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Associative Structures Underlying Discriminated Three-Response Behavior Chains

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ASSOCIATIVE STRUCTURES UNDERLYING DISCRIMINATED THREE-RESPONSE BEHAVIOR CHAINS

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ABSTRACT

Instrumental behavior often consists of sequences of responses, or chains, that lead to a primary reinforcing outcome. These responses often differ in terms of both topography and the discriminative stimuli that set the occasion for them. Previous studies have focused on two response chains. They have shown that extinction of R1 weakens the associated R2, and conversely that extinction of R2 also weakens R1. To expand what little we know about discriminated instrumental chains, as well as the associative structure that underlies them, in the present experiments we test the effects of separately extinguishing individual responses on other target responses within an S1-R1-S2-R2-S3-R3 chain. In Experiment 1, extinction of R2, but not R3, weakened R1. In Experiment 2, extinction of both R1 and R3 weakened R2. Finally, in Experiment 3, Extinction of R2 weakened R3 more than did extinction of R1. The results support the role of adjacency in discriminated chains, with importance being given to the immediately-preceding and following responses in supporting a target response. The results do not support the role of a psychological representation of the chain as a whole or a special role of the first response, which "launches" the chain, or the last response, which leads most directly to the primary reinforcer.

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CHAPTER 1: LITERATURE REVIEW

1.1 Characterizing Types of Behavior Chains

Instrumental behavior often consists of a sequence, or chain, of linked behaviors that are all necessary to produce a reinforcer. A chain involves at least two behaviors: a response that directly results in the primary reinforcer (R2) and a preceding response that provides access to R2 (R1). Nondiscriminated chains and discriminated chains have both been studied in the previous literature, but the number of studies is limited. Nondiscriminated chains involve behaviors that are not preceded by a stimulus. For example, both lever and nose-poke manipulanda could be present in the rodent operant chamber, with the rat learning to perform a certain number of lever presses followed by a certain number of nose-pokes in order to acquire a reinforcer. In contrast, discriminated chains involve behaviors that are each preceded by a unique discriminative stimulus (SD). For example, the same lever and nose-poke manipulanda could be present in the operant chamber, but the rat must learn that a light sets the occasion for a certain number of lever presses, which turns off the light and turns on a tone, which then sets the occasion for a certain number of nose-pokes in order to turn off the tone and acquire a reinforcer. Most research to date has actually studied partially-discriminated chains with drugs as reinforcers. In such chains, R1 is often known as “drug seeking” and R2 is known as “drug taking.” Typically, a lever is freely available without a preceding SD. After a certain number of lever presses (R1) are made, a different lever is inserted into the chamber (S2) which provides access to the pressing of that lever (R2), which is followed by administration of a drug (such as cocaine). In these studies, seeking responses (R1) for cocaine reinforcers were facilitated by the association between R1 and R2, as

extinction of taking responses (R2) decreased R1 (Zapata, Minney, & Shippenberg, 2010; see also Olmstead, Lafond, Everitt, & Dickinson, 2001). In other words, extinction of drug taking responses decreased drug seeking responses.

There are, however, certain advantages to studying fully discriminated chains, where separate discriminative stimuli (SDs) set the occasion for each behavior in the chain. As suggested earlier, here an R1 SD (or S1) sets the occasion for R1. Making R1 then turns off S1 and produces S2, setting the occasion for R2. Making R2 then turns off S2 and earns the reinforcer (e.g., Thrailkill & Bouton, 2016). Such discriminated chains may be more related to chains that individuals often perform in their everyday lives, because in principle there is always a separate SD for each response. They might, for example, model the characteristics of consuming drugs of abuse more closely than nondiscriminated chains, because seeking and taking usually occur in the presence of different stimuli; cues specifically associated with drug taking are widely acknowledged to play a role in drug behavior (Ostlund & Balleine, 2008). Additionally, a discriminated chain has analytical advantages for research purposes. For example, with separate SDs for each response, we are able to analyze how each cue influences the animal's choice of which response to perform, and we can also set the occasion for each behavior outside the context of the full chain itself (Thrailkill & Bouton, 2016).

1.2 Studies of Discriminated Heterogenous Chains

Given this, it is surprising how little research has been conducted on discriminated heterogenous chains. Recently, Thrailkill and Bouton (2015, 2016) reported several experiments addressing instrumental chains in discriminated settings. In addition to exploring the effect of R2 extinction on R1 responding in a discriminated

chain, no one had ever investigated the effect of R1 extinction on R2 responding. In the first series of experiments (Thrailkill & Bouton, 2015), a two-response chain was trained with a different SD setting the occasion for each response. For example, a stimulus light turned on which signaled the opportunity to press a lever, which then turned on a different stimulus light, signaling the opportunity to pull a chain hanging from the ceiling, resulting in a reinforcer. In some experiments, S1 and R1 were then extinguished over a number of trials by presenting S1 such that R1 responding was not followed by S2. The rats were then tested with R2 in extinction (S2 was presented and R2 responses were recorded). Results indicated that the extinction of R1 weakened the subsequent performance of R2 in this paradigm (Thrailkill & Bouton, 2015). This result is interesting because it suggests for the first time that something analogous to mediated extinction can take place in instrumental learning (cf. Holland & Forbes, 1982). Mediated extinction has been studied primarily in Pavlovian paradigms, such that pairings of the CS and the US provide the CS with the ability to activate a representation, or memory, of the US. Even after devaluation of the US, with later extinction of the CS rats begin to consume the US again as if the evoked representation of the CS is enough to extinguish the aversion to the US (Holland and Wheeler, 2009).

In a subsequent series of experiments by Thrailkill and Bouton, the complementary extinction effect was addressed: a two-response chain was trained, R2 was extinguished, and R1 was finally tested. Results indicated that extinction of R2 weakened the performance of R1 (Thrailkill & Bouton, 2016). In this sense, two-response discriminated chains seem to follow similar patterns and goals as two-response partially-discriminated chains. This seems interesting because there are alternative

associations in fully discriminated chains, as each response is also associated with its own cue.

Perhaps most importantly, it was pertinent to investigate whether the primary reinforcer is truly the goal of a heterogenous chain. In nondiscriminated chains, studies have shown that devaluation of the reinforcer (see below) decreases R2 responding, but not R1 responding (Balleine, Garner, Gonzales, & Dickinson, 1995; Balleine, Paredes-Olay, & Dickinson, 2005). For example, Balleine et al. trained rats with a nondiscriminated heterogenous chain in which a chain pull was followed by a lever press that resulted in a sucrose reinforcer. The reinforcer was then paired with injections of lithium chloride, causing the rat to form an association between the sucrose and sickness (the rat therefore now rejected the reinforcer). R1 and R2 were then tested in extinction separately. Rats that had sucrose paired with lithium chloride decreased R2 responding, but not R1 responding (Balleine et al., 2005). This result suggests that in a nondiscriminated chain, the goal of R2 is the reinforcer, but the goal of R1 was unknown. Recently, the effects of outcome devaluation were assessed in a discriminated chain setting, where S1 signaled R1, leading to S2 which set the occasion for R2, resulting in a primary reinforcer (Thrailkill & Bouton, 2017). Here, after devaluation of the reinforcer with lithium chloride injections (again forming a pellet-sickness association), neither R1 nor R2 were affected, suggesting that the reinforcer may not be the goal of either response in a heterogeneous discriminated chain. Additionally, given the results of Thrailkill and Bouton (2016) where extinction of R2 reduced R1, the results overall suggest that the goal of R1 in a discriminated chain is R2 and not the primary reinforcer.

