

Extinction of Food-Reinforced Instrumental Behavior in Japanese Quail (*Coturnix japonica*)

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Japanese quail (*Coturnix japonica*) were reinforced with food for traversing a runway for either 18 or 36 trials, administered at a rate of 1 trial per day. Then, all animals received 18 extinction trials. The latency to run from the start box to the goal box was the dependent variable. Extinction was significantly slower in animals that had received 50% partial reinforcement during acquisition, whether relative to a group matched in terms of acquisition trials (36 trials, twice the number of reinforced trials) or relative to a group matched in terms of reinforcements (18 trials). The latter group was also matched in terms of the temporal distribution of acquisition trials with the partial reinforcement group, being trained only on days when the partial group was scheduled to receive a reinforced trial. Thus, there was evidence of a spaced-trial partial reinforcement extinction effect. A comparison of groups receiving large versus small reward magnitudes yielded no evidence of the spaced-trial magnitude of reinforcement extinction effect, even though the large-reward group consumed approximately 3 times more food than the small-reward group. Moreover, a comparison of groups that received 36 versus 18 acquisition trials produced no evidence of the spaced-trial overtraining extinction effect, even though acquisition latencies were significantly lower for the group that received 36 acquisition trials. These results are discussed in relation to comparative research on learning phenomena involving incentive downshift manipulations.

Keywords: partial reinforcement extinction effect, magnitude of reinforcement extinction effect, overtraining extinction effect, spaced-trial training, reward downshift, Japanese quail

Changes in responding after incentive shifts are of great interest because they reflect the adaptive nature of learning. Although often such shifts are followed by a decrease in responding, in some cases the response shows a different pattern. In the partial reinforcement extinction effect (PREE), acquisition under a variable reinforcement schedule results in a slower decline of behavior during extinction, compared with the decline of behavior after acquisition under continuous reinforcement (Amsel, 1992). As summarized in Table 1, comparative research with vertebrates on the PREE and related phenomena (including the magnitude of reinforcement extinction effect, MREE, the overtraining extinction effect, OEE, and successive negative contrast in consummatory, cSNC, and instrumental behavior iSNC) shows a discontinuous

pattern of outcomes that might shed light on the evolution of learning mechanisms (Papini, 2002, 2003, 2006). Not all the effects have been studied systematically in all the species shown in Table 1, or under analogous training conditions, a fact opening the possibility for comparative testing of this discontinuity hypothesis. Under spaced-trial conditions (i.e., one trial per day), mammalian species produced consistent results in four of these effects (for examples in rats, *Rattus norvegicus*, see Crespi, 1942; Vogel, Mikulka, & Spear, 1968; Wagner, 1961):

- (1) a higher response level in extinction after partial rather than continuous reinforcement (PREE);
- (2) a higher response level in extinction after small rather than large reinforcers (MREE).
- (3) a lower response level after a downshift in reinforcer magnitude (cSNC and iSNC), relative to an unshifted control.

Analogous experiments with turtles, toads, and goldfish have produced the opposite pattern, that is, partial and small reinforcers lead to lower response level in extinction compared with continuous and large reinforcers (reversed PREE and reversed MREE), and a downshift in incentive magnitude leads to the gradual adjustment of behavior without contrast (reversed cSNC and reversed iSNC) (for examples in toads, *Rhinella arenarum*, see

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Table 1
Outcomes of Spaced-Trial Comparative Experiments on Learning Effects Involving Incentive Shifts

Class	Species	PREE	MREE	OEE	cSNC	iSNC
Mammals	Rat (<i>Rattus norvegicus</i>)	+	+	?	+	+
	Mouse (<i>Mus musculus</i>)	?	?	?	+	?
	White-eared opossum (<i>Didelphis albiventris</i>)	?	?	?	+	?
	Red opossum (<i>Lutreolina crassicaudata</i>)	?	?	?	+	?
Birds	Pigeon (<i>Columba livia</i>)	+	—	—	?	—
	Quail (<i>Coturnix japonica</i>)	+*	—	?	?	?
	Starling (<i>Sturnus vulgaris</i>)	?	?	?	+	?
Reptiles	Turtle (<i>Chrysemys picta</i>)	—	—	?	?	—
	Turtle (<i>Geoclemys reevesii</i>)	—	—	?	?	—
	Iguana (<i>Dipsosaurus dorsalis</i>)	—	?	?	?	?
Amphibians	Toad (<i>Rhinella arenarum</i>)	—	—	—	—	—
Bony fish	Goldfish (<i>Carassius auratus</i>)	—	—	—	—	—
	African mouthbreeder (<i>Tilapia macrocephala</i>)	—	—	?	?	?

