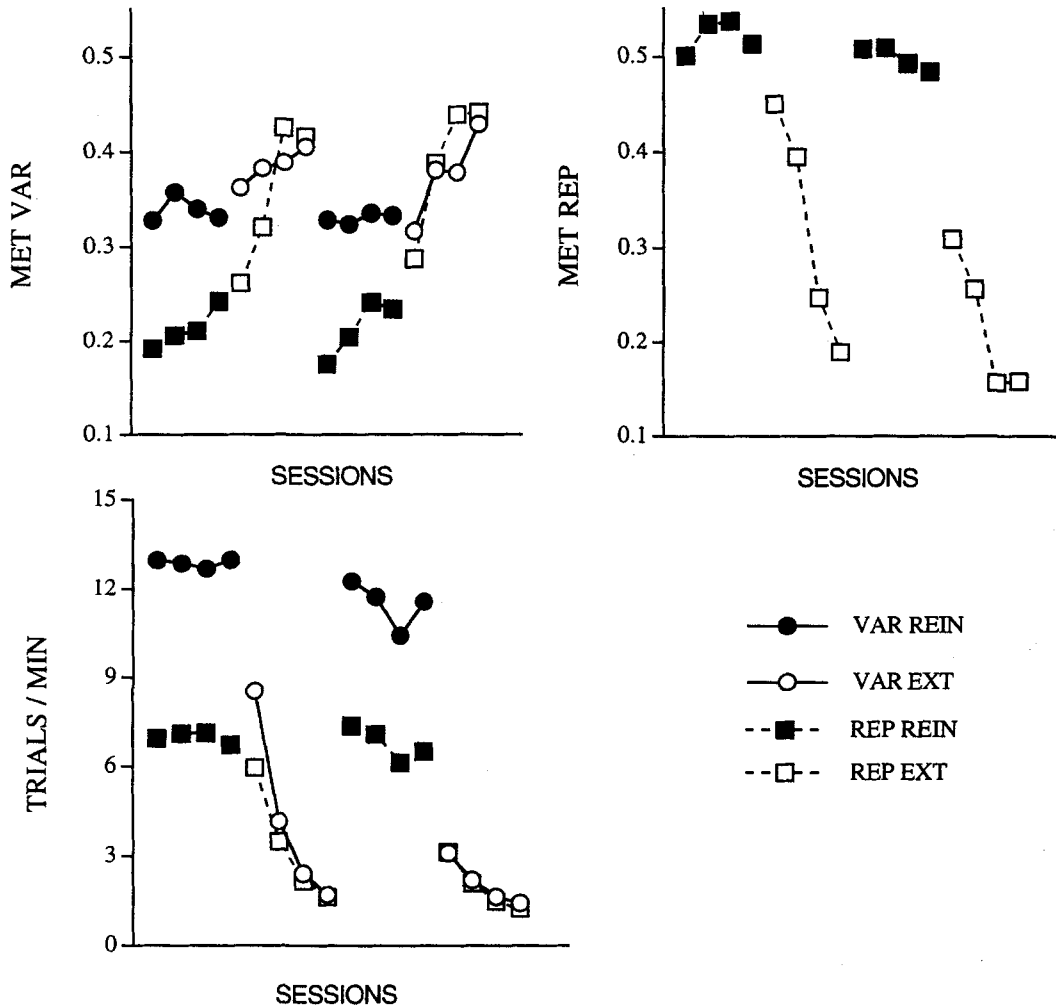
Figure 7. The upper-left graph shows probability of varying, in other words, of meeting the variability criterion (MetVar contingency) during reinforcement (REIN; solid points) and extinction (EXT; open points) phases. Circles represent the Var group (reinforced for variations) and squares, the Rep group (reinforced for a single sequence). The upper-right graph shows the Rep group's probability of emitting the required sequence. The bottom graph shows rates of responding (trials per minute) during the same sessions. Note that there were four sessions per phase and that each phase was repeated twice.