1.3 Introducing Three-Response Discriminated Chains

Based on this preexisting data, we know that in two-response discriminated chains, the goal of R1 is R2, extinction of R1 also weakens R2, and the reinforcing outcome plays little to no role in motivating either R1 or R2. However, all of this literature involves two-response chains: a first behavior gives access to the opportunity to perform a second behavior. In many cases of human behavior, behavior chains are not only discriminated but consist of more than two responses (e.g., driving to a late-night gas station, purchasing a pack of cigarettes, opening the pack, and smoking), each with its own distinct SD. Studying three-response chains allows us to study chained behavior that may be more likely to occur in everyday life. A three-response chain has an extra behavior between the first response and the last response that leads to the primary reinforcer. Analytically, in a three-response chain we can ask questions about adjacency (whether behaviors that are immediately next to one another have more control over each other than behaviors that are not immediately adjacent) and we can directly compare the effectiveness of extinguishing preceding behaviors (Thrailkill & Bouton, 2015) vs. following behaviors (Thrailkill & Bouton, 2016) on a target response. Also, do the first and last responses in a chain hold special status? It seems logical, then, to ask what information we can extract from an analysis of three-response chains. This is the subject of the current experiments, the designs of which are illustrated in Table 1.

The first experiment was designed to test the feasibility of studying three-response discriminated chains and asked what the goal of R1 is in a three-response chain. Is it the next response (R2), or is it the final response that leads most directly to the primary reinforcer (R3)? (These two possibilities are confounded in a two-response

chain.) Rats acquired a chain consisting of S1-R1, which led to S2-R2, leading to S3R3. R3 was reinforced by a food pellet (see Table 1). Rats then received extinction sessions consisting of either R2 extinction or R3 extinction. Once the animals stopped performing R2 or R3, the rats all received a test with S1 and R1 in extinction. Experiment 2 targeted R2 and allowed us to compare the effect of extinguishing the preceding and following responses (R1 and R3), which could not be compared in a two-response chain. Experiment 3 then targeted R3, and examined the effects of extinguishing R1 and R2, testing whether R1 has a special status as the first response in the chain. The target response in each experiment was a nose-poke response (occasioned by a tone) in order to keep the target entirely consistent in all three experiments (see Table 1).

Table 1. Designs of the Experiments

Group	Acquisition	Extinction	Test
Experiment 1			
R2 Extinction	S1:R1→S2:R2→S3:R3+	S2:R2 -	S1:R1-
R3 Extinction	S1:R1→S2:R2→S3:R3+	S3:R3 -	S1:R1-
Handle	S1:R1→S2:R2→S3:R3+	——	S1:R1-
Experiment 2			
R1 Extinction	S1:R1→S2:R2→S3:R3+	S1:R1 -	S2:R2-
R3 Extinction	S1:R1→S2:R2→S3:R3+	S3:R3 -	S2:R2-
Handle	S1:R1→S2:R2→S3:R3+	——	S2:R2-
Experiment 3			
R1 Extinction	S1:R1→S2:R2→S3:R3+	S1:R1 -	S3:R3-
R2 Extinction	S1:R1→S2:R2→S3:R3+	S2:R2 -	S3:R3-
Handle	S1:R1→S2:R2→S3:R3+	——	S3:R3-

Note. R refers to response (either nose poke, chain pull, or lever press), and S refers to the discriminative stimuli (either left panel light, right panel light, or tone). + designates primary reinforcement, - designates nonreinforcement (extinction) and —— designates handling without exposure to the experimental apparatus.

CHAPTER 2: EXPERIMENT 1: TARGETING R1

2.1 Introduction

In the first experiment, rats acquired a chain consisting of S1-R1 (tone setting the occasion for nose-poke), which terminated S1 and led to S2-R2 (light setting the occasion for lever press or chain pull), which terminated S2 and led to S3-R3 (light setting the occasion for chain-pull or lever press). R3 was finally reinforced by a food pellet. Rats then received extinction sessions consisting of either R2 extinction or R3 extinction (made possible by presenting either S2 or S3 with R2 and R3 available over a series of trials). Once the animals stopped performing R2 or R3, they all received a test with S1 and R1 in extinction. If the goal of R1 is the next response, then extinction of R2 should decrease R1 responding and extinction of R3 should not. However, if the goal of R1 is the response that leads most directly to the primary reinforcer, then extinction of R3 should decrease R1 responding. Notice again that these two possibilities are confounded in a simpler two-response chain.

2.2 Methods

Subjects

Twenty-four female Wistar rats (75-90 days old; Charles River, Canada) were individually housed in plastic sawdust-filled cages and maintained at 80% of their free-feeding weights. Rats had unlimited access to water in their home-cages and were given supplementary feeding approximately 3hr after each experimental session.

Apparatus

The apparatus consisted of two unique sets of four conditioning chambers located in separate rooms of the laboratory (Model ENV-007-VP; Med Associates, St. Albans, VT). Each chamber was housed in its own sound-attenuating chamber. All boxes measured 31.75 × 24.13 × 29.21 cm (length × width × height). A recessed food cup was centered on the front wall approximately 2.5 cm above the floor. A retractable lever (Model ENV-112CM, Med Associates) was positioned to the left of the food cup. The lever was 4.8 cm wide and 6.3 cm above the grid floor. It protruded 2.0 cm from the front wall when extended. A chain-pull response manipulandum (Model ENV-111C, Med Associates) was positioned to the right of the food cup. The chain, which was suspended from the ceiling, was 23.5 cm long and 5.7 cm above the grid floor. It was spaced 2.0 cm from the front wall. Two 28-V (2.8 W) panel lights (diameter = 2.5 cm) were mounted on the wall near each manipulandum. One light was immediately above the lever and the other was behind the chain. A nose-poke response manipulandum (ENV-114AM, Med Associates) was positioned directly above the food cup (17.8 cm above the grid floor). A 2,900-Hz tone (80 dB) could be delivered through a Sonalert tone system (ENV-223AM; Med Associates) centered on the back wall of the chamber. The chambers were illuminated by 7.5-W incandescent bulbs mounted to the ceiling of the sound-attenuation chamber. Reinforcement consisted of the delivery of a 45 mg grain food pellet into the food cup (MLab Rodent Tablets; TestDiet, Richmond, IN).

Procedure

Food restriction began one week prior to the beginning of training. During training, one session was conducted seven days a week at approximately the same time each day. Animals were handled each day and maintained at their target weight with supplemental feeding.

Acquisition

Rats first received two 30-min sessions of magazine training with all response manipulanda removed. In each session, there were 30 noncontingent pellet deliveries scheduled according to an RT 60- schedule. In the next 30-min session, R3 (counterbalanced across subjects as lever press or chain pull) was trained. Only the R3 manipulandum (chain or lever) was present. No stimulus (S) was presented. Reinforcers were scheduled on an FR-1 schedule for 30 responses. The next session was the same as the previous day, except that it ended with 20 trials that this time involved presentations of S3, the panel light near the R3 manipulandum. An R3 response during S3 turned S3 off and immediately produced a food pellet. Responses that occurred in the absence of S3 were not reinforced. During these two days, a trial was terminated if a response was not made within 60 s of stimulus onset. In the following two sessions, the R2 manipulandum was added to the chamber (lever or chain counterbalanced). At the start of each of 30 trials, S2 (panel light near the R2 manipulandum) was turned on. A single R2 response in the presence of S2 turned off the stimulus and immediately turned on S3, in the presence of which a single R3 response produced a food pellet. In both S2 and S3, a trial was terminated if a response was not made within 60 s of either stimulus onset. Next, there

were two sessions in which the R1 manipulandum (nose poke for all rats) was added to the chamber. At the start of each of 30 trials, S1 (tone) was turned on. A single R1 response in the presence of S1 turned off the stimulus and immediately turned on S2, in which a single R2 response immediately terminated S2 and turned on S3, in which a single R3 response immediately terminated S3 and delivered a food pellet. In S1, S2, and S3, a trial was terminated if the appropriate response was not made within 60 s of stimulus onset. Over the next six days, the response requirement was gradually increased to a random ratio (RR) 4 in all three links, while also gradually decreasing the maximum stimulus time from 60 s to 20 s. On day one of this six-day period, the response requirement was RR-2 with a 60 s stimulus, day two was RR-3 with a 60 s stimulus, day three was RR-4 with a 60 s stimulus, day four was RR-4 with a 45 s stimulus, day five was RR-4 with a 30 s stimulus, and day six was RR-4 with a 20 s stimulus.

