

## Role of Reinforcement in Spaced-Trial Operant Learning in Pigeons (*Columba livia*)

Mauricio R. Papini  
Texas Christian University

The author designed 3 experiments to study pigeons' adjustment to unexpected shifts in reinforcer magnitude with a single trial per day. Extinction was faster or poorer after training with a small magnitude (1 food pellet) than after training with a large magnitude (10 or 15 pellets). A shift from 15 to 1 pellet was accompanied by a gradual adjustment, with no indication of a successive negative contrast effect. Pigeons discriminated the reinforcer magnitudes but yielded no evidence of spaced-trial simultaneous negative contrast. Moreover, extinction was faster for a stimulus paired with 1 pellet than for a stimulus paired with 15 pellets. The results can be interpreted in terms of simple strengthening–weakening learning rules and without reference to anticipatory frustration.

The acquisition and extinction of simple instrumental responses is affected by variables such as the magnitude and probability of reinforcement in a variety of vertebrate species. However, when training is administered on a spaced-trial basis (i.e., a single trial per day, with intertrial intervals of 24 hr or longer), the generality of some of these learning phenomena is severely limited. Such spaced-trial procedures are useful to reduce and perhaps eliminate the influence on one trial of events (e.g., stimuli, reinforcers, and responses) that occur on previous, recent trials, on the assumption that the traces of such events decay in time (Weinstock, 1954). For example, acquisition rate and asymptote are generally a direct function of reward magnitude. In contrast, in rats (*Rattus norvegicus*) extinction is faster after relatively larger magnitudes than after smaller ones (Hulse, 1958), or after continuous reinforcement rather than after partial reinforcement (Rashotte & Surridge, 1969; Weinstock, 1954); however in fish (*Carassius auratus*, *Tilapia macrocephala*), toads (*Bufo arenarum*), and turtles (*Chrysemys picta*, *Geoclemys reevesii*), extinction is slower after acquisition with large rewards rather than with small rewards, or with continuous reinforcement rather than with partial reinforcement in a wide range of conditions (Boitano & Foskett, 1968; Gonzalez, Behrend, & Bitterman, 1965; Gonzalez & Bitterman, 1962; Gonzalez, Holmes, & Bitterman, 1967; Graf, 1972; Ishida & Papini, 1993; Longo & Bitterman, 1960; Muzio, Segura, & Papini, 1992, 1994; Papini & Ishida, 1994; Schutz & Bitterman, 1969).

Researchers have considered the effects of magnitude and probability of reinforcement in the rat to be odd in light of the classic Thorndikian assumption that the strength of stimulus–response associations is a direct function of reward

magnitude and probability (Thorndike, 1911). Accordingly, these effects have been referred to as paradoxical (Amsel, 1992). The two paradoxical effects described above are the magnitude of reinforcement extinction effect (MREE) and the partial reinforcement extinction effect (PREE).

The successive negative contrast effect (SNCE) is another paradoxical reward effect that has been studied from the comparative perspective. In this situation, mammals that are trained with a relatively larger reward magnitude (or with a more preferred reward) reject a smaller magnitude (or a less preferred reward) significantly more than do control animals that are exposed only to the lower value (Crespi, 1942; Elliott, 1928; Papini, Mustaca, & Bitterman, 1988; Tinklepaugh, 1928). Again, in this case, analogous spaced-trial experiments involving fish, toads, and turtles have produced no evidence of the SNCE (Couvillon & Bitterman, 1985b; Gonzalez, Potts, Pitcoff, & Bitterman, 1972; Lowes & Bitterman, 1967; Papini & Ishida, 1994; Papini, Muzio, & Segura, 1995; Pert & Bitterman, 1970). These animals appear to adjust gradually, if at all, to the new conditions of reinforcement without the performance-undershooting characteristic of the SNCE. In this article, I refer to the behavior of mammals as paradoxical, whereas I refer to the behavior of fish, amphibians, and reptiles tested under analogous conditions as nonparadoxical. Moreover, the classic terms *higher vertebrates* (Mammalia and Aves) and *lower vertebrates* (Agnatha and Chondrichthyes, Osteichthyes, Amphibia, and Reptilia) are used as purely descriptive terms and without any reference to such concepts as the “scala naturae . . . inevitable progress, goal or perfection” (Bullock, 1993, p. 89).