the second; Var group: .869 to .884 in the first replication and .857 to .867 in the second). Rep group differences were significant, $t(24) = 7.731, p < .0001$ and $t(24) = 9.696, p < .0001$ for the two replications, respectively. The Var group's differences were significant in the first replication but not the second, $t(24) = 3.771, p < .0009$ and $t(24) = 1.472, ns.$

Variability as a function of trial duration again confirmed maintained response structure (Figure 9, top). The Rep functions differed markedly from the Var functions. For Var rats, probability of satisfying the contingency increased with trial duration, as in Experiments 1 and 2. For Rep rats, variability decreased and then increased. For comparison, the bottom of Figure 9 shows that the corresponding probabilities of satisfying the Rep contingency (LKR) changed in opposite fashion. The most important finding was that despite the marked differences between Var and Rep

groups, their respective functions during extinction were highly correlated with those during the reinforcement phase, Var: $r(17) = .87$; Rep: $r(17) = .92$ for the variability functions and $r(17) = .98$ for the LKR target functions, all $ps < .0001$. Thus, as before, distributions generated by the reinforcement contingencies were maintained during extinction.

Two additional analyses further tested the stability of response structure. We asked first whether the sequence hierarchies changed across the four sessions of extinction. Figure 10 shows the distributions for the Var group separately for each session of extinction (first replication). The same general pattern is characteristic of all four extinction sessions except that the most frequent sequences, such as KKK and RRR, tended to increase across the four sessions, whereas sequences beginning with K and ending with leverpresses tended to decrease, such as KRR and KLL. The similarity across
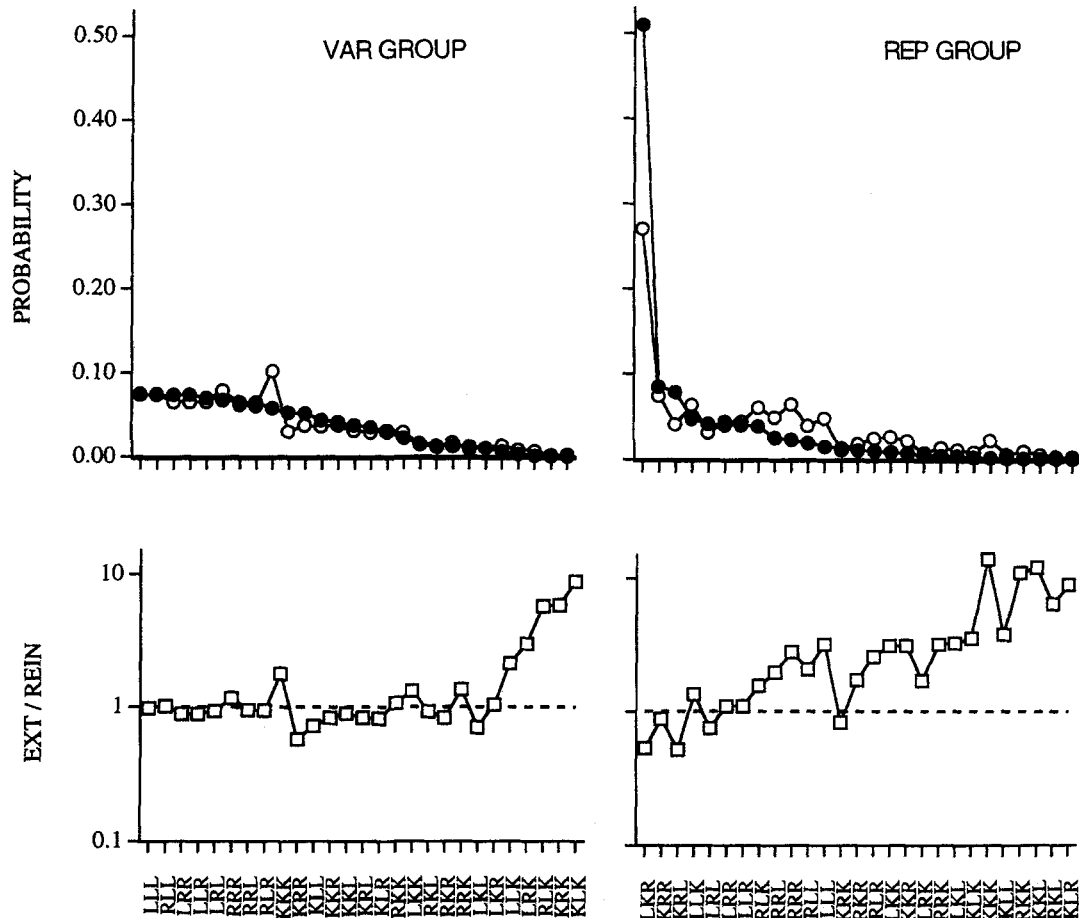
Figure 8. The top graphs show the probabilities of each of the 27 possible response sequences during reinforcement (REIN; solid circles) and extinction (EXT; open circles) phases. The Var group (reinforced for variations) is on the left and the Rep group (reinforced for a single sequence), on the right. The order of sequences was based on each group's hierarchy during the reinforcement phase and is given along the *x*-axis. The bottom graph shows the ratios of these probabilities, in other words, extinction probabilities divided by reinforcement probabilities.