Extinction

Once acquisition was completed, rats were randomly assigned to one of three groups: Group R2 Extinction (n=8), Group R3 Extinction (n=8), or Group Handle (n=8). During each of the next three daily sessions, Group R2 Extinction was presented with 30 trials of S2. Making the R2 response terminated S2 on an RR4 schedule, but was not followed by S3 or any other event. Group R3 Extinction was similarly presented with 30 trials of S3. Making the R3 response terminated S3 on an RR4 schedule, but was not followed by a food pellet or any other event. In both of these groups, all response manipulanda were continuously present in the chambers. There were three extinction sessions that each involved 30 trials with a 45-s variable ITI, and if responding failed to

meet the RR4 requirement in either S, trials ended with termination of S after 20 s. The rats in Group Handle received no extinction, but were handled in an equivalent manner to the other groups (transported from the home cage to the operant chamber, but instead of being placed in the chamber were transported back to the home cage).

R1 Test

All rats then received a final test session in which all response manipulanda were present. There were 30 S1 test presentations separated by a 45-s variable ITI. Responses on the R1 manipulandum during S1 turned off the stimulus tone according to RR4, but did not turn on S2. Trials otherwise ended with S1 terminating after 20 s.

Data Analysis

All data were analyzed using elevation scores to describe and compare R1, R2, and R3 responding with analyses of variance using a rejection criterion of $p < .05$. Elevation scores are the pre-stimulus responses subtracted from the rate of responses that occur during the stimulus. Elevation scores therefore depict the increase of behavior from the 10 seconds of intertrial interval immediately before S1 occurs to the behavior the occurs during the S itself. To describe R1 responding occasioned by S1 in the test, we calculated elevation scores by subtracting the response rate on R1 manipulanda during the 10 s immediately before S1 was presented from the response rate during S1. The elevation scores were evaluated with analyses of variance (ANOVAs) using a rejection criterion of $p < .05$, along with planned comparisons.

2.3 Results

Acquisition

All rats learned to perform the three-response chain during the acquisition phase. The acquisition of the full chain for each group is illustrated in Figure 1. Responding increased over sessions, and there was a clear pattern of increasing response rates from R1 to R2 to R3. Elevation scores for all responses were compared in a Response (3) x Session (8) ANOVA. There was a significant effect of session, $F(7, 483) = 49.83$, $MSE = 3111.52$, $p < .01$, as well as response, $F(1, 69) = 25.58$, $MSE = 23{,}082.81$, $p < .01$, with no interaction ($F < 1$).

Groups were also compared in a Group (3) x Session (8) ANOVA for each response in the chain. There was a significant effect of session for R1, $F(7, 147) = 22.36$, $MSE = 1159.80$, $p < .01$, and no group differences or interactions, $Fs < 1$. The same analysis for R2 response elevation scores revealed a significant effect of session, $F(7, 147) = 20.07$, $MSE = 1275.39$, $p < .01$, and no group differences or interactions, $Fs < 1$. A final ANOVA for R3 elevation scores showed another significant effect of session, $F(7, 147) = 9.64$, $MSE = 773.73$, $p < .01$, and no group differences or interactions, $Fs < 1$. The results simply confirm that the groups learned and responded similarly before entering the crucial extinction phase.

We then compared response rates during the Pre-S period for all three S-R pairings in the chain. The comparisons did not reveal a result that challenged the use of elevation scores. The average R1 response rates during the pre-S1 period in the first session of acquisition for groups R2 Extinction, R3 Extinction, and Handle were 3.98,

4.06, and 4.19; in the final session they were 6.32, 6.43, and 6.38, respectively. The average R2 response rates during the pre-S1 period in the first session for these three groups were 3.91, 3.50, and 1.84, and in the final session were 4.43, 5.88, and 2.44, respectively. Finally, the average R3 response rates during the pre-S1 period in the first session for the three groups were 4.39, 4.18, and 3.33, and in the final session were 5.08, 4.10, and 3.35. For all Pre-S rates, a Group (3) x Response (3) x Session (8) ANOVA showed a significant effect of session, $F(7, 147) = 6.10$, $MSE = 35.52$, $p < .01$, as well as a significant Response x Session interaction, $F(14, 294) = 2.17$, $MSE = 9.59$, $p = .01$, with no other main effects or interactions (highest $F = 1.67$). The significant interaction reflects the fact that there were increasingly higher rates from R1 to R3 and across acquisition sessions.

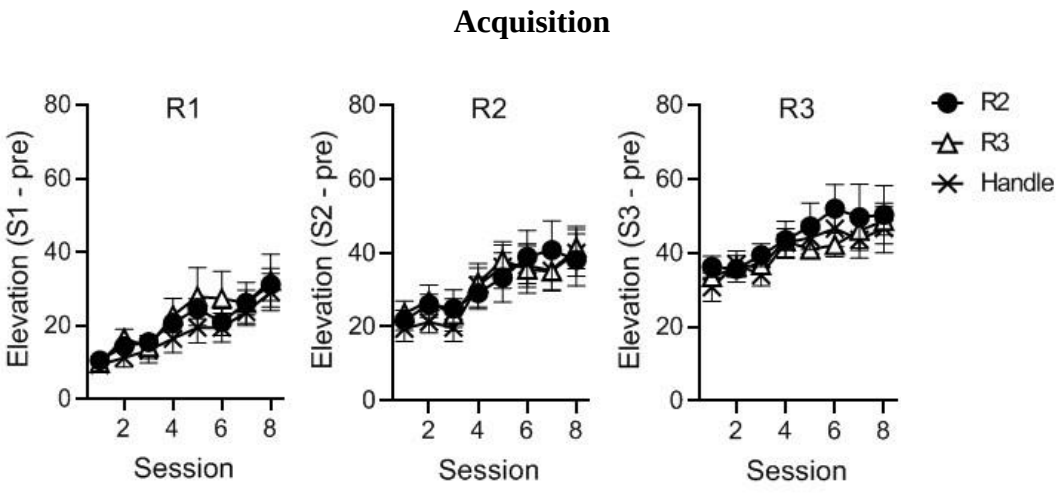

Figure 1. Elevation scores for R1, R2, and R3 during acquisition of the chain in each group of Experiment 1. Error bars represent the standard errors of the means.

Extinction

The results of the extinction phase are presented in Figure 2. The two extinction groups (R2 Extinction and R3 Extinction) decreased their responding within each session and over the three sessions of extinction. A Group (R2 Extinction vs. R3 Extinction) x Session (3) x Trial Block (7) ANOVA confirmed these observations, with significant effects of session, $F(2, 42) = 37.21$, $MSE = 2960.93$, $p < .01$, and trial block, $F(6, 252) = 48.25$, $MSE = 1402.27$, $p < .01$, as well as a Session x Block interaction, $F(12, 252) = 8.41$, $MSE = 244.53$, $p < .01$. There were also significant effects of group, $F(1, 42) = 7.06$, $MSE = 561.96$, $p = .01$, as well as significant interactions between Block x Group, $F(6, 252) = 5.05$, $MSE = 146.85$, $p < .01$, Group x Session, $F(2, 42) = 3.41$, $MSE = 271.32$, $p = .042$, and Block x Group x Session, $F(12, 252) = 2.78$, $MSE = 80.74$, $p = .001$. The effects involving the Group factor confirm that R3 was emitted at a higher rate than R2, consistent with what was observed in acquisition.

Figure 3 describes the levels of responding (elevation scores) of the other available responses in the 10-s period after each S terminated on the extinction trials. These scores were initially negative because the rats tended to persist on the extinguishing response (i.e., R2 or R3) after each trial, and this presumably suppressed performance of the other behaviors relative to the pre-S baseline. The scores clearly suggest that presentation of S2 and S3 did not evoke behaviors other than R2 and R3 (respectively) during the extinction phase.

