



## Determinants of instrumental extinction in terrestrial toads (*Bufo arenarum*)<sup>☆</sup>

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### Abstract

Previous research in a water-reinforced instrumental training situation with toads (*Bufo arenarum*) has shown that performance in both acquisition and extinction is poorer after partial, rather than continuous reinforcement training. In Experiment 1, the performance of a group receiving 24 trials on a 50% partial reinforcement schedule was poorer in acquisition and extinction than that of continuously reinforced groups matched for trials or reinforcements. However, partially reinforced toads extinguished at the same rapid rate as a continuously reinforced group that received training only on the days in which the partial toads received water reinforcement. In Experiment 2, extinction was faster after 10 reinforced acquisition trials than after 30 trials. This evidence suggests that the deleterious effects of partial reinforcement in toads can be explained by a combination of two factors, namely, the distribution of reinforced trials across days and the total number of reinforcements.

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Terrestrial toads such as *Bufo arenarum* have evolved a complex system for detecting and consuming water by absorption through a patch of ventral skin in the pelvic region

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(Christensen, 1974; Reboreda, Muzio, Viñas, & Segura, 1991). As in all amphibians, these toads are exposed to desiccation by water loss, so they are highly dependent on access to water on a daily basis for survival (Stebbins & Cohen, 1995). Toads rapidly learn to locate water in a straight runway, showing typical learning phenomena including acquisition, extinction, and spontaneous recovery across sessions, as well as the ability to improve water uptake across training trials (Muzio, Segura, & Papini, 1992).

A series of experiments has shown that such runway learning is affected by the consistency and magnitude of water reinforcement (Muzio et al., 1992, Muzio, Segura, & Papini, 1994; Papini, Muzio, & Segura, 1995). The present experiments concentrate on the effects of reinforcement consistency on acquisition and extinction and were designed to understand the following phenomenon. Toads exposed to a situation in which water is accessible in a random half of the trials, but inaccessible in the rest of the trials (called partial reinforcement, PR), display poorer acquisition performance and faster extinction than toads exposed to a situation in which water is always accessible (called continuous reinforcement, CR; Muzio et al., 1992, 1994). Analogous runway experiments with rats (e.g., Weinstock, 1954) and pigeons (e.g., Roberts, Bullock, & Bitterman, 1963) typically yield the opposite effect, that is, greater resistance to extinction after PR rather than CR. Since this phenomenon is called the partial reinforcement extinction effect (PREE), the toad version is referred to as a reversed PREE. The reversed PREE is not unique to toads; it occurs in analogous experiments with a variety of fish and reptilian species (for reviews, see Bitterman, 1975, 2000; Papini, 2003) and also with rats and pigeons under certain training conditions, such as in within-group experiments (e.g., Papini, Thomas, & McVicar, 2002).

What causes toads to extinguish instrumental behavior faster after PR than CR training? There are at least four possible answers to this question. *First, PR toads extinguish faster because they consume less water than CR toads.* Since water uptake is sensitive to experience in the situation, usually increasing as a function of trials, it seems possible that inconsistent reinforcement could disrupt such water uptake. A comparison of water uptake on reinforced trials showed, however, that PR and CR toads consumed about the same amount of water per trial (Muzio et al., 1992). Thus, this possibility can be safely discarded. *Second, PR toads extinguish faster because nonreinforced trials reduce the associative strength accrued on previous reinforced trials, thus resulting in a net loss relative to CR toads.* This account is consistent with the trial-by-trial effects of PR. Toads walked significantly faster the day after a reinforced trial than the day after a nonreinforced trial (Muzio et al., 1992, 1994). This phenomenon, called the reward following effect, seems to suggest that nonrewarded trials weaken the associative strength of the stimuli controlling instrumental behavior, much as reinforced trials are supposed to strengthen control of behavior (Hull, 1943; Thorndike, 1911). However, the reward following phenomenon does not offer unambiguous evidence for the weakening role of nonreinforcement, as will be shown next. *Third, PR toads extinguish faster than CR toads because the interreinforcement interval is twice as long.* Given the sequence of reinforced and nonreinforced trials used in these experiments, PR toads are usually reinforced every 48 h on average, whereas CR toads receive water reinforcement every 24 h. A longer interreinforcement interval may promote forgetting or weakening of the reinforcer representation (Delamater, 2004). According to this view, poorer acquisition performance during PR training is not a consequence of experience with nonreinforcement; rather, runway behavior deteriorates as a consequence of the increasing time (either because of decay or increasing memory interference) since the last water reinforcement episode. The present Experiment 1 tests this hypothesis by including a group receiving CR training, but with R trials spaced apart every 48 h on average. If faster