sessions was also found when we analyzed the probability distributions from the other experiments as well as variability as a function of trial durations. Thus, response structure stability was maintained across extinction sessions.

Second, we asked whether the average functions accurately represented individual subjects. Figure 11 shows the probability distributions for 6 randomly selected Var subjects. For individual animals as well as for the group averages, the distributions were similar across reinforcement and extinction phases. In summary, according to all analyses in each of the three experiments, the structures of responding generated by reinforcement were maintained during extinction.

This section concludes with one additional analysis, the data for which were not available in Experiments 1 and 2. In each of the three experiments, the least probable sequences increased most. Also increased was the KKK sequence. These results suggest a tendency during extinction for the rats to respond differently and possibly to respond distantly from the area in which reinforcement had previously been experienced. As one test of this conjecture, we

measured responding on two peripheral keys located on either side of the lighted and operative key in the rear of the chamber. These peripheral keys differed in that they were dark and that responses to them never had an effect. In Experiments 1 and 2, responses to them were not recorded, but in the present experiment, we recorded peripheral responses in 8 of 10 chambers (the peripheral keys being inoperative in the 2 remaining chambers), and therefore, 23 Rep and 17 Var animals are included in the analysis. The main question was whether responses to these keys would increase during extinction, and Figure 12 shows that the answer is yes, $F(1, 38) = 44.271$, $p < .0001$, with similar increases occurring in both Var and Rep groups. Extinction increased responses to operanda that were not contained within the previously reinforced set.

General Discussion

How is it possible that extinction leaves the structure or pattern of learned responses unchanged while at the same time increases response variability? As outlined in our introduction, there is
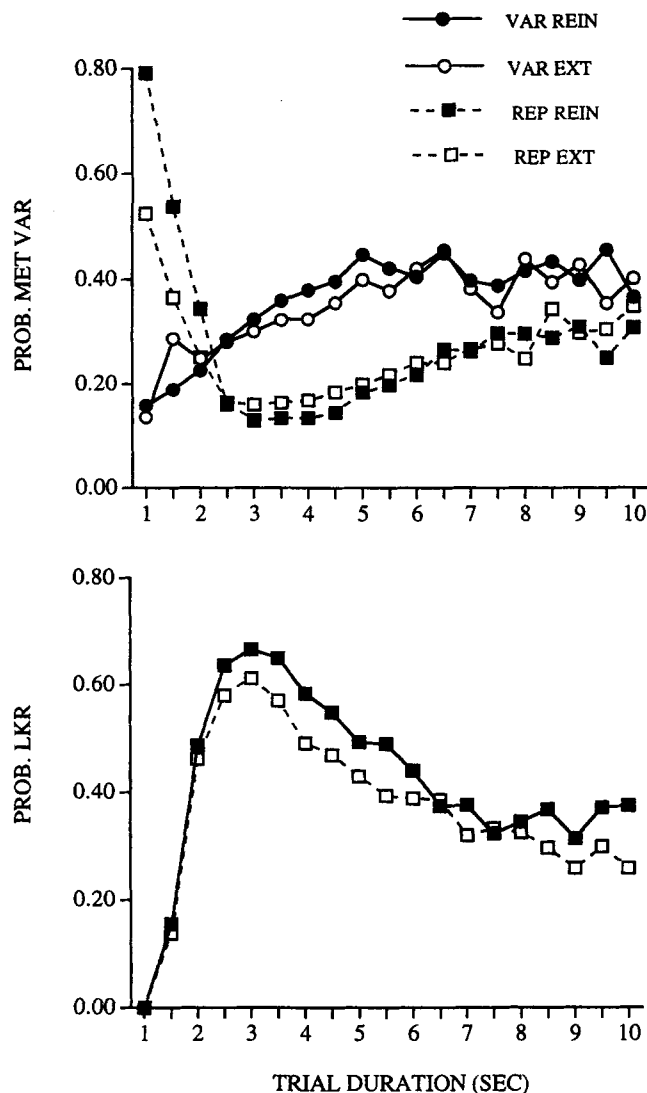
Figure 9. The top graph shows probabilities of meeting the variability contingency (MetVar) as a function of trial duration during reinforcement (REIN; solid points) and extinction (EXT; open points) phases for the Var group (reinforced for variations; circles) and Rep group (reinforced independently of variations; squares). The bottom graph shows the Rep group's probability of emitting the LKR sequence.