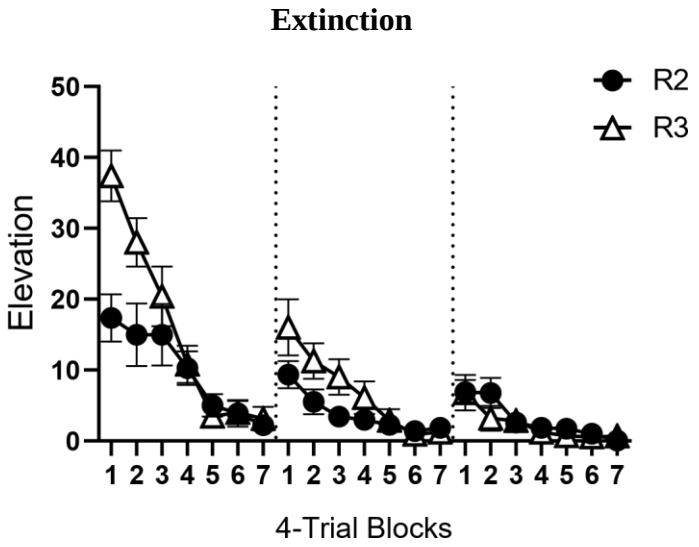

Figure 2. Elevation scores of R2 and R3 extinction groups in four-trial blocks across sessions of extinction of Experiment 1. Error bars represent the standard errors of the means.

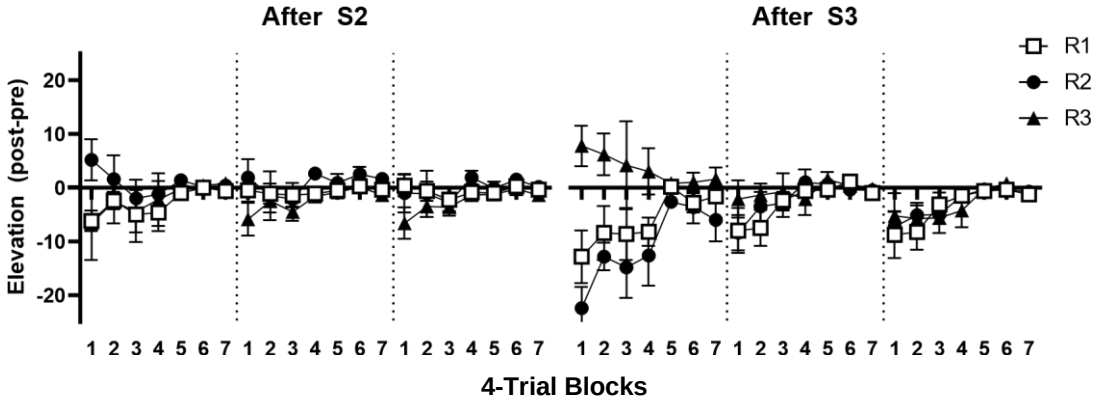

Figure 3. Elevation scores (post – pre S) of all available responses during extinction in Experiment 1. Error bars represent the standard errors of the means.

Test

The results of the R1 test are illustrated in Figure 4. Visually, Group R2 Extinction made fewer R1 responses than either Group R3 Extinction or Group Handle. These observations were supported by a Group (3) x Trial Block (7) ANOVA, which revealed significant effects of group, $F(2, 21) = 3.83$, $MSE = 641.45$, $p = .038$, and trial block, $F(6, 126) = 7.21$, $MSE = 511.35$, $p < .01$, with no interaction, $F(12, 126) = 1.57$, $MSE = 111.06$, $p = .11$. Separate planned analyses were conducted to compare each pair of groups with Group (2) x Block (7) ANOVAs. Group R2 Extinction had a lower rate of responding than Group Handle over the test session, $F(1, 14) = 5.11$, $MSE = 1046.91$, $p = .04$, and R1 responding decreased over blocks, $F(6, 84) = 2.67$, $MSE = 154.18$, $p = .02$, with no interaction between the two factors ($F < 1$). Group R2 also had a lower rate of R1 responding than Group R3 Extinction over the test session, $F(1, 14) = 15.15$, $MSE = 869.18$, $p = .002$, and R1 responding in both groups decreased over blocks, $F(6, 84) = 7.47$, $MSE = 401.20$, $p < .001$, with a significant interaction, $F(6, 84) = 3.13$, $MSE = 167.81$, $p = .008$. Lastly, there was no difference in R1 responding between Groups R3 Extinction and Handle, as evidenced by no main effect of group and no interaction (Fs < 1). Overall, the results suggest that extinction of R2 was more successful at suppressing R1 than extinction of R3 or Handling alone.

Test

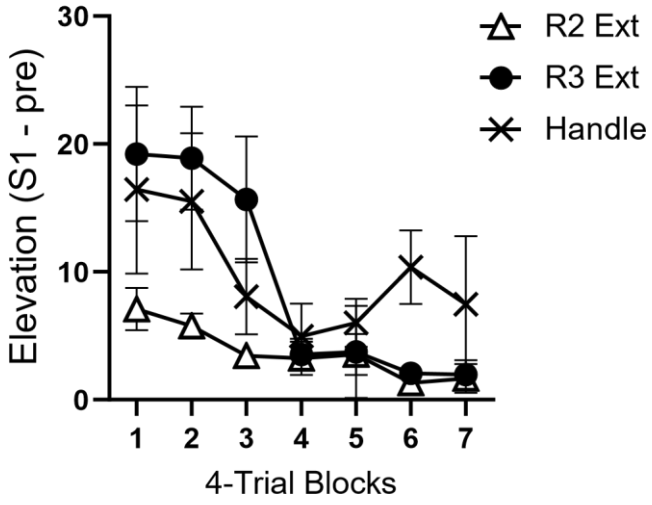

Figure 4. R1 response rate elevation scores across blocks of five S1 presentations during the test phase of Experiment 1. Error bars represent the standard errors of the means.

2.4 Discussion

Rats acquired the discriminated heterogeneous three-response chain and learned to make the appropriate responses in S1, S2, and S3 over eight sessions of training. Extinction of R2 then weakened the performance of R1, while extinction of R3 had no effect. As noted earlier, a previous study (Thrailkill & Bouton, 2016) had shown related results in which extinction of R2 decreased R1, but differed critically in that it utilized a two-response chain. The present results are thus the first to investigate the effects of R2 and R3 on R1 responding, and therefore the first to indicate that extinction of the "nearer" response (R2) had more effect than response after that (R3). This is consistent with the idea that the goal of R1 is the next response in the chain, and not the response that ultimately results in the primary reinforcer. Additionally, the fact that extinction of R3 had no impact on R1 rules out nonspecific effects of extinction that might suppress

R1, such as a general frustration effect, or movement of the rat away from the front panel of the chamber where all response manipulanda were located. Instead, the results suggest that R1 was specifically sensitive to extinction of the response that immediately followed it.

CHAPTER 3: EXPERIMENT 2: TARGETING R2

3.1 Introduction

The goal of Experiment 2 was to target R2 (see Table 1). Recall that the results of Thrailkill and Bouton (2015, 2016) indicate that the strength of a target response can be weakened by extinguishing either the preceding or the following response in a two-response chain. In the current experiment, we explore which effect is stronger in a three-response chain. Rats acquired a chain similar to Experiment 1, differing only in that S2:R2, instead of S1:R1, consisted of the tone setting the occasion for nose-poke. Following acquisition, rats received extinction sessions consisting of either R1 extinction or R3 extinction. Once the animals stopped performing R1 or R3, the rats all received a test with S2 and R2 in extinction. Results of Thrailkill and Bouton (2015, 2016) led us to expect that extinction of either the preceding (R1) or following (R3) response might weaken the target response (R2). The use of a three-link chain, however, allowed us to compare the two effects directly.