extinction in the PR condition is the result of a relatively longer interreinforcement interval, then toads trained under these conditions should extinguish at the same fast rate as a group administered conventional PR training. *Fourth, PR toads extinguish faster because they receive half the number of reinforcements that CR toads received during acquisition.* This follows from the fact that experiments comparing PR and CR training in toads have generally been designed such that the total number of acquisition trials is equated across groups (Muzio et al., 1992, 1994). It takes a minimum number of reinforced trials to develop stable runway performance; thus, it is plausible that lower acquisition and extinction performance may be the result of an insufficient number of reinforcements to generate a level of performance similar to that of CR animals. This issue is explored in the two experiments reported in this paper.

## Experiment 1

Experiment 1 was designed to provide answers to two questions. First, is the reversed PREE a function of the spacing of reinforced trials in the PR condition? The key comparison is between a group receiving PR training and one receiving CR training matched for the daily distribution of reinforced trials. If rapid extinction after PR training is the result of a long interreinforcement interval in acquisition (48 h on average), then these two groups should not differ in extinction rate. Moreover, the matched CR condition should extinguish faster than a CR group exposed to a shorter interreinforcement interval (24 h).

Second, is the reversed PREE a function of the total number of reinforced trials in the PR and CR conditions? The key comparison is between two CR conditions, one receiving 12 reinforced trials and the other receiving 24 reinforced trials. If the reversed PREE reflects different number of reinforcements, then the CR group receiving 12 reinforced trials should extinguish faster than the group trained with 24 reinforced trials. Moreover, the group receiving 12 reinforced trials should extinguish at the same rate as a partial reinforcement group also receiving 12 reinforced trials.

## Method

### Subjects

The subjects were 25 adult male toads (*B. arenarum*) captured in ponds around Buenos Aires, Argentina, and maintained in group cages with water during at least 2 weeks after arrival in the laboratory. The vivarium was kept at a constant temperature (21–23 °C) and humidity (48–52%), and under a 16:8 h cycle of light and dark periods (light from 03:00 to 19:00 h). Before the start of the experiment, toads were transferred to individual cages with freely available deionized water, also used as water reinforcement during training trials. At the start of training, toads were experimentally naive and their standard weights varied between 60.7 and 123.0 g. The standard weight is the weight of a hydrated toad with an empty urinary bladder (Ruibal, 1962).

### Apparatus

The runway was built with black Plexiglas and was divided into a start box (20 cm long), an alley (60 cm long), and a goal box (20 cm long). The unit was 12 cm wide and 20 cm high and was tilted 5°, so that an animal moved upward from the start to the goal box. This procedure was adopted to increase response effort (Muzio et al., 1994). Guillotine doors controlled the entrance to the alley from the start compartment and to the goal box from



start of each daily trial. Animals were trained in different orders every day, a procedure that resulted in a water deprivation time ranging between 14 and 15 h.

## Results and discussion

The top panel of Fig. 1 shows the performance of Groups P/24, C/12m, and C/12c on both acquisition and extinction of runway behavior. To plot an equal number of acquisition trials, only trials following a reinforcement were plotted for Group P/24 (trials 1, 2, 4, 5, 7, 9, 12, 15, 17, 19, 20, and 22). Acquisition seems to be faster in the two CR groups than in Group P/24, but a Group  $\times$  Trial analysis detected only significant decreases across trials,  $F(11, 176) = 18.46$ ,  $p < .001$ . The differences between groups and the group  $\times$  trial interaction failed to reach statistical significance,  $F_s < 1.05$ . Groups did not differ during the first extinction trial,  $F(2, 18) = 1.35$ ,  $p < .30$ ; post hoc pairwise comparisons with the LSD test also failed to detect any group difference,  $p_s > .05$ . Whereas these groups did not differ in acquisition and during the initial extinction trial, they did show differential extinction performance during the 7 trials as a whole. Extinction was analogous in the two groups, P/24 and C/12m, matched for the distribution of reinforcement across days and, in both cases, faster than the extinction performance of Group C/12c, which received a reinforced trial every day. A Group  $\times$  Trial analysis indicated a significant difference across groups,