Note. PREE = partial reinforcement extinction effect; MREE = magnitude of reinforcement extinction effect; OEE = overtraining extinction effect; cSNC = consummatory successive negative contrast; iSNC = instrumental successive negative contrast; + = effect; — = reversed effect; ? = no evidence available. See references in text.

* Present experiment.

Muzio, Pistone-Creydt, Iurman, Rinaldi, Sirani, & Papini, 2011; Muzio, Segura, & Papini, 1992; Papini, Muzio, & Segura, 1995). The co-occurrence of the PREE, MREE, and SNC, either all present (rats) or all absent (toads), has led to the hypothesis that the mechanisms of emotional learning underlying the reaction to incentive downshifts (traditionally called frustration; Amsel, 1992) are present in mammals but not in representatives of older vertebrates lineages (Papini, 2003, 2006).

Birds complicate this comparative view of incentive downshift effects because the few studies available depart from this covariation of PREE, MREE, and SNC. In pigeons (*Columba livia*), for example, spaced-trial experiments with food reinforcement have yielded evidence of the PREE in the runway (Roberts, Bullock & Bitterman, 1963; Thomas & Papini, 2003) and Skinner-box situations (Papini, Thomas & McVicar, 2002). However, analogous experiments have produced reversed MREE and SNC effects (Papini, 1997; Thomas & Papini, 2003). In fact, the PREE and reversed MREE have been observed within a single experiment in the runway situation (Thomas & Papini, 2003). In Japanese quail (*Coturnix japonica*), spaced-trial runway experiments with sexual reinforcement yielded evidence of a reversed MREE (Baquero, Puerta, & Gutiérrez, 2009), whereas in starlings (*Sturnus vulgaris*), a downshift from mealworms (more preferred) to turkey crumbs (less preferred) yielded clear evidence of cSNC (Freidin, Cuello, & Kacelnik, 2009). The dissociation of these effects in birds clearly merits additional research.

The experiment reported here was designed to determine whether Japanese quail trained under more conventional conditions, with food reinforcement and in a runway, would yield evidence of the PREE and MREE. The four groups included in this experiment allowed for three comparisons. First, a comparison between a 50% partial reinforcement condition with two continuous reinforcement groups, one matched in terms of trials and the other matched in terms of reinforcements and their distribution in time. These three groups received a relatively large reward. Matching the number and temporal distribution of reinforcements has become interesting in light of the discovery that toads trained

under such conditions exhibit an extinction profile similar to that of partially reinforced animals (Muzio, Ruetti, & Papini, 2006), a fact suggesting that their reversed PREE is more related to reward distribution than to the partial schedule per se. Second, a group also receiving continuous reinforcement, but with a small reward allow for a test of the effects of reward magnitude on extinction. Finally, the two continuously reinforced conditions included as comparison groups to assess the PREE afford the study of a third, less studied phenomenon: the overtraining extinction effect (OEE). The presence of the OEE can be determined by a comparison between the two large-reward, continuously reinforced groups receiving different amounts of acquisition training. The comparative database for the OEE is less consistent procedurally and thus more difficult to assess. Under massed-training conditions, faster extinction after extensive, rather than limited acquisition training (i.e., the overtraining extinction effect, OEE) has been reported in rats (Ison, 1962) and turtles (Ishida & Papini, 1997). However, under spaced-training conditions, the OEE has failed to occur in goldfish (Ishida, 1977), toads (Muzio et al., 2006), and pigeons (Thomas & Papini, 2003). Because the distribution of trials is one key factor determining whether at least some of these effects are observed (for the PREE in toads, see Muzio et al., 1992), it is difficult to assess whether the OEE can help detecting species differences in learning phenomena. The present experiment then provides input on these learning effects, under spaced-training conditions, using a species from a vertebrate class (Aves) that has yielded a complex pattern of results.