3.2 Methods

Subjects and Apparatus

Twenty-four naïve female Wistar rats were purchased from same supplier and maintained under the same conditions as in Experiment 1. The apparatus consisted of the same conditioning chambers used in Experiment 1.

Procedure

Food restriction began one week prior to the beginning of training. During training, one session was conducted seven days a week at approximately the same time

each day. Animals were handled each day and maintained at their target weight with supplemental feeding.

Acquisition

The acquisition procedure was the same as that of Experiment 1, with only a difference in arrangement of stimuli and responses. Here, S1:R1 consisted of panel light and either lever press or chain pull (counterbalanced), S2:R2 was tone and nose poke for all rats, and S3:R3 was panel light and chain pull or lever press.

Extinction

Once acquisition was completed, rats were randomly assigned to one of three groups: Group R1 Extinction (n=8), Group R3 Extinction (n=8), or Group Handle (n=8). Similar to Experiment 1, during each of the next three daily sessions Group R1 Extinction was presented with 30 trials of S1. Making the R1 response terminated S1 on an RR4 schedule, but was not followed by S2 or any other event. Group R3 Extinction was similarly presented with 30 trials of S3. Making the R3 response terminated S3 on an RR4 schedule, but was not followed by a food pellet. All response manipulanda were available during extinction. The rats in Group Handle received no extinction but were handled in an equivalent manner to the other groups.

R2 Test

All rats then received a final test session in which all response manipulanda were present. There were 30 S2 test presentations, separated by a 45-s variable ITI. Responses on the R2 manipulandum during S2 turned off the stimulus tone according to RR4, but did not turn on S3. Trials otherwise ended with S2 terminating after 20 s.

3.3 Results

Acquisition

All rats learned to perform the three-response chain during the acquisition phase. The acquisition of the full chain for each group is illustrated in Figure 5. Responding increased over sessions, with response rates highest for R2 (nose poke). Elevation scores for all responses were compared in a Response (3) x Session (8) ANOVA. There was a significant effect of session, $F(7, 483) = 55.18$, $MSE = 4436.90$, $p < .01$, as well as response, $F(1, 69) = 47.62$, $MSE = 96{,}616.09$, $p < .01$, with a significant interaction, $F(14, 483) = 12.90$, $MSE = 1037.15$, $p < .01$. Two Response (2; R1 vs R2 or R3 vs R2) x Session (8) ANOVAs were completed to explore the previous interaction. Results comparing R1 and R2 revealed significant effects of session, $F(7, 322) = 51.06$, $MSE = 4599.65$, $p < .01$ and response, $F(1, 46) = 81.62$, $MSE = 171{,}157.20$, $p < .01$, as well as a significant response x session interaction, $F(7, 322) = 16.81$, $MSE = 1514.38$, $p < .01$. Results comparing R2 and R3 revealed significant effects of session, $F(7, 322) = 43.81$, $MSE = 4492.93$, $p < .01$, as well as a response x session interaction, $F(7, 322) = 15.45$, $MSE = 1584.73$, $p < .01$, with no effect of response ($F = 2.20$).

Groups were also compared in a Group (3) x Session (8) ANOVA for each response in the chain. There was a significant effect of session for R1, $F(7, 147) = 12.02$, $MSE = 433.54$, $p < .01$, and no group differences or interactions, $Fs < 1$. The same analysis for R2 response elevation scores revealed a significant effect of session, $F(7, 147) = 37.99$, $MSE = 5680.48$, $p < .01$, and no group differences or interactions, $Fs < 1$. A final ANOVA for R3 elevation scores showed another significant effect of session,

$F(7, 147) = 6.21$, $MSE = 397.18$, $p < .01$, and no group differences or interactions, $Fs < 1$. The results simply confirm that the groups learned and responded similarly before entering the crucial extinction phase.

We then compared response rates during the Pre-S1 period for all three responses. The average R1 response rates during the pre-S1 period in the first session of acquisition for groups R1 Extinction, R3 Extinction, and Handle were 12.58, 11.44, and 15.12, while in the final session they were 15.11, 12.98, and 18.13, respectively. The average R2 response rates during the pre-S1 period in the first session for these three groups were 2.83, 5.14, and 3.47, and in the final session were 2.31, 2.95, and 1.80, respectively. Finally, the average R3 response rates during the pre-S1 period in the first session for the three groups were 1.04, 1.44, and 1.06, and in the final session were 0.53, 0.44, and 0.60. For all Pre-S rates, a Group (3) x Response (3) x Session (8) ANOVA showed a significant effect of session, $F(7, 147) = 3.92$, $MSE = 16.06$, $p = .001$, response, $F(2, 42) = 98.11$, $MSE = 9957.73$, $p < .01$, as well as a significant Response x Session interaction, $F(14, 294) = 8.57$, $MSE = 33.33$, $p < .01$, with no other main effects or interactions (highest $F = 1.27$).

Acquisition

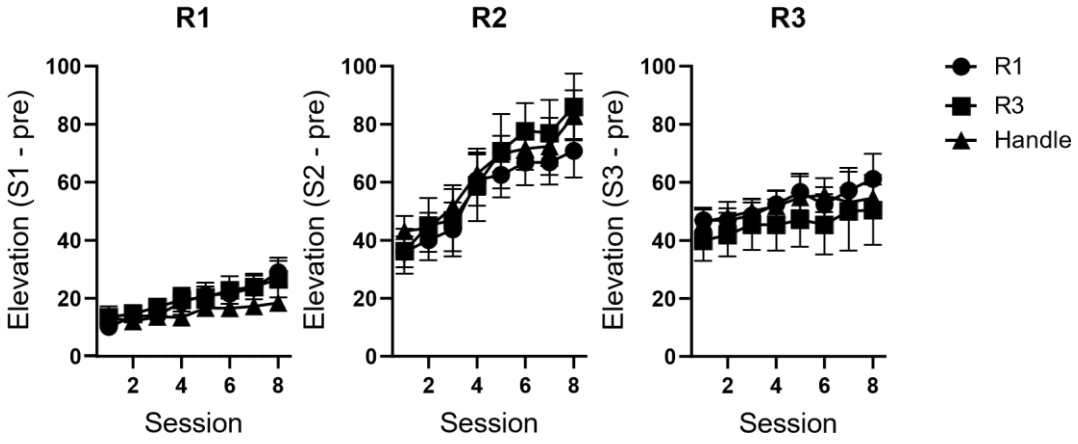

Figure 5. Elevation scores during acquisition of R1, R2, and R3 in each group of Experiment 2. Error bars represent the standard errors of the means.

Extinction

The results of the extinction phase are presented in Figure 6. The two extinction groups (R1 Extinction and R3 Extinction) decreased their responding within each session and over the three sessions of extinction. A Group (R1 Extinction vs. R3 Extinction) x Session (3) x Trial Block (7) ANOVA confirmed these observations, with significant effects of session, $F(2, 42) = 26.45$, $MSE = 7901.82$, $p < .01$, and trial block, $F(6, 252) = 54.48$, $MSE = 4169.33$, $p < .01$, as well as a Session x Block interaction, $F(12, 252) = 4.82$, $MSE = 368.65$, $p < .01$. There was also a significant effect of group, $F(1, 42) = 5.19$, $MSE = 1549.58$, $p = .028$, with no other significant interactions (Fs < 2). The group effect is due to Group R1 Extinction responding more than Group R3 Extinction, possibly due to extinction conditions being more similar to acquisition conditions for R1 than R3.

Figure 7 depicts the level of the other available responses (as elevation scores) during the 10-s period following the extinction trials of the extinction phase. Once again, the non-zero elevation scores of the alternative responses were negative, suggesting suppression to the baseline (pre-S) period, perhaps because of competition created by some persistence of the extinguishing response.