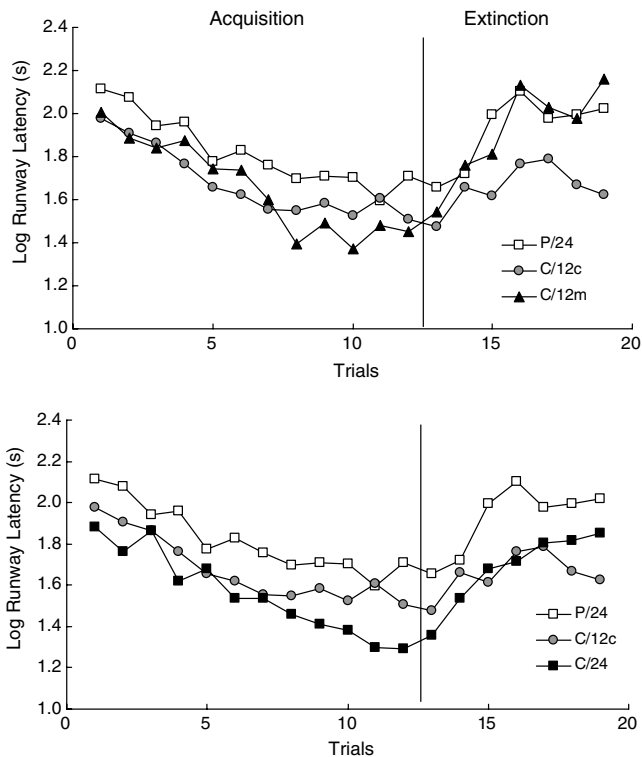


Fig. 1. The runway performance of triples of groups designed to determine whether the spacing of trials across days plays a role in the reversed PREE (top panel) or whether the absolute number of reinforced trials contributes to the reversed PREE (bottom panel).

$F(2,16)=3.79$ ,  $p<.05$ , and a significant extinction effect,  $F(6,96)=10.24$ ,  $p<.001$ , but a nonsignificant interaction,  $F(12,96)=1.31$ ,  $p<.30$ . Pairwise comparisons across groups with the LSD test indicated that, overall, latencies were lower in Group C/12c than in both Groups P/24 and C/12m,  $ps<.04$ ; the latter two groups did not differ from each other,  $p>.05$ . Therefore, the distribution of reinforced trials appears to be a major determinant of performance in toads, thus suggesting that the reversed PREE may not be as tightly connected to nonreinforced trials as heretofore thought.

The bottom panel of Fig. 1 shows the performance of Groups P/24, C/24, and C/12c, for both acquisition and extinction. Twelve trials were selected in Groups P/24 and C/24, so that all groups could be compared on an equal number of trials. The selected trials were those after reinforcement for Group P/24 and the equivalent trials for Group C/24 (trials 1, 2, 4, 5, 7, 9, 12, 15, 17, 19, 20, and 22). Acquisition replicates the differences between Groups P/24 and C/24 that were described in previous experiments (e.g., Muzio et al., 1992). Group C/12c performed at a level that was somewhat intermediate between the other two groups. A Group  $\times$  Trial analysis indicated, however, no differences across groups,  $F(2,16)=1.97$ ,  $p<.18$ , and no group  $\times$  trial interaction,  $F<1$ , but only a significant acquisition effect,  $F(11,176)=19.33$ ,  $p<.001$ . Groups did not differ in their performance during the first extinction trial,  $F(2,16)=2.75$ ,  $p<.10$ . Similarly, extinction performance was not statistically different among the three groups,  $F(2,16)=2.43$ ,  $p<.13$ , nor was there a significant group  $\times$  trial interaction,  $F(12,96)=1.12$ ,  $p<.36$ , but only a significant extinction effect,  $F(6,96)=9.16$ ,  $p<.001$ . Post hoc pairwise comparisons with the LSD test indicated that none of the groups differed from another group during extinction,  $ps>.05$ . It is obvious from the lower panel of Fig. 1 that Groups C/12 and C/24 displayed virtually identical extinction performance. This suggests that the difference in the number of reinforced trials does not contribute to the reversed PREE, at least under the current conditions of training.