These species differences can be theoretically analyzed at the mechanistic and evolutionary levels (Tinbergen, 1963). At the level of the underlying mechanisms, there are essentially two possibilities. One is to argue that the differences among higher and lower vertebrates are only superficial and probably attributable to the particular choice of training parameters and the effects of these variables on such factors as motivation, sensory-perceptual processes, and motor control. This view, appropriately labeled the null

---

The research reported in this article was supported in part by a grant from Texas Christian University (TCU/RF 5-23710). I thank Dana Shaw for her contribution to this project.

Correspondence concerning this article should be addressed to Mauricio R. Papini, Department of Psychology, Texas Christian University, TCU Box 298920, Fort Worth, Texas 76129. Electronic mail may be sent via Internet to papini@gamma.is.tcu.edu.

hypothesis (Macphail, 1982), implicitly suggests that the mechanisms underlying these learning phenomena are homologous; behavioral differences emerge as a function of whether or not the environmental conditions of a particular experiment engage these mechanisms.

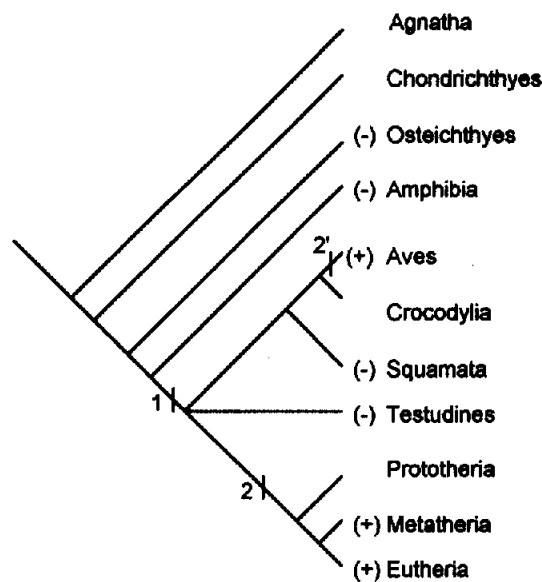
A second possibility is that these behavioral differences reflect a divergence in learning mechanisms across higher and lower vertebrates (Bitterman, 1975). The general strategy to identify species differences in learning processes, as opposed to differences in contextual factors also affecting behavior, involves control by systematic variation (Bitterman, 1960). Factors affecting behavior are systematically varied, whereas the focus is the functional relationship between the independent variables (e.g., reinforcer magnitude) and dependent variables (e.g., extinction rate). Obviously, a hypothesis of divergence in mechanisms requires a more detailed statement about the precise nature of the differences. One possible explanation of these species differences is that paradoxical behavior reflects the availability of mechanisms that allow animals to both react emotionally to transitions in reward magnitude and learn to anticipate such emotional reactions (for other hypotheses, see Bitterman, 1975; Macphail, 1982). Within the framework of frustration theory (Amsel, 1992), the initial emotional reaction to surprising reward omissions or reductions is termed *primary frustration*, whereas the conditioned form of this reaction is termed *anticipatory frustration*. Nonparadoxical performance could reflect either the absence of these emotional reactions or the inability of these reactions to control instrumental behavior. Nonparadoxical behavior would then be primarily under the control of simple associative rules, such as the strengthening–weakening rules first suggested by Thorndike (1911; see Couvillon & Bitterman, 1985a).

Amsel (1992) reviewed evidence that a transition from nonparadoxical to paradoxical behavior occurs in the ontogeny of the rat and suggested that the emergence of paradoxical behavior is correlated with the maturation of the mammalian septo-hippocampal system. If a similar transition from nonparadoxical to paradoxical behavior has occurred phylogenetically, it may be an instance of what Bullock (1993) called *vertical grades of complexity*. In evolutionary biology, *grade* refers to a level of organization that has been achieved by a group of species, not necessarily because of common ancestry. *Complexity* in brain and behavior is defined in terms of “the number of distinguishable different kinds of parts, operations and interrelations, discriminable stimuli (including social situations), and discriminable outputs (including the whole behavioral repertoire)” (Bullock, 1993, p. 89; see McShea, 1996). It is important to emphasize that the notion of complexity grade is orthogonal to that of adaptation. More complex vertebrate brains and behaviors have generally evolved more recently but cannot be considered to provide a greater level of adaptation compared with simpler brains and behavioral patterns. Indeed, it is assumed here that new levels of complexity evolved by natural selection (Bonner, 1988).