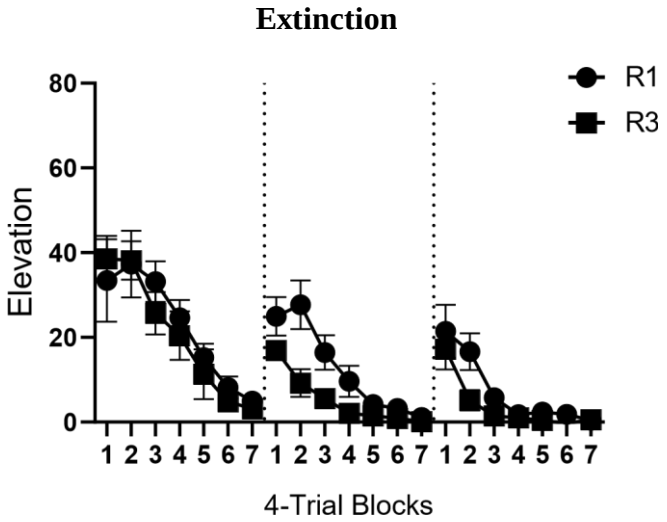

Figure 6. Elevation scores of R1 and R3 extinction groups in 5-trial blocks across sessions of extinction in Experiment 2. Error bars represent the standard errors of the means.

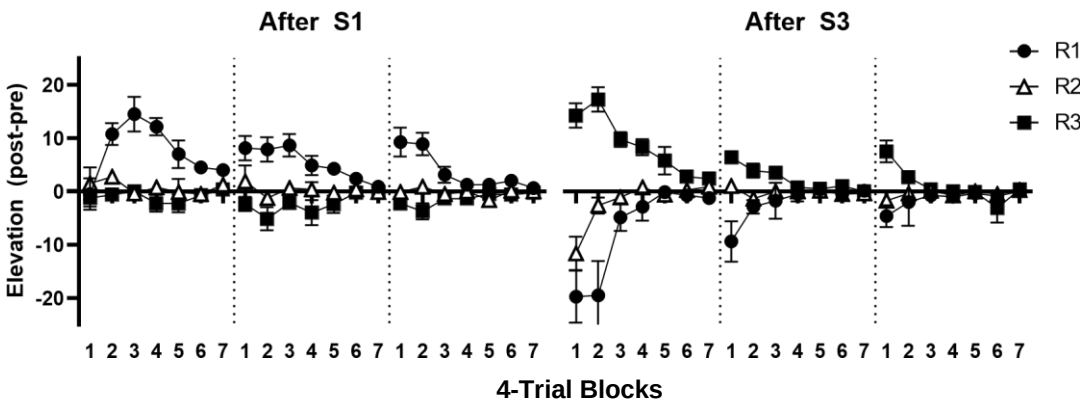

Figure 7. Elevation scores (post – pre S) of all responses available during the 10-s period after the extinction trials in Experiment 2. Error bars represent the standard errors of the means.

Test

The results of the R2 test are illustrated in Figure 8. Visually, both Group R1 and Group R3 Extinction had lower R2 responding than the Handle control, a pattern that was especially noticeable in the fourth block. These observations were supported by a Group (3) x Trial Block (7) ANOVA, which revealed significant effects of group, $F(2, 21) = 4.82$, $MSE = 1132.04$, $p = .019$, and trial block, $F(6, 126) = 15.26$, $MSE = 1510.04$, $p < .01$, with no interaction ($F < 1$). Separate planned analyses were conducted to compare each pair of groups with Group (2) x Block (7) ANOVAs. There were no significant differences in responding over the test session between Groups R1 and R3 Extinction, $F(1, 14) = .965$, $MSE = 58.41$, $p = .343$, and no Block x Group interaction, $F < 1$. Group R1 Extinction had a lower rate of responding than Group Handle over the test session, $F(1, 14) = 4.13$, $MSE = 1358.01$, $p = .062$, and R2 responding decreased over blocks, $F(6, 84) = 7.70$, $MSE = 981.39$, $p < .01$, with no interaction between the two, $F <$

1. Group R3 Extinction also had a lower rate of R2 responding than Group Handle throughout the test session, $F(1, 14) = 6.28$, $MSE = 1979.70$, $p = .025$, and R2 responding in both groups decreased over blocks, $F(6, 84) = 10.50$, $MSE = 1070.22$, $p < .001$, with no interaction, $F(6, 84) = 1.41$, $MSE = 143.56$, $p = .221$. Overall, the results suggest that extinction of R1 and R3 were both successful at suppressing R2 responding.

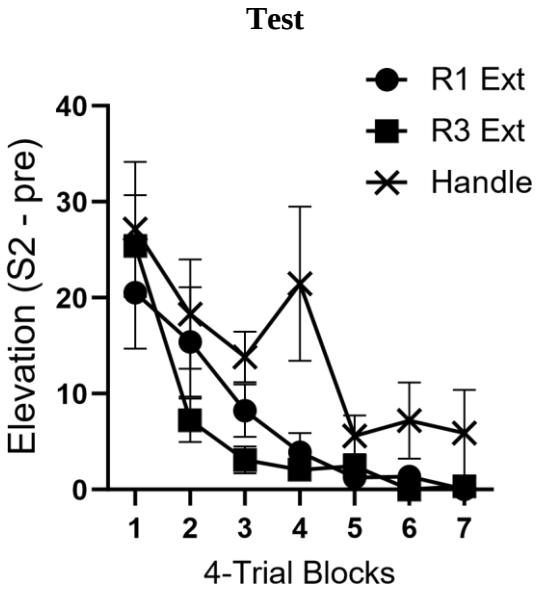

Figure 8. R2 response rate elevation scores during the test phase of Experiment 2. Error bars represent the standard errors of the means.

3.4 Discussion

Rats again acquired the discriminated heterogeneous three-response chain and learned to make the appropriate responses in S1, S2, and S3. Extinction of both R1 and R3 weakened the performance of R2. This result is consistent with both of Thrailkill and Bouton's findings indicating that extinction of either the preceding or following response weakened the target response in a two-response chain (2015, 2016). Notice that the fact that presentations of S1 did not generate R2 responding (see Figure 7) rules out the

possibility that presentation of S1 (and emitting R1) caused direct extinction of R2 by promoting unreinforced performance of it. Critically, the current experiment also allowed us to test and compare the effects of extinguishing both preceding and following responses in the same procedure. The results support the idea that the adjacent responses in a three-response chain are equally important, but one is not particularly special compared to the other.

CHAPTER 4: EXPERIMENT 3: TARGETING R3

4.1 Introduction

The goal of Experiment 3 was to target R3 and compare the effects of extinction of R1 or R2 on that response (see Table 1). Rats acquired a three-response chain similar to Experiments 1 and 2, except that S3:R3 was now the tone setting the occasion for nose-poke (R1 and R2 were counterbalanced between lever press and chain pull). Following chain acquisition, rats received extinction sessions consisting of either R1 extinction or R2 extinction. Once the animals stopped performing R1 or R2, the rats all received a test with S3 and R3 in extinction. Since R2 immediately precedes R3, we could see an adjacency effect with extinction of R2 having a greater effect than extinction of R1. On the other hand, because R1 is the "lead" response in the chain, it is possible that extinction of R1 might have an especially powerful effect on subsequent responses. Notice that these possibilities are confounded in the two-response chain.

4.2 Methods

Subjects and Apparatus

Twenty-four naïve female Wistar rats were purchased from same supplier and maintained under the same conditions as in Experiments 1 and 2. The apparatus consisted of the same conditioning chambers used in Experiment 1 and 2.

Procedure

Food restriction began one week prior to the beginning of training. During training, one session was conducted seven days a week at approximately the same time each day. Animals were handled each day and maintained at their target weight with supplemental feeding.

Acquisition

This procedure was consistent with Experiments 1 and 2, with only a difference in arrangement of stimuli and responses: S1:R1 and S2:R2 both consisted of a panel light and either lever press or chain pull, followed by S3:R3 tone and nose poke.