Water uptake, expressed as grams gained per 100 g of weight (thus correcting for individual differences in body weight), was calculated for all groups after 10, 11, and 12 reinforced trials. The following means ( $\pm$ SEM) were obtained: 4.7 ( $\pm$ 1.0) for P/24, 6.7 ( $\pm$ 1.5) for C/24, 6.4 ( $\pm$ 0.5) for C/12c, and 5.5 ( $\pm$ 0.4) for C/12m. A one-way analysis of variance indicated nonsignificant differences,  $F<1$ . Furthermore, LSD pairwise post hoc tests failed to detect any differences among groups,  $ps>.05$ . A second analysis was calculated on the last 3 trials of training for Groups C/24 (trials 22–24) and C/12c (trials 10–12) to determine whether the amount reinforcement practice influenced water uptake. Mean uptake (SEM) was 6.0 (1.1) for Group C/24 and 6.4 (0.5) for Group C/12c, and the difference was not statistically significant,  $F<1$ . Thus, partial reinforcement (as in Group P/24), spaced continuous reinforcement (as in Group C/12m), or regular continuous reinforcement (as in Groups C/24 and C/12c) led to similar amounts of water uptake. Group differences cannot thus be attributed to differential magnitudes of water uptake.

## Experiment 2

The number of reinforced trials proved ineffective to account for the reversed PREE. However, an intriguing aspect of the previous experiment is the apparent crossing over of the functions corresponding to Groups C/24 and C/12 during the last two extinction trials. Such crossing over corresponds to a phenomenon known as the overlearning extinction effect (OEE). OEE occurs when animals receiving a greater amount of acquisition training actually extinguish faster than animals receiving a lower amount of

training (Ishida & Papini, 1997). Theoretically, the OEE has been related to the PREE and other learning effects involving transitions in reinforcement conditions (see, e.g., Amsel, 1992; Daly & Daly, 1982). Because the PREE and related effects do not appear in experiments with toads (Muzio et al., 1992, 1994; Papini et al., 1995; Schmajuk, Segura, & Ruidíaz, 1981), the potential presence of the spaced-trial OEE in toads would suggest a functional dissociation and point to different underlying mechanisms. Thus, the present experiment explored this issue by increasing the disparity in the amount of acquisition training and extending the number of extinction trials. Toads received 12 vs. 24 acquisition trials and seven extinction trials in Experiment 1, whereas they received 10 vs. 30 acquisition trials and 14 extinction trials in the present experiment. These changes in the training protocol were introduced to maximize the chances of observing an OEE.

Increased disparity in acquisition training would also help in determining whether the number of reinforced trials could contribute to a reversed PREE. Experiment 1 provided no evidence for an explanation of the reversed PREE in terms of the number of reinforced trials in acquisition when a 50% partial reinforcement schedule is used. However, a more lean partial reinforcement schedule could produce a difference in extinction performance that may be accounted for in terms of the total number of reinforced trials. The data from this experiment could provide evidence for this possibility in terms of a reversed OEE.

## *Methods*

### *Subjects and Apparatus*

We used 16 adult male toads (*B. arenarum*). Their standard weights varied between 82.1 and 164.5 g. The same runway described previously was used in the present experiment.

### *Procedure*

Toads received pretraining as described in Experiment 1. Animals were randomly assigned to one of two groups ( $n = 8$ ). Toads in Group 30 received a total of 30 reinforced acquisition trials, whereas those in Group 10 received a total of 10 reinforced acquisition trials. Each trial ended with a 300-s period of access to deionized water in the goal box. All the toads received 14 extinction trials similar in all respects to the acquisition trials except that the deionized water located in the goal box was inaccessible. A single trial per day was administered throughout the experiment. The two groups started training at the same time; because different numbers of acquisition trials were administered (30 vs. 10), the start of extinction occurred at different moments for each group. All other aspects of the procedure were as described in Experiment 1.