substantial evidence for each of these claims, but they seem inconsistent. The present research shows that the most common responses established by reinforcement were maintained intact—their structures and patterns were unchanged, and they continued to be most common—whereas unlikely responses increased relative to their baseline levels, including those that rarely, if ever, occurred in the past. The first of these results accounts for maintained stability, the second for increased variability. A more detailed overview of the evidence follows.

Different groups of rats were reinforced for variable sequences (Var group), for a single, repeated sequence (Rep group), and independently of both variations and repetitions (Yoke group). This is the first study to compare extinction after reinforcement

across these three diverse contingencies and the first ever to study extinction after reinforced variability.

Most results were common across the three contingencies, thereby supporting their generality. First, in all cases and as has been commonly reported elsewhere, rates of responding decreased consistently across the period of extinction. Whether they had been reinforced for varying, repeating, or without regard to either, the animals responded less and less when reinforcement was withheld.

Second, sequence variability increased during extinction, and this was observed across all contingencies. The increase was most clearly demonstrated by the MetVar statistic because of its sensitivity to low-probability sequences. Those sequences that had only rarely been emitted increased most, relative to their levels during the reinforcement phase. Another measure of variability, U value, also increased, although especially for the Var groups, this measure was less affected. U value represents overall probability distributions, and as will be discussed below, these were generally unaffected. It should be noted that variability has many dimensions (there are many different ways for a phenomenon to vary or not) and that significant effects in any one or more measures suffice to show a variability difference across two conditions (Knuth, 1969). The conclusion reached from the present experiments is consistent with and extends other studies (e.g., Balsam, Deich, Ohyama, & Stokes, 1998): Variability increases in extinction because of the relatively large increases in low-probability behaviors. When reinforcers are no longer forthcoming, subjects occasionally try something different.

Two other results supported the try-something-different effect. Responses to inoperative operanda (dark keys that provided no feedback and were located in the rear of the chamber) significantly increased during extinction (Experiment 3). A related finding was that probabilities of the KKK sequence increased in extinction, KKK being the sequence whose members were most distant from
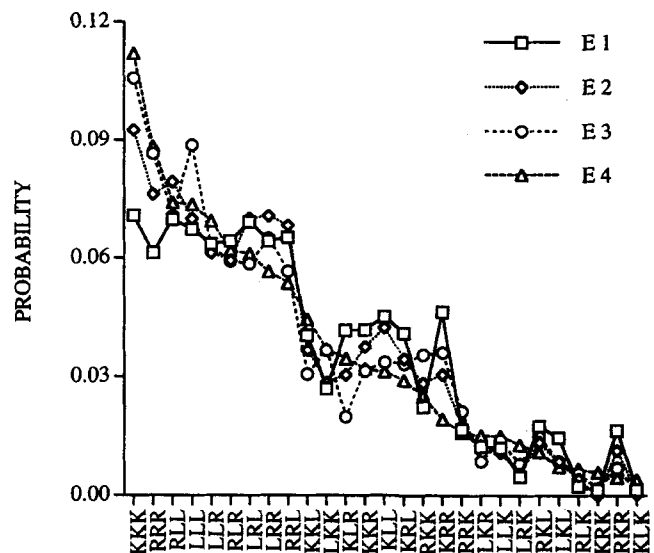