Extinction

Once acquisition was completed, rats were randomly assigned to one of three groups: Group R1 Extinction, Group R2 Extinction, or Group Handle. Similar procedurally to Experiments 1 and 2, during each of the next three daily sessions, Group R1 Extinction was presented with 30 trials of S1 and Group R2 Extinction was similarly presented with 30 trials of S2. The rats in Group Handle received no extinction, but were handled in an equivalent manner to the other groups.

R3 Test

All rats then received a final test session in which all response manipulanda were present. There were 30 S3 test presentations, separated by a 45-s variable ITI. Responses on the R3 manipulandum during S3 turned off the stimulus tone according to RR4, but did not turn on S3. Trials otherwise ended with S2 terminating after 20 s.

4.3 Results

One rat assigned to Group Handle was lost due to sudden illness, and another assigned to Group R1 Extinction failed to acquire the three-response chain. Data of both rats were therefore excluded from the analyses, leaving *n*'s of 7, 7, and 8 for Groups Handle, R1 Extinction, and R2 Extinction, respectively.

Acquisition

The acquisition of the full chain for each group is illustrated in Figure 9. Responding increased over sessions, and there was a clear pattern of increasing response rates from R1 to R2 to R3. Elevation scores for all responses were compared in a Response (3) x Session (8) ANOVA. There was a significant effect of session, $F(7, 462) = 67.01$, $MSE = 4236.47$, $p < .01$, as well as response, $F(2, 66) = 129.57$, $MSE = 70{,}274.06$, $p < .01$, with a significant interaction, $F(14, 462) = 17.92$, $MSE = 1132.82$, $p < .01$.

Groups were also compared in a Group (3) x Session (8) ANOVA for each response in the chain. There was a significant effect of session for R1, $F(7, 140) = 13.70$, $MSE = 224.43$, $p < .01$, and no group differences or interactions, $Fs < 1.5$. The same analysis for R2 response elevation scores revealed a significant effect of session, $F(7, 140) = 14.95$, $MSE = 541.17$, $p < .01$, and no group differences or interactions, $Fs < 1$. A final ANOVA for R3 elevation scores showed another significant effect of session, $F(7, 140) = 39.64$, $MSE = 5735.23$, $p < .01$, and no group differences or interactions, $Fs < 1$. The results simply confirm that the groups learned and responded similarly before entering the crucial extinction phase.

We then compared response rates during the Pre-S1 period for all three responses. The average R1 response rates during the pre-S1 period in the first session of acquisition for groups R1 Extinction, R2 Extinction, and Handle were 5.98, 5.86, and 5.35, while in the final session they were 12.03, 7.63, and 7.12, respectively. The average R2 response rates during the pre-S1 period in the first session for these three groups were

2.64, 3.83, and 3.20, and in the final session were 2.20, 2.23, and 2.54, respectively. Finally, the average R3 response rates during the pre-S1 period in the first session for the three groups were 3.56, 1.21, and 3.13, and in the final session were 1.02, 1.64, and 1.32. For all Pre-S rates, a Group (3) x Response (3) x Session (8) ANOVA showed a significant effect of session, $F(7, 133) = 2.66$, $MSE = 12.79$, $p = .013$, response, $F(2, 38) = 34.65$, $MSE = 1809.84$, $p < .01$, as well as a significant Response x Session interaction, $F(14, 266) = 4.46$, $MSE = 17.24$, $p < .01$, with no other main effects or interactions (highest $F = 1.40$).

Acquisition

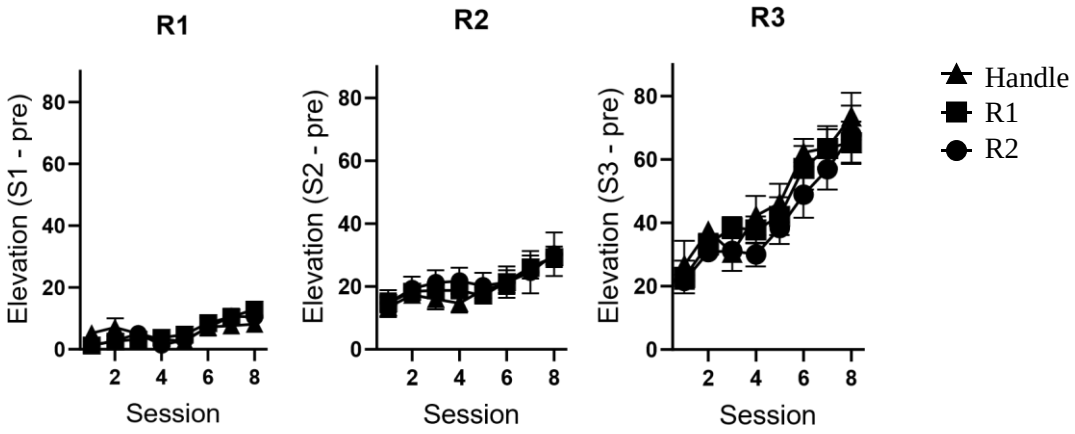

Figure 9. Elevation scores during acquisition of R1, R2, and R3 in each group of Experiment 3. Error bars represent the standard errors of the means.

Extinction

The main results of the extinction phase are presented in Figure 10. The two extinction groups (R1 Extinction and R2 Extinction) decreased their responding within each session and over the three sessions of extinction. A Group (R1 Extinction vs. R2 Extinction) x Session (3) x Trial Block (7) ANOVA confirmed these observations, with

significant effects of session, $F(2, 42) = 28.48$, $MSE = 2196.49$, $p < .01$, and trial block, $F(6, 252) = 31.60$, $MSE = 1140.29$, $p < .01$, as well as a Session x Block interaction, $F(12, 252) = 3.42$, $MSE = 123.37$, $p < .01$. The effects of group, as well as all other interactions, did not reach significance.

Figure 11 also depicts the level of responding for the alternative responses (in elevation scores) in the 10-s period following each extinction trial. As in the other experiments, the alternate response scores were close to or below zero throughout, suggesting that there was very little responding on the alternative manipulanda during extinction.

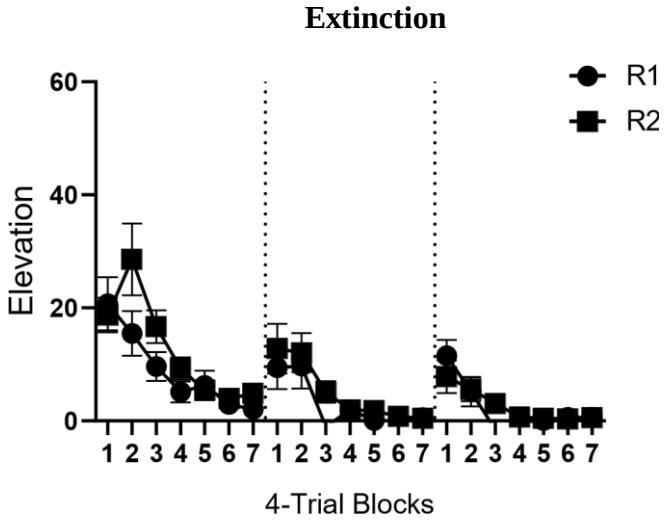

Figure 10. Elevation scores of R1 and R2 extinction groups during extinction in Experiment 3. Error bars represent the standard errors of the means.