Method

Subjects

Forty 4-month-old male Japanese quail, purchased from a private farm near Bogotá, Colombia, were used as subjects. Subjects were housed at the Animal Learning and Behavior Lab, National University of Colombia, for two months before the beginning of the experiment. Subjects were maintained in individual cages and

on a 14:10 light:dark cycle (lights on at 06:00 h). All subjects had free access to water, but food (mixed grain) was restricted so they were maintained at 80–85% of their ad libitum weight.

Apparatus

Animals received training in a straight alley made of acrylic and divided in three compartments: a start box, a central runway, and a goal box (see Figure 1). The central runway was 302 cm long, 20 cm wide, and was surrounded by walls that were 25 cm high. Both the start box and the goal box were located at each end of the alley. The start and goal boxes were separated from the runway by vertical sliding doors, 10 cm wide and 15 cm high. The doors were operated by a string and pulley system. The start and goal boxes were 40 cm wide, 42 cm long, and 25 cm high. There was a transparent acrylic ceiling covering the entire alley. The floor was covered with white bond paper. Mixed grain served as the reinforcer and was delivered in a food cup, in the goal box.

Two pairs of photocell sensors were located at the beginning and the end of the central runway, located as shown in Figure 1. These sensors were connected to a chronometer Casio HS-5 that registered the time that each animal took to traverse the runway. Running latencies were registered in 0.01-s units and transformed to the \log_{10} to improve normality and allow for parametric analyses of the data.

Procedure

One trial per day was administered throughout the experiment. In each of four trials of food-cup pretraining, animals were introduced directly in the goal box for 5 min and allowed to eat 5 g of mixed grain. The amount of food consumed by the subject was measured. By the fourth trial, most animals had eaten at least 1.5 g of food. Four animals failed to consume food consistently and were thus discarded from the experiment.

During runway pretraining trials, animals were introduced in the start box; after 30 s, the door was opened and the animals had 3 min to reach the goal box. Subjects failing to reach the goal within 3 min were gently guided with an acrylic pad. Once at the goal box, animals received 3 min of access to 5 g of mixed-grain. This phase ended when each animal had reached the goal box for 2 consecutive trials without guidance.

At the end of pretraining, animals were matched in terms of ad libitum weight and pretraining duration and randomly assigned to one of four groups. Acquisition trials were similar to pretraining trials, except for the availability of food in the goal box. Group PR/5/36 received 50% partial reinforcement training in which 18 trials ended with 5 min of access to food in the goal box and the

rest of the trials ended in 5 min of retention in the goal box (a total of 36 trials). The sequence of reinforced and nonreinforced trials was determined using Gellerman's (1933) series. Group CR/5/36 received continuous reinforcement training in which each trial ended in a 5-min period of access to food and received 36 acquisition trials. These animals were matched in terms of trials with the partially reinforced animals. Group CR/5/18 received continuous reinforcement training with access to 5 min of food in each of 18 trials. Thus, these quail received the same number of reinforced trials as did the partially reinforced animals. In addition, reinforced trials were administered only the days in which partially reinforced birds were scheduled to receive a reinforced trial, thus also matching the temporal distribution of reinforcement. Finally, Group CR/1/36 received continuous reinforcement training in which each of 36 acquisition trials ended with a 1-min access to food.

Extinction trials were identical to the nonreinforced trials of Group PR/5/36, that is, no food was delivered and animals were kept in the goal box during 5 min. Animals in Group CR/1/36 were kept for 1 min in the goal box during extinction trials. As in pretraining trials, animals that failed to reach the goal box within 3 min were gently guided. For these animals, a latency of 180 s was recorded. All animals received 18 extinction trials.

Three comparisons can be made with these four groups based on their extinction performance (Thomas & Papini, 2003). First, PR/5/36 versus CR/5/36 and CR/5/18 would provide information on the PREE (schedule effect). Second, CR/5/36 versus CR/1/36 would assess the MREE (magnitude effect). Third, CR/5/36 versus CR/5/18 would assess the OEE (amount of training effect).