Figure 10. Probabilities of each of the 27 possible response sequences during each of the four extinction sessions E1 through E4. Data are from the first replication for the Var group (reinforced for variations) in Experiment 3.
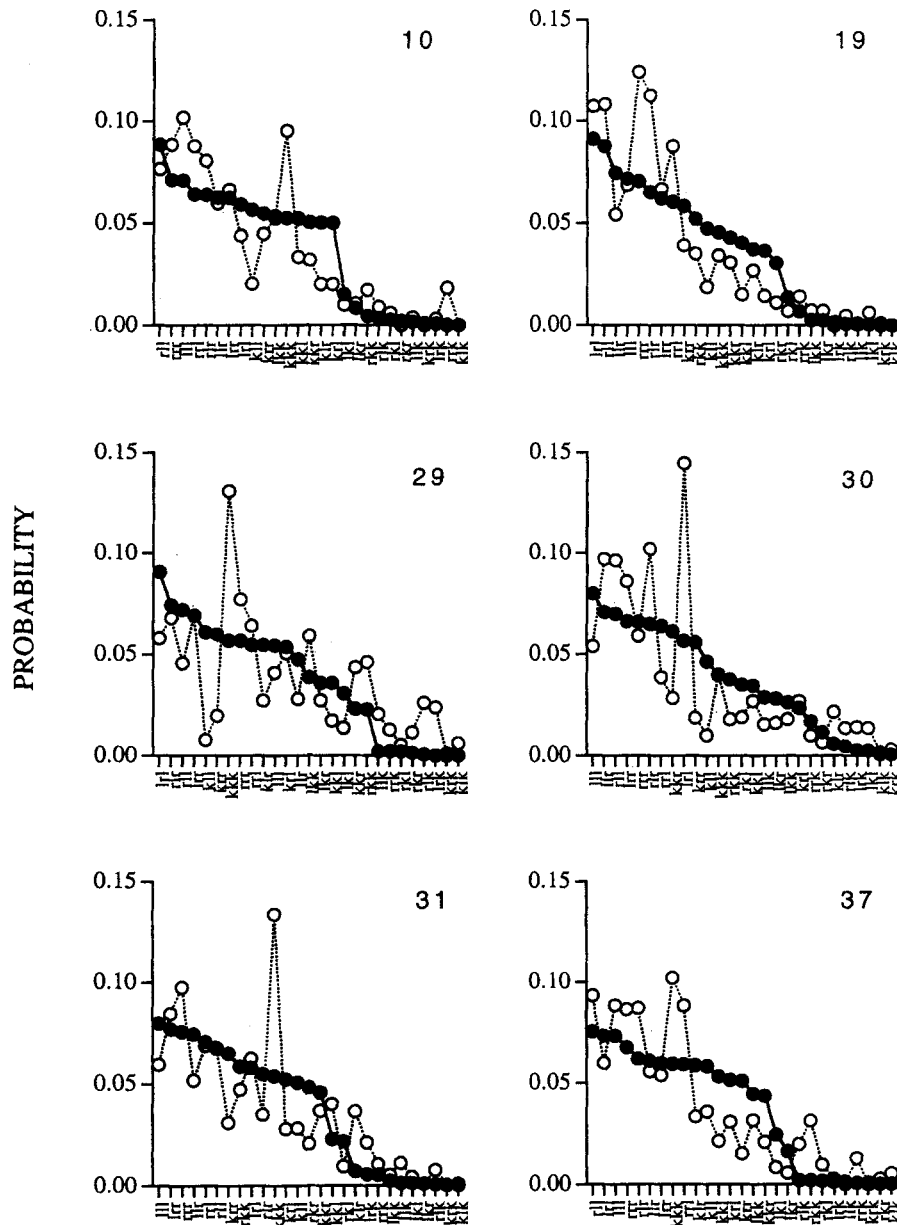
Figure 11. Probabilities of each of the 27 possible response sequences for 6 randomly selected subjects from the Var group (reinforced for variations) in Experiment 3. Solid circles represent the reinforcement phase and open circles represent extinction.

the pellet dispenser. Lowest probability sequences, responses on novel operanda, and repetitions of K responses all represent doing something different and distant during extinction and all increased significantly.