A second level of analysis of the hypothetical divergence in learning mechanisms is that of the evolutionary origin of

that divergence. Figure 1 shows a cladogram of Vertebrata (based on Benton, 1990) and indicates for each taxon whether there is evidence of spaced-trial paradoxical performance (+) or of spaced-trial nonparadoxical performance (–). The distribution of these characters is based on the references cited earlier, except for Aves (see below). Such evidence comes from the study of one or a few species, according to the groups. If it is assumed that the mechanisms underlying these two phenotypes (paradoxical and nonparadoxical performance) are analogous to morphological characters, then the phylogenetic stability of these learning phenomena justifies expressing the hypotheses in terms of a cladogram. Behavioral, neurochemical, and neurobiological characters are commonly used in cladistic analyses (e.g., Butler, 1994; Kennedy, Spencer, & Gray, 1996; Northcutt & Kaas, 1995). This cladogram also helps visualization of the taxonomic groups that need to be studied.

As for Aves, there appears to be only one published experiment (Roberts, Bullock, & Bitterman, 1963) on the paradoxical performance of birds in a spaced-trial situation. Roberts et al. trained pigeons (*Columba livia*) to locate food in a runway and measured their running latency. Two of the four groups included in that experiment are relevant here. One of them received continuous reinforcement for 50 daily trials, whereas the other received partial reinforcement with



- 1 Single origin, subsequent loss in Testudines and Squamata.
- 2 Independent origin in Mammalia.
- 2' Independent origin in Aves.

Figure 1. Cladogram representing the phylogenetic relationships of major vertebrate groups (Benton, 1990). Positive and negative signs refer, respectively, to reports of paradoxical and nonparadoxical instrumental performance in experiments involving manipulations of reward magnitude and probability (see text for references).

25 trials ending in access to reward (5 g of grain) and 25 trials ending in nonreward, in Gellermann order. Extinction showed a crossing over of group latencies, with the continuously reinforced group starting at a lower latency than the partially reinforced group but rapidly extinguishing the running response. This is a clear demonstration of the PREE. Given this result, I have characterized birds as exhibiting paradoxical behavior in Figure 1.

Two possible hypotheses of the origin of the underlying mechanisms of paradoxical behavior, presumably evolving by natural selection, are represented in Figure 1. I used teleost fish and amphibians as the outgroups and considered nonparadoxical mechanisms to be the primitive vertebrate condition (i.e., plesiomorphy in the language of cladistics), whereas I considered the paradoxical mechanisms to be a derived condition (i.e., apomorphy). The first possibility, labeled the *single-origin hypothesis* (see No. 1 in Figure 1), is that the paradoxical mechanisms evolved only once. This hypothesis implies that mammalian and avian paradoxical mechanisms are homologous and it also implies the selective evolutionary loss of these mechanisms in the lines leading to extant lizards (Squamata) and turtles (Testudines), which have so far yielded evidence of nonparadoxical performance.

The second possibility, labeled the *independent-origin hypothesis* (see Nos. 2 and 2' in Figure 1), is that the paradoxical behavior of mammals and birds is only superficially similar because of convergent evolution (homoplasy). Convergence in biological systems is usually detected when the underlying mechanisms are studied in detail, at the molecular, physiological, or developmental levels (Avers, 1989). There are several examples of evolutionary convergence among mammals and birds, including relative brain size, thermoregulation, rates of morphological evolution, and sleep-wakefulness cycles (Burghardt, 1988; Cai, 1991; Northcutt, 1987; Ruben, 1995; Wyles, Kunkel, & Wilson, 1983). In this particular case, convergence would be supported if it could be shown that the paradoxical performance of mammals and birds depends on different behavioral factors, after systematic variation of those variables (Bitterman, 1975), or on different brain structures or neurochemical systems (Muzio, Segura, & Papini, 1993). Convergence would also be consistent with different developmental profiles in species showing paradoxical behavior (Amsel, 1992). It is plausible then that an analysis of the paradoxical effects in pigeons would provide evidence of either homology, divergence, or convergence in learning mechanisms across vertebrates. As with any other evolutionary theory, critical evidence for choosing among these hypotheses will come from a study of the comparative pattern of distribution of these paradoxical learning phenomena (Papini, 1987).