### *Results and discussion*

Fig. 2 shows the runway latencies of the two groups during acquisition and extinction. The performance of Group 10 is repeated twice in this figure, once so as to coincide with the start of Group 30's data and once so as to coincide with the end of Group 30's data. The former shows that the toads assigned to these two conditions learned the runway task at about the same speed. The latter shows that the ending performance of these groups seemed different. A Group  $\times$  Trial analysis comparing the last 10 trials of Group 30 with all the trials of Group 10 indicated significant effects for all the factors. Group 30 performed significantly below Group 10,  $F(1,14) = 7.37$ ,  $p < .02$ ; latencies decreased



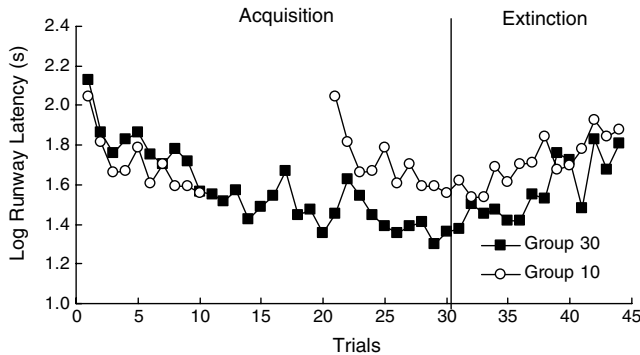


Fig. 2. Acquisition and extinction performance of groups receiving either 30 (Group 30) or 10 (Group 10) reinforced trials. The function for Group 10 is repeated twice so that its start or end coincides with those of Group 30.

significantly across trials,  $F(9,126)=4.58$ ,  $p<.001$ ; and the decrease was significantly greater for Group 10 than for Group 30,  $F(9,126)=2.01$ ,  $p<.05$ .

Extinction yielded no evidence of the OEE. Toads in Group 30 traversed the runway faster than those in Group 10, at least during the initial extinction trials. A Group  $\times$  Trial analysis covering all extinction trials indicated that only the extinction effect was significant,  $F(13,182)=6.33$ ,  $p<.001$ . Nonsignificant effects were obtained across groups,  $F(1,14)=2.78$ ,  $p<.12$ , and for the group  $\times$  trial interaction,  $F(13,182)=1.53$ ,  $p<.12$ . Thus, overall, there was no evidence of a crossing-over of extinction functions that would indicate the presence of an OEE. Because extinction performance was maximally differentiated during the initial 8 trials, a subsequent analysis was calculated on just these trials. The analysis showed that Group 30 performed significantly below Group 10 during the initial 8 extinction trials,  $F(1,14)=5.16$ ,  $p<.04$ . There was also a significant extinction effect,  $F(7,98)=2.35$ ,  $p<.03$ , but the interaction was nonsignificant,  $F(7,98)=1.17$ ,  $p<.33$ .

Water uptake recorded in the last 3 acquisition trials (trials 28–30 for Group 30 and 8–10 for Group 10) indicated differential amounts of reinforcement. Thus, the mean (SEM) for Group 30 was 2.0 (0.2), whereas the mean for Group 10 was 1.3 (0.1). The difference was statistically significant,  $F(1,14)=7.34$ ,  $p<.02$ .

As a whole, these data suggest that the absolute number of reinforcements during acquisition can potentially contribute to the reversed PREE when one group received at least three times more reinforced trials than the other. The underlying mechanism appears to be related to the increased efficiency in water uptake that occurs across reinforced trials.

## General discussion

The results reported in these two experiments provide a new view of the determinants of extinction in toads. Earlier research had shown that PR training retards acquisition and leads to faster extinction compared to CR training (Muzio et al., 1992, 1994). This effect, labeled a reversed PREE, was interpreted as providing evidence for the classic Thorndikian and Hullian assumption that reinforcement strengthens instrumental responses while nonreinforcement weakens them (see Papini, 2002). The key postulate that the present results bring into question is the weakening side of this classic learning mechanism. Two experiments were designed to test the role of two acquisition factors on the reversed PREE:



the spacing of reinforcements across days and the absolute number of reinforcements before extinction.