Third, for all three contingencies, the response structures established during the reinforcement phases were maintained during extinction, this being shown in two ways. (a) When the 27 possible sequences were ordered from most probable to least, it was found that the hierarchies were highly correlated across reinforcement and extinction phases. That is, those sequences that were most probable during reinforcement generally continued to be most

probable throughout extinction. This is an important finding, for it indicates that consistent with the literature showing maintenance of previously learned responses (e.g., Bouton & Nelson, 1998; Rescorla, 1998), previous learning is not wiped out. The different reinforcement contingencies generated different hierarchies; for instance, when variability was reinforced, distributions were relatively flat, whereas when repetitions were reinforced, distributions were peaked, anchored around the single reinforced sequence, but whatever the distribution generated by reinforcement, it was retained throughout extinction. (b) When an animal took a long time to complete a trial, the sequence in that trial tended to be less
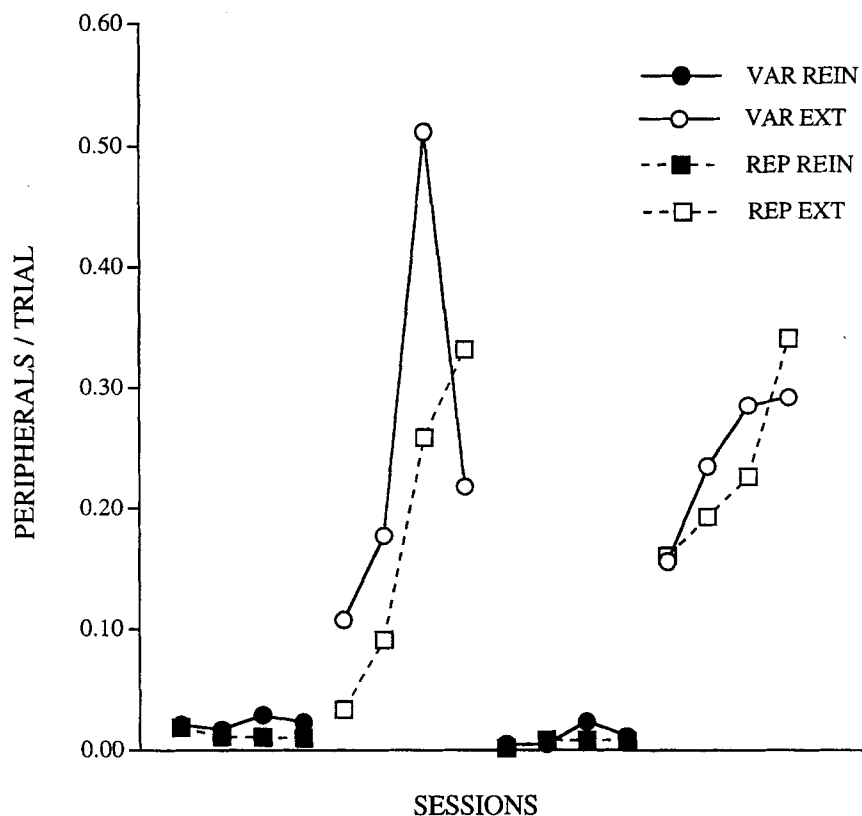
Figure 12. Number of responses per trial to the two peripheral keys during each of four sessions of reinforcement (REIN; solid points) and extinction (EXT; open points). Circles represent the Var group (reinforced for variations) and squares represent the Rep group (reinforced for a single sequence).

common—it was a low-probability sequence—than when the animal rapidly completed a trial. In the cases of Var and Yoke contingencies, variability increased monotonically with trial durations, with Yoke variability consistently lower than that of Var. The function differed for Rep contingencies, first decreasing and then increasing. But the important finding was that although specific reinforcement contingencies produced different functions, those functions were maintained during extinction. Stated differently, the variability versus time functions generated during extinction were highly correlated with those generated during the reinforcement period. Taken together, these results support the claim that response structures are retained during extinction.