In the present series of experiments, I sought evidence for the MREE and SNCE using a conventional key-pecking situation. As in the spaced-trial experiments reviewed earlier, there was one trial per session and an intertrial interval of 24 hr. According to the single-origin hypothesis, on the basis of the outcome reported by Roberts et al. (1963), these paradoxical phenomena were expected to occur under the present conditions. The independent-origin hypothesis could

in principle accommodate either paradoxical or nonparadoxical behavioral outcomes. If paradoxical performance were found, this hypothesis would stress the possibility that the avian effects would be sensitive to a different set of independent variables from that affecting mammalian paradoxical performance. If nonparadoxical performance were found, the dissociation between instrumental (e.g., Roberts et al., 1963) and operant situations (i.e., the present key-pecking experiments), a dissociation that is not observed in rats (McNaughton, 1984; Weinstock, 1954), could be interpreted as providing support for convergent evolution.

## Experiment 1

Pigeons were pretrained to peck at an illuminated key in sessions involving multiple trials. Once individual birds achieved a behavioral criterion, they were shifted to the acquisition phase of the experiment. In this phase, each session consisted of a single trial, preceded and followed by an interval of time. During the trial, the key was illuminated with a different stimulus from that used in pretraining and responding resulted in some outcome. Acquisition was followed by extinction, in which reinforcements were withheld but all other aspects remained constant.

The first experiment in which this procedure was used did not yield significant results, so I do not report it in detail and refer to it as the preliminary experiment. Two continuous reinforcement groups were reinforced with either 1 or 10 food pellets. A partial reinforcement group also received 10 pellets but in only 50% of the trials. There were 52 acquisition trials followed by 48 extinction trials. Despite the null results, the experiment suggested two main conclusions. First, latencies were notoriously variable both across animals and across trials for a single animal. In an attempt to decrease behavioral variability, the response requirement was increased from a fixed ratio (FR) 1 to an FR 10. This provided not only the latency to the first response but also the latency to complete the ratio. Moreover, paradoxical effects have been reported to emerge more clearly in rats when response effort is increased (Eisenberger, 1992; Lawrence & Festinger, 1962). Second, it was clear that the largest group differences were in the comparison in terms of reinforcer magnitude rather than in terms of partial reinforcement. Accordingly, in the experiments reported in this article, I concentrated on the effects of reinforcer magnitude shifts on the pigeon's key-pecking behavior.

## Method

**Subjects.** The subjects were the same pigeons that had been assigned to the groups reinforced with 1 and 10 pellets in the preliminary experiment. The pigeons were obtained from a local dealer. Their sex and age were not determined, but they were all sexually mature. Pigeons were housed in individual wire cages, with grit and water continuously available, and they were maintained at 75% of their ad libitum weights. A 12-hr light-dark cycle was in effect in the colony room, with light beginning at 07:00.

**Apparatus.** Three standard conditioning boxes for pigeons were used. Each animal was trained in one specific box during the entire experiment. Each conditioning box was enclosed in a

soundproof chamber equipped with a fan, which provided both ventilation and masking background noise. The conditioning boxes measured  $32.2 \times 29.9 \times 32.2$  cm (width  $\times$  length  $\times$  height). Two walls and the ceiling were made of clear Plexiglas, and the other two walls were made of aluminum. A feeder cup made of opaque Plexiglas and measuring  $4.5 \times 5.5 \times 4$  cm was located in the center of one of the aluminum walls, 3 cm above the floor. Noyes precision pellets (pigeon formula, 45 mg) were automatically delivered into this cup by a pellet dispenser. A lamp (General Electric 1820), located on the top left corner of the wall with the feeder, provided diffuse illumination. A key light (diameter = 1.8 cm) was placed 18.5 cm above the floor. The key was illuminated from behind with either a white light or a white plus sign on a black background. A computer located in an adjacent room controlled all the events and recorded response latencies.