Results

There were nonsignificant group effects for ad libitum weight, grain consumption, and average trial duration during pretraining, $F_s < 1$, $\eta_p^2 < 0.04$ (see Table 2). As shown in Figure 2, the groups that received 5 min of access to grain per trial consistently consumed more food than the group receiving 1 min of access per trial (Group CR/1/36). A one-way analysis was calculated on the average consumption over the entire acquisition trials (36 trials for CR/5/36 and CR/1/36, and 18 trials for PR/5/36 and CR/5/18). Groups were significantly different, $F(3, 32) = 87.84$, $p < .001$, $\eta_p^2 = 0.89$. Pair wise LSD tests determined that Group CR/1/36 consumed significantly less food than the other three groups, $ps < 0.001$, which did not differ from each other, $ps > 0.09$. Therefore, the reward magnitude procedure actually led to differential food consumption.

Figure 3 shows the results of the three groups that evaluate the effects of partial reinforcement: PR/5/36, CR/5/36, and CR/5/18. A Group by Trial analysis only of those acquisition trials when Group PR/5/36 received reinforcement (Trials 1, 3–4, 6–7, 11, 13–14, 17–18, 22–24, 27, 30, 32–33, 36) indicated only a significant reduction in latencies across trials, $F(17, 408) = 13.66$, $p < .001$, $\eta_p^2 = 0.36$. Neither the group nor the group by trial interaction were significant, $F_s < 2.22$, $ps > 0.13$, $\eta_p^2 < 0.17$. An analysis of the two groups traditionally included in comparative studies of the PREE, PR/5/36 versus CR/5/36, including all 36 acquisition trials, also yielded the same results. There was a significant decline in latencies across acquisition trials, $F(35, 560) = 8.63$, $p < .001$, $\eta_p^2 = 0.35$, but no evidence of a group or group by trial interaction effect, $F_s < 1.70$, $ps > 0.21$, $\eta_p^2 < 0.11$.

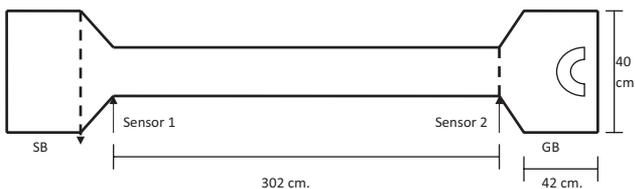


Figure 1. Diagram of the straight alley. SB, Star Box; GB, Goal Box. The dotted lines indicate the location of the doors. See text for details.

Table 2

Mean [95% Confidence Intervals] Ad Libitum Weights, Grain Consumption, and Pretraining Trial Durations for Each Group

Group	Ad libitum weight (g)	Grain consumption (g)	Pretraining (s)
CR/5/36	155.07 [145.7–164.4]	2.13 [1.9–2.4]	51.36 [34.2–68.5]
PR/5/36	155.70 [150.1–161.3]	2.11 [1.8–2.5]	44.36 [25.7–63.0]
CR/1/36	153.96 [144.4–164.3]	2.03 [1.8–2.2]	44.83 [30.8–61.3]
CR/5/18	154.37 [145.6–162.3]	1.98 [1.9–2.2]	46.06 [32.9–56.8]

Figure 3 also shows the extinction performance of these three groups. Two major outcomes were observed. First, a very clear PREE emerged in these data, with the two CR groups extinguishing faster than the PR group. Second, the PREE emerged whether trials (CR/5/36) or reinforcements and their temporal distribution (CR/5/18) were equated relative to Group PR/5/36. A Group \times Trial (37–54) analysis indicated a significant interaction, $F(34, 408) = 3.65, p < .001, \eta_p^2 = 0.23$. The group effect, $F(2, 24) = 12.78, p < .001, \eta_p^2 = 0.52$, and the trial effect, $F(17, 408) = 20.08, p < .001, \eta_p^2 = 0.46$, were also significant. LSD pair wise tests indicated that PR/5/36 extinguished significantly more slowly than either of the two CR groups, $ps < 0.002$, which, in turn, did not differ from each other, $p > .31$.

Figure 4 shows the results for the groups differing in terms of incentive magnitude. Despite these groups eating significantly different amounts of grain during acquisition trials (see above), and despite an observable trend for CR/5/36 to exhibit shorter running latencies during acquisition than CR/1/36 (i.e., a trend in the expected direction), a Group \times Trial (1–36) analysis did not confirm a behavioral effect during acquisition. There was a significant decline in latencies, $F(35, 560) = 6.82, p < .001, \eta_p^2 = 0.30$, but neither the interaction nor the group effect were significant, $F_s < 1.87, ps > 0.19, \eta_p^2 < 0.11$. Similar results were obtained for the extinction trials. The extinction effect was significant, $F(17, 272) = 23.71, p < .001, \eta_p^2 = 0.60$, but the interaction and group effects were not significant, $F_s < 1.22, ps > 0.25, \eta_p^2 < 0.08$.