In a single set of experiments, therefore, evidence was provided showing that variability increased during extinction but, at the same time, that response structures were largely unaffected. This seems puzzling at first, but the results provide a reconciliation. The least likely sequences increased relative to their baseline levels, but in absolute terms, the increases were small. The result was to significantly raise variability but not so much as to affect the hierarchies. It is as if the subjects generally bet on what had worked in the past but occasionally probed to see whether anything better might appear by doing something completely different, a combination of conservative and radical behavioral strategies. The combination is presumably functional in a world in which reinforcers are sometimes intermittent and other times depleted (if

intermittent, it is functional to continue with the previously effective behavior; if depleted, then it is not), but the two cases may be difficult for an animal to discriminate; therefore, the combination of conservative and radical strategies.

There remains the question of why the particular mix; our data indicate that the common behaviors continued with high probability throughout extinction and that the uncommon ones, although increased in relative frequency, were rare in absolute terms. A hint at an answer might come from a parallel with evolutionary processes. Mutations generate the genetic variability necessary for the evolution of species. However, most mutations are nonfunctional or lethal. At the behavioral level, doing something totally different may have a low probability of success and be associated with risks, such as entering the location of a predator or aggressive conspecific. Thus, when things are going poorly, animals generally do what has succeeded in the past and only rarely do something completely different.

The stability–variability mix may differ as a function of species, personality, motivation, and schedule variables. For example, although the present results show increased variability during extinction, a recent study found that under extremely stringent variability contingencies (requiring even higher levels of variability than in the present experiments), decreases in frequency of reinforcement led to decreased variability (Grunow & Neuringer, 2000). Thus, schedule variables may influence the direction of

effects. Species differences may be related to the constancy of environmental niches: the more constant, the more an organism is likely to persist in previously reinforced behaviors; the more variable the niche, the more likely the do-something-different strategy. Individual differences might be related to such variables as shyness versus boldness, with bold individuals more likely quickly to employ the variability strategy and shy individuals more likely to persist in a stable mode. For a given individual, contextual control may also play a role; in other words, in a context in which contingencies often change, the variability strategy may predominate, whereas in another context, in which reinforcement contingencies are constant, stability may be the dominant strategy (see Denney & Neuringer, 1998). Last, and related to the above, different response systems may manifest different mixes of variability and stability under extinction conditions. For example, it would be of considerable interest to compare levels of extinction-induced variability versus stability in Pavlovian-conditioned responses with those of similar operants. The key peck response in the pigeon is an obvious candidate for such study.

We turn next to a discussion of possible explanations of the increased variability during extinction. Two findings in the present study are informative. First, as indicated above, variability increased with trial duration. As indicated above, one contributor may have been that the most unlikely sequences—those requiring multiple crossings of the chamber from key to one of the levers— took more time than did the more common repetitions on a single operandum or than the alternations across only the levers. However, the linear relationship between variability and trial duration extended to durations well beyond what was required to cross the chamber. Furthermore, other evidence suggests that when responses are independently manipulated under conditions in which variability is reinforced, variability is affected; in other words, that experimentally slowing response rates in fact increases variability (e.g., Baddeley, Emslie, Kolodny, & Duncan, 1998; Neuringer, 1991). Thus, one possible contributor to the increased variability in extinction may be the slowing of responding, a major consequence of extinction.