**Procedure.** Immediately after the end of the preliminary experiment, all pigeons were returned to pretraining. In pretraining, each session had 20 trials separated by an average intertrial interval of 60 s (range = 40–80 s). Each trial was begun with the illumination of the key with a white light. A single response to the key resulted in the immediate delivery of a 45-mg Noyes pellet (pigeon formula). If the pigeon failed to respond, a pellet was automatically delivered after 6 s. At the end of each session, the probability of response was determined for each bird. Whenever a particular pigeon achieved a probability of response equal to or greater than 0.8 in two consecutive sessions, the FR requirement was increased in the following session. Pigeons were trained in FRs of 1, 2, 4, 6, 8, and 10. Sessions were run under the new FR requirement until the subject again met the criterion described above. After reaching the FR 10 terminal requirement, pigeons were run for a minimum of 5 sessions and had to meet a criterion of a probability of response of 0.8 or better in three consecutive sessions to be shifted to the acquisition phase.

The groups of this experiment were labeled Group 1 ( $n = 5$ ) and Group 10 ( $n = 6$ ), depending on the number of pellets received during acquisition trials. The acquisition phase involved 40 daily trials. Each daily session involved a single trial. The pigeons were

transferred from the colony room to the conditioning lab in their cages and then manually placed in the conditioning box. The start of the session was marked by turning on the house light. A pretrial interval ranging from 30 to 90 s was followed by the illumination of the key with a white plus sign on a black background. The subject had a maximum of 30 s to start responding and a maximum of 20 s to complete the ratio once key pecking started. The trial ended either when 10 key pecks had been recorded or after the maximum time elapsed. In either case, the subjects received 1 or 10 pellets according to group assignments. The 10 pellets were delivered in a rapid succession, one every 170 ms. After the key stimulus was turned off, a posttrial interval ranging from 30 to 90 s started. At the end of this interval, the house light was turned off and the pigeon was returned to its cage and colony room. Extinction trials were equal in every respect, except that no pellets were delivered at the end of the trial. There were 32 extinction trials.

Two latencies were recorded in each trial. The initial latency was defined as the time between the onset of the stimulus (the plus sign) and the emission of the first key-peck response. The FR latency was defined as the time to complete the FR 10 requirement. In all the experiments reported here, the latencies obtained in each trial were transformed to the natural logarithm ( $\ln$ ) to improve normality and allow for the use of parametric statistics. Transformed latencies were then collapsed in blocks of four trials and subjected to mixed-design analysis of variance. The value for alpha was set to .05.

## Results

All pigeons could be shaped to an FR 10. Group 1 took an average of 32.2 sessions (range = 16–84), whereas all the subjects in Group 10 took 16 sessions to achieve the pretraining criterion.

Figure 2 presents the results in terms of the  $\ln$  of the initial latency (left panel) and the  $\ln$  of the FR latency (right panel). Acquisition performance starts at a low level because these

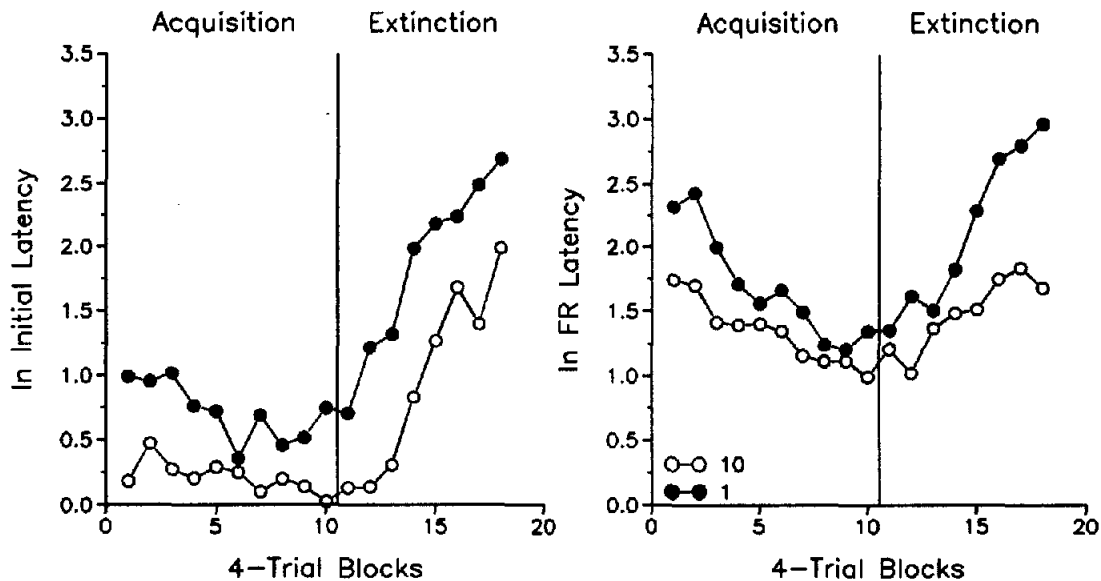


Figure 2. Initial and fixed-ratio (FR) latency (natural logarithm [ $\ln$ ]) results are presented in the left and right panels, respectively, for groups of pigeons reinforced with either 1 or 10 food pellets during acquisition and subsequently shifted to extinction.