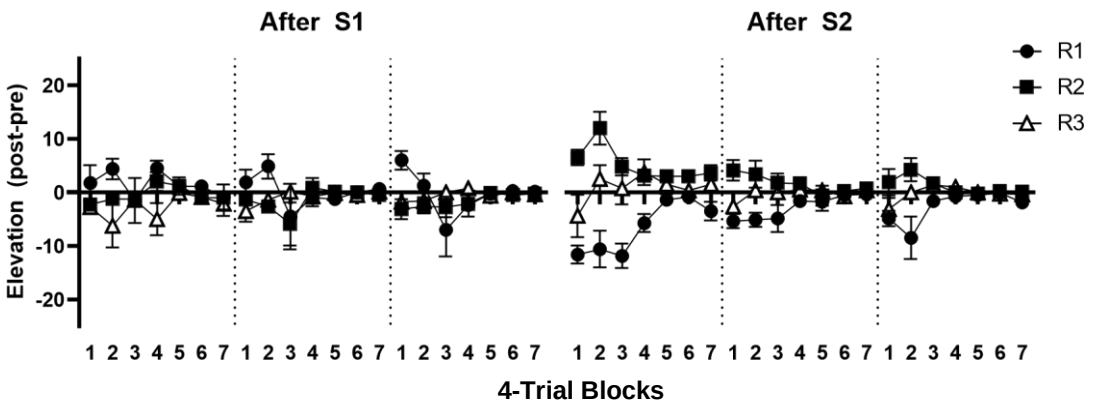

Figure 11. Elevation scores (post – pre S) of all available response manipulanda during extinction in Experiment 3. Error bars represent the standard errors of the means.

Test

The results of the final R3 test are illustrated in Figure 12. Visually, extinction of R2 had the greatest effect on R3 responding, especially after the first block. A Group (3) x Trial Block (7) ANOVA, revealed significant effects of trial block, $F(6, 114) = 21.19$, $MSE = 2401.20$, $p < .01$, with a significant group x trial interaction, $F(12, 114) = 1.99$, $MSE = 225.09$, $p = .032$, but a nonsignificant group effect, $F(2, 19) = 2.48$, $MSE = 1098.51$, $p = .11$. Separate planned analyses were conducted to compare each pair of groups with Group (2) x Block (7) ANOVAs. Responding over the test session in Group R1 Extinction did not differ from Group Handle, $Fs < 1$. However, Group R2 Extinction trended toward a lower rate of R3 responding than Group Handle over the entire test session, $F(1, 13) = 4.25$, $MSE = 2176.37$, $p = .060$. R3 responding in both groups decreased over blocks, $F(6, 78) = 20.14$, $MSE = 1873.87$, $p < .001$, and there was a significant interaction indicating a more rapid loss of responding in Group R2 Extinction, $F(6, 78) = 3.69$, $MSE = 343.36$, $p = .003$. Lastly, R3 responding between Groups R1 and

R2 Extinction approached significance with Group R2 Extinction responding at a lower rate than Group R1 Extinction, $F(1, 13) = 3.42$, $MSE = 665.12$, $p = .087$, with no block effect or interaction (Fs < 1). Overall, the results suggest that extinction of R2 was more successful at suppressing R3 than extinction of R1 or Handling alone.

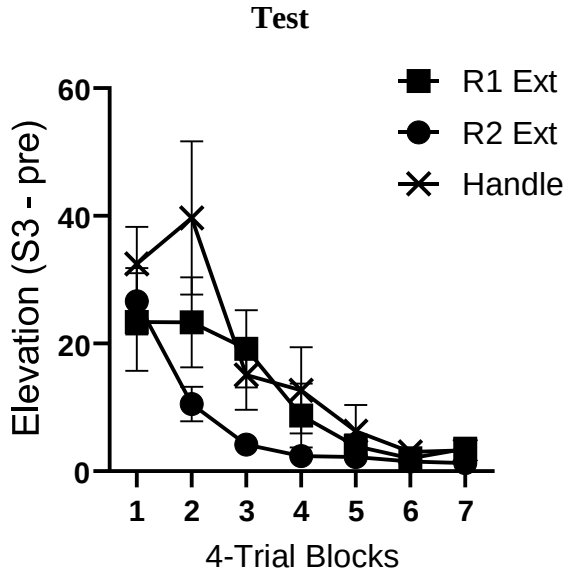

Figure 12. R3 response rate elevation scores during testing in Experiment 3. Error bars represent the standard errors of the means.

4.4 Discussion

Rats again acquired the discriminated heterogeneous three-response chain and learned to make the appropriate responses in S1, S2, and S3. Extinction of R2 then had a greater effect on the performance of R3 compared to extinction of R1. It is important to note that extinction of R2 had an effect on R3 even though there was very little R3 responding in extinction. Thus, the presentation of S2 (and performance of R2) did not weaken R3 because it caused the rat to perform that response and made it available for direct extinction. The results support the results of Thrailkill and Bouton (2015), where extinction of the immediately preceding response decreases the following response,

whether or not the target response was available in extinction. They also continue to suggest evidence of an adjacency effect.

CHAPTER 5: GENERAL DISCUSSION

The present series of experiments further characterize the effects of extinction and the learned associative structure that underlies discriminated instrumental chains. In all three experiments, rats learned to perform a chain or sequence of behaviors in which separate SDs set the occasion for three different responses in order to earn a primary reinforcer. Results from the three experiments clearly demonstrated that 1.) extinction of R2 weakens R1, 2.) extinction of R1 and R3 equally weaken R2, and 3.) extinction of R2 weakens R3 more than extinction of R1. These results support the idea of an adjacency effect in discriminated three-response chains, where importance is given to immediately preceding and following responses in supporting a target response instead of use of a psychological representation of the chain as a whole.

Given earlier studies of two-response chains, it was also possible that the first response in the chain, or the last response in the chain, may have special status, such that the first response acts as a "launch" into the chain itself and the last response leads to the primary reinforcer. However, the current findings suggest there is nothing particularly special about these responses and instead underscore the importance of adjacent responses in the chain. For example in Experiment 1, R3 extinction was not as effective as R2 extinction, and in Experiment 2 it was no better than extinction of R1. In Experiment 2, R1 extinction was likewise no better than R3, and in Experiment 3 it was inferior to R2. We can conclude, then, that R2 is important for R1, both R1 and R3 are important for R2, and R2 is important for R3. While the following response seems to be the "goal" of the target response, the preceding response may be just as important.

Expanding on this, the importance of the next response in the chain is straightforward to explain; it appears to be the goal of the target response, and such a setup can guide the rat through the entire chain. The importance of the preceding response is less straightforward; however, the evidence suggests this may be an instrumental example of mediated extinction. Mediated extinction has been studied primarily in Pavlovian paradigms, in which pairings of the CS and the US provide the CS with the ability to activate a representation, or memory, of the US (Holland, 1990; Holland & Wheeler, 2009). For example, Holland and Wheeler (2009) paired two auditory stimuli with two different reinforcing USs, then paired both outcomes with illness, therefore decreasing the value of those outcomes. Each rat then received extinction of one auditory stimulus. Since the auditory stimuli evoke a representation of the USs, a consumption test of both reinforcers revealed higher consumption of the US whose auditory CS was extinguished, as if the evoked representation was enough to extinguish the aversion (Holland and Wheeler, 2009). Results of the present Experiments 2 and 3, as well as those of Thrailkill and Bouton (2016) demonstrate the possibility of mediated extinction occurring in instrumental learning, such that making the preceding response in extinction leads to the hypothetical activation of a representation of the next response, thereby allowing the target response to undergo mediated extinction and suppress responding during the test. Note that the results of the extinction phases of Experiments 2 and 3 suggest that it is retrieval of a representation of the next response, rather than actual performance of that response, that yields extinction of the following response when the preceding response is extinguished, because there was no evidence that the target behavior was evoked during extinction.

The combined results also suggest that rats undergo something similar to "tunnel vision" in these chains; there is no evidence that they have learned or use a global representation of the entire chain, but rather enter the chaining process and perform according to immediately-adjacent responses. Something else that future research needs to consider is the importance of the primary reinforcer in three-response chains. While the effects of reinforcer devaluation suggest that the primary reinforcer is not the ultimate "goal" in a two-response chain (Thrailkill & Bouton, 2017), this idea has not been tested with a longer chain.

The results of these experiments provide information about how individuals may learn about each response in a chain of behaviors, how these responses are inter-associated, and how learned inhibition of each response can affect the other responses in the chain. This series of experiments provides new information that could be useful in application to addiction, clinical treatments, and positive real-life applications. For example, extinction-based treatments that inhibit earlier links in chained addiction behavior could reduce associated consumption or self-administration responses.

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