As shown in Experiment 1, toads receiving CR training that matches the distribution across days of reinforced trials with that of the PR condition exhibited essentially the same extinction rate. The implication is that nonreinforced trials in the PR condition have no measurable effects on extinction. Of course, this finding also questions the role of nonreinforcement in extinction, suggesting that it is not nonreinforcement per se that causes behavior to extinguish, but the progressive remoteness of the last reinforced trials. Rate expectancy theory (Gallistel & Gibbon, 2000) also assumes that the time intervals in the presence of the signal and between reinforcers is an important determinant of the PREE. Although this theory was designed for conditions involving multiple trials per session, a direct application to the current conditions fails to predict the key result in Experiment 1. Rate expectancy theory still predicts a PREE in a comparison between Groups P/24 and C/12m because the former has twice as much exposure to the discriminative stimulus as the latter, while both groups are exposed to the same reinforcement rate. We suggest, instead, that the encoding of the critical associations renders them labile and prone to decay in time. The spacing of reinforcement can thus be viewed as weakening the ability of the relevant stimuli to control the instrumental response by a process akin to forgetting. This forgetting hypothesis leads to several counterintuitive testable predictions. As an example, it should be possible to obtain a pseudo-PREE by administering reinforced trials at a longer interreinforcement interval in the CR group than in a 50% PR group. As the interreinforcement interval in the CR group reaches a critical value above that of the PR group, extinction should be faster in the CR group than in the PR group (i.e., a PREE-like result). Of course, exactly that pattern was shown in Experiment 1 between two CR groups receiving the same absolute number of reinforced trials but with a different interreinforcement interval (Groups C/12c and C/12m).

The second factor was the total number of reinforced trials. In Experiment 1, with a 2:1 ratio of reinforcements between the PR and CR conditions (i.e., with 50% reinforcement), no support was found for the hypothesis that the reversed PREE is produced by the differential number of reinforcers received by PR and CR groups when trials are matched. That is, CR groups receiving either 12 or 24 reinforced trials in acquisition extinguished runway performance at essentially the same rate. With a 3:1 ratio, as in Experiment 2, at least the early extinction performance was better for the group that had received a larger number of reinforced trials (Group 30) than for the group with the smaller number of reinforced trials (Group 10). Extrapolating this to a PR condition, this would correspond to a 33% partial reinforcement schedule. It is possible, then, that the absolute number of reinforced trials may play a significant role in producing a reversed PREE when leaner partial reinforcement schedules are employed. Experiment 2 also provided a potential mechanism for this effect: variation in the amount of water intake. In toads, water uptake is modulated by experience with the consummatory situation (e.g., Muzio et al., 1992). This is not unique to toads; rats, for example, typically drink progressively larger amounts of sucrose solutions across trials in consummatory contrast situations (see Flaherty, 1996). One consequence of these dynamic changes in consummatory behavior is that toads that are subject to a larger number of runway trials experienced a larger amount of reinforcement than toads receiving a smaller number of trials. Given that extinction rate is slower as the magnitude of reinforcement increases (e.g., Muzio et al., 1992, Experiment 4), it is not surprising that, in Experiment 2, Group 30 exhibited better performance during early extinction trials than Group 10.

What is the importance of these findings? This new forgetting hypothesis of the reversed PREE may apply to species other than the toads tested in these experiments. Reversed PREEs occur under spaced-trial conditions (typically, one trial per day) in several species of teleost fish and reptiles (for reviews of this extensive literature, see Bitterman, 1975, 2000; Papini, 2003). In fact, the spaced-trial PREE has only been described in pigeons (Papini et al., 2002; Roberts et al., 1963; Thomas & Papini, 2003) and rats (McNaughton, 1984; Wagner, 1961; Weinstock, 1954). Interestingly, appetitive experiments with rats and pigeons show significant PREEs even when the frequency of reinforcement is equated across PR and CR groups (Haselgrove, Aydin, & Pearce, 2004; Thomas & Papini, 2003). These results reflect species differences in the processing of nonreinforcement events that may underlie the emergence of the PREE. Because, to our knowledge, the spacing of reinforced trials has not been explored in experiments with teleosts and reptiles, the present forgetting hypothesis offers an alternative to the classic strengthening–weakening learning model.

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