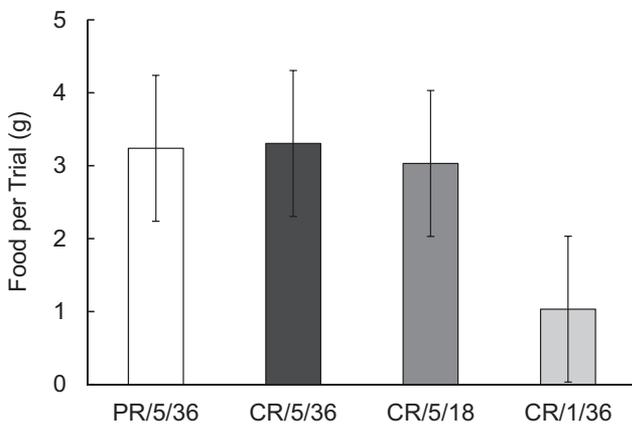


Figure 2. Mean ($\pm 95\%$ confidence intervals) food consumed per trial during acquisition trials for each of the groups.

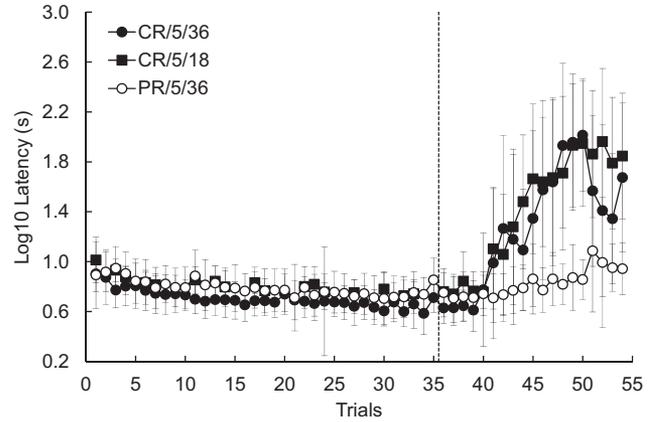


Figure 3. Mean ($\pm 95\%$ confidence intervals) latency, transformed to the \log_{10} to enhance normality, in groups receiving continuous reinforcement (CR), partial reinforcement (PR), and either 18 or 36 acquisition trials. All animals had access to grain in the goal box for 5 min. The dotted line separates acquisition from extinction trials.

The comparison in terms of the number of acquisition trials between Groups CR/5/36 and CR/5/18 is also presented in Figure 3. A Group by trial analysis including only trials when both groups were run (Trials 1, 3, 4, 6, 7, 11, 13, 14, 17, 18, 22, 23, 24, 27, 30, 32, 33, and 36), confirmed that Group CR/5/36 displayed significantly shorter latencies in acquisition than Group CR/5/18, $F(1, 16) = 4.91, p < .05, \eta_p^2 = 0.23$. The acquisition effect was also significant, $F(17, 272) = 9.73, p < .001, \eta_p^2 = 0.38$, but the interaction was nonsignificant, $F < 1, \eta_p^2 = 0.04$. A similar analysis of extinction performance indicated a significant extinction effect, $F(17, 272) = 18.66, p < .001, \eta_p^2 = 0.54$, but nonsignificant group or interaction effects, $F_s < 1.05, ps > 0.38, \eta_p^2 < 0.07$.

Discussion

Three effects involving incentive downshifts were sought within a single experiment using a four-group design. First, there was

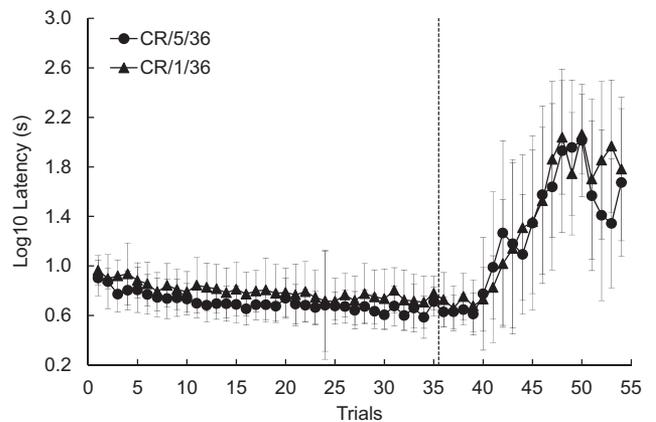


Figure 4. Mean ($\pm 95\%$ confidence intervals) latency, transformed to the \log_{10} to enhance normality, in groups receiving continuous reinforcement (CR) and either 5 or 1 min of access to food in the goal box. All animals received 36 acquisition trials.