Second, when variability is explicitly reinforced, the reinforcers appear to exert two opposing effects, a contingency and a contiguity effect. During the reinforcement phase, the reinforcement *contingency* required low levels of repetitions, but reinforcement *contiguity* (i.e., follows in time) might have produced the opposite tendency, causing the just-reinforced sequence to be repeated. We tested this conjecture by comparing the probability of repeating a sequence given that the sequence had just been reinforced, with the same probability given that the sequence had not been reinforced. Figure 13 shows data from the Var group in Experiment 3. (Only 21 sequences are represented because there was insufficient data from the other 6.) The closed circles show the probabilities of sequence repetitions when a reinforcer did not intervene. The function is flat, and across many of the sequences, the probabilities approximate the variability threshold requirement, namely, .05. The open triangles show a different pattern. Probabilities of repeating some sequences were much higher when the first member of the pair was reinforced. For example, repetitions of LLL, RRR, and KKK were increased more than fourfold by reinforcement, whereas LKL, LKR, and RKL were increased not at all. Thus, repetitions of only the most common sequences were increased by reinforcement. Responding after nonreinforcement was similar to
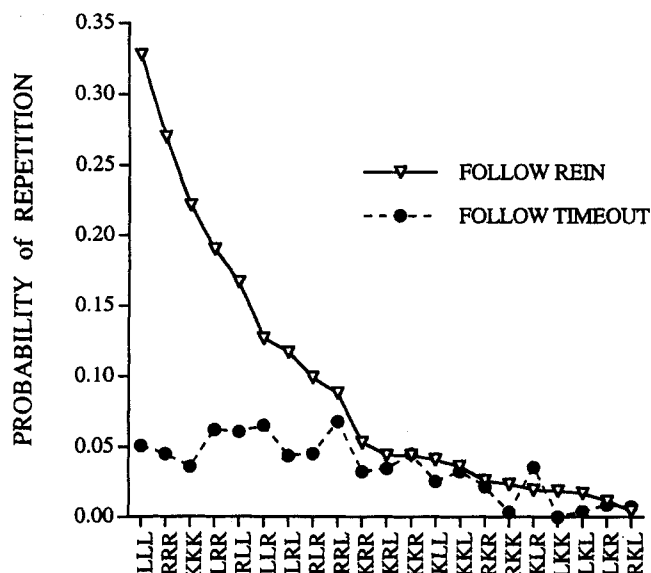

Figure 13. Probabilities of sequence repetitions given that a reinforcer (REIN) followed the first instance (open triangles) or did not (solid circles).

that during extinction, as can be seen by comparing Figures 13 and 8. Similar effects were found for the Var groups in Experiments 1 and 2 and for the Yoke group in Experiment 2, in which reinforcement increased repetitions, mainly of the LLL, RRR, and KKK sequences.

A second reason, therefore, why variability was higher during extinction than reinforcement is that some sequences were repeated immediately after their reinforcement, this being especially the case for the most common sequences. Supporting evidence is seen in that the Var animals in Experiment 3 were less likely to meet the variability contingency immediately after reinforced than nonreinforced trials, $F(1, 24) = 12.169$, $p < .01$. This same contingency–contiguity antagonism has been reported under related conditions (Cherot, Jones, & Neuringer, 1996; McElroy & Neuringer, 1990; Neuringer, 1991). In summary, extinction-induced variability is explained, at least in part, by slowed responding and removal of reinforcement contiguity effects. These same considerations may also be relevant to extinction of repeated operants.

Before this study, little was known about the effects of extinction on operant variability. Because variability was itself reinforced, would it decrease during extinction, as indicated by decreases in frequency of operant responses during extinction, or would it increase, as indicated by studies showing that extinction induces variability? The question is important for the many cases in which variability is adaptive, for example, in problem-solving, creativity, skilled motor learning, and development of cognitive strategies (e.g., Manoel & Connolly, 1995; Siegler, 1996). In operant-shaping procedures as well, reinforcement presentations are intermixed with temporary withholding of reinforcements, it being thought that withholding reinforcement induces the variability necessary for shaping (Page & Neuringer, 1985; Stokes, 1995). Thus, short-term extinction is part of the shaping process, but what, in fact, is the result of such extinction? The present results suggest that in these cases, just as in the more commonly studied

pattern of extinction after repetitions, variability may be increased when reinforcement is withdrawn. However, what had been learned will be retained.

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