clear evidence for the PREE in quail, whether the partial reinforcement group was compared with a continuously reinforced group matched in trials or matched in reinforcements and their temporal distribution. Second, there was no evidence of an MREE, and, third, there was also no evidence of an OEE. There was no evidence of biased assignment, at least as assessed in terms of weight differences, amount of food consumed during pretraining, and duration of pretraining trials. Furthermore, the absence of an MREE cannot be attributed to a nondifferential amount of food eaten during acquisition trials; Group CR/5/36 ate about three times more food than Group CR/1/36. Moreover, the absence of an OEE cannot be attributed to a lack of effect of the amount of training manipulation during acquisition trial because latencies in Group CR/5/36 were significantly lower than latencies in Group CR/5/18.

Figure 5 summarizes the available evidence on the spaced-trial experiments involving incentive shifts superimposed on a phylogenetic tree of the vertebrate species that have been studied thus far. Although the present experiment did not assess the SNC effect, it is included in this discussion because there is relatively more comparative information. The comparative database underlying Figure 5 is presented in Table 1. The relevant experiments involved food reinforcement for all species, except for toads (access to water), and instrumental tasks for all species. There are additional data available for spaced-trial experiments in a variety of other species concerning some of these effects. For example, the spaced-trial SNC effect was reported for consummatory behavior in two species of didelphid marsupials (*Didelphis albiventris* and *Lutreolina crassicaudata*, Papini, Mustaca, & Bitterman, 1988) and in mice (*Mus musculus*, Mustaca, Bentosela, & Papini, 2000), in all cases with access to sucrose solutions in a one trial per day

situation. A reversed PREE was also reported in an experiment with iguanas (*Dipsosaurus dorsalis*, Graf, 1972) trained to run in an L-shaped runway for access to a heated surface for 3 min, in a one trial per day situation. As for the evidence from experiments with Japanese quail, although there is evidence of a reversed MREE with sexual reinforcement (Baquero et al., 2009) and the absence of group effects with food reinforcement (present experiment), there is no available evidence on the SNC effect.

The covariation of these incentive downshift effects is violated in experiments involving birds. Pigeons and quail show the PREE, but not the MREE. A reversed SNC effect was also reported in pigeons (Papini, 1997). To complicate matters further, a consummatory SNC effect was observed in starlings (Freidin et al., 2009). The distribution of these spaced-trial effects in vertebrates suggests the following hypotheses. First, the primitive mechanism underlying adjustment to reward downshift leads to reversed effects, as shown in goldfish, toads, and turtles. Second, the mechanisms underlying the PREE in mammals and birds have evolved independently. This is supported by the covariation of PREE, MREE, and SNC in rats but not in pigeons and quail. These hypotheses must be taken with caution and only as guides for future research. An advantage of stating these hypotheses clearly is that they can be tested.

Testing these hypotheses requires research along two main lines. One line involves the systematic variation of relevant factors in search for parameters that might produce these effects under spaced-trial conditions (Bitterman, 1975). For example, recent research with toads has focused on using isotonic solutions of different concentrations leading to hydration or dehydration as incentives (e.g., Daneri, Papini, & Muzio, 2007; Muzio et al., 2011). Confidence about the possibility that these behavioral effects are not attributable to a peculiar combi-

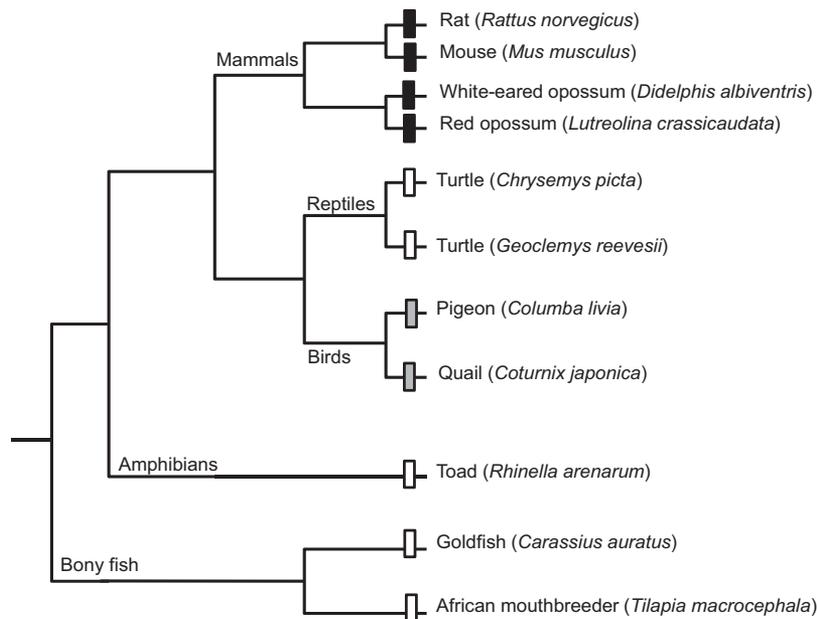


Figure 5. Phylogenetic relations of vertebrate species studied in situations involving incentive shifts under spaced-trial conditions. The vertical rectangle illustrates whether the species displays all the effects (black), none of them (white), or some (gray). References for specific effects (PREE, MREE, OEE, cSNC, and iSNC) and species are in Table 1 and text.

nation of parameters grows to the extent that similar effects are found under a variety of training parameters. However, certainty is elusive because it is impossible to be absolutely sure that all conditions affecting behavior independent of learning mechanisms (so-called contextual variables) can be equated across species (Bitterman, 1975). What can be guaranteed is that the designs of the experiments are reasonably analogous in some critical aspects. Examples of variables that might affect the outcome of comparative experiments include the type of incentive, the way in which it is delivered, response biases, and amount of training, among others. For example, despite significant reduction in latency in all comparisons, the acquisition performance in the present experiment started quite low, surely as a result of effective pretraining. One can ask whether differences in pretraining procedures might affect these effects differentially or might affect behavior differently for different species. To this we need to add the possibility that similar behavioral outcomes observed in different species may arise from different mechanisms (e.g., Thomas & Papini, 2003). The fact that Japanese quail have produced a rather strong PREE in the present experiment does not demonstrate that this effect is based upon the same brain mechanisms known to underlie the PREE in rats (Amsel, 1992; Papini, 2002, 2006).

A second line of evidence concerns an analysis of the brain circuitry and neurochemical systems activated by an experience of incentive downshift in a comparative framework (Papini, 2002). For example, Thomas and Papini (2003) selected drugs known to have effects on the PREE in rats and tested them in pigeons. Haloperidol, a dopamine receptor antagonist, shown to have no effect on the PREE in rats (Feldon, Katz, & Weiner, 1988; Feldon & Weiner, 1991), actually eliminated the PREE in pigeons. Similar discrepancies were found for nicotine (a stimulant that binds to cholinergic nicotinic receptors) and chlordiazepoxide (an anxiolytic that binds selectively to the benzodiazepine site of GABA_A receptors). Japanese quail offer a suitable model for a systematic analysis of incentive downshift effects using different rewards (sexual and food reinforcers), training conditions, and neurobiological manipulations (e.g., Can, Domjan, & Delville, 2007; Mills, Crawford, Domjan, & Faure, 1997; Taziaux, Kahn, Moore, Balthazart, & Holloway, 2008).

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Correction to Gonzalo, López, and Martín (2012)

In the article “Adaptive Forgetting in Iberian Green Frog Tadpoles: Learned Irrelevance and Latent Inhibition May Avoid Predator Misidentification,” by Adegá Gonzalo, Pilar López, and José Martín (*Journal of Comparative Psychology*, Advance online publication August 6, 2012. doi:10.1037/a0029173), the title should have read “Adaptive Forgetting in Iberian Green Frog Tadpoles (*Pelophylax perezi*): Learned Irrelevance and Latent Inhibition May Avoid Predator Misidentification.” All versions of this article have been corrected.

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