birds had received training in this situation in the preliminary experiment. The FR 10 requirement resulted in a pattern of acquisition and extinction data that resembled the data obtained in the preliminary experiment with an FR 1 schedule, although the magnitude of the group differences in extinction was larger. There was no evidence for the MREE; in fact, extinction yielded evidence of an anti-MREE, that is, better and slower extinction performance after acquisition with the large reward magnitude than after acquisition with the small reward magnitude.

Group  $\times$  Block analyses of variance yielded the following results. For the acquisition data, the only significant result was an acquisition effect in the FR latency,  $F(9, 81) = 6.35$ . None of the other factors reached a significant level ( $F_s < 2.08$ ). Analyses of the extinction data yielded for both dependent measures significant extinction effects,  $F_s(7, 63) > 7.27$ . More important, the Group  $\times$  Block interaction was significant for the FR latency measure,  $F(7, 63) = 2.17$ . The other effects did not achieve a significant level ( $F_s < 2.85$ ). The significant interaction in FR latencies indicates that extinction was faster after reinforcement with 1 pellet than after reinforcement with 10 pellets.

## Experiment 2

The results of Experiment 1 were unexpected. On the basis of Roberts et al.'s (1963) successful demonstration of the PREE in a runway situation, I anticipated that other related paradoxical effects would be observed in the key-pecking situation. Experiment 2 was designed to provide further information on the control of key-pecking performance by reward magnitude under spaced-trial conditions. Naive pigeons were again trained on an FR 10 schedule reinforced with either 1 or 15 pellets and subsequently extinguished. One of the groups trained with 15 pellets was shifted to 1 pellet after 40 trials and remained in the shifted condition for a total of 20 trials. A comparison of this 15-to-1 group with a control group receiving always 1 pellet allowed for an evaluation of the SNCE. The choice of 20 postshift trials and the increase from 10 (Experiment 1) to 15 pellets in the large reward condition are justified in light of available evidence. In rats, the spaced-trial SNCE is notable by its rapid development: Significant behavioral changes are typically observed after the first shift trial, and behavior deteriorates further within the following few trials (e.g., Crespi, 1942; DiLollo, 1964; Elliott, 1928; Spence, 1956). Moreover, the size of the SNCE is known to increase directly with the size of the magnitude shift (DiLollo & Beez, 1966).

The design also allowed for a comparison of extinction performance after acquisition with either 1 or 15 pellets. This time, however, there were 60 acquisition trials (rather than 40, as in Experiment 1); overtraining generally accelerates extinction (Ishida & Papini, 1997), and thus I assumed that extending the acquisition phase would enhance the chances of observing the paradoxical MREE.

## Method

*Subjects and apparatus.* The subjects were 15 white carneaux pigeons obtained from the Palmetto Pigeon Plant, South Carolina. Pigeons were sexually mature and experimentally naive. The housing and maintenance conditions and the apparatus used during the experiment were those described in Experiment 1.

*Procedure.* Preliminary training was as described in Experiment 1 with one exception: Subjects were shifted from an FR 1 to an FR 10 by increasing the ratio requirement in steps of one response. This made the pretraining phase longer but reduced behavioral disruptions that had been occasionally seen in previous experiments when incrementing an FR value by two responses. At the end of the pretraining phase, subjects were randomly assigned to three groups ( $n = 5$ ). The structure of the daily sessions was the same as described in Experiment 1. The presentation of the plus stimulus ended in either the delivery of 1 pellet, the delivery of 15 pellets, or nonreward, depending on the group and phase of training. Groups 1 and 15 received 1 and 15 pellets during 60 daily trials and thereafter were shifted to extinction for an additional 40 daily trials. Subjects in Group 15-1 received 15 pellets during the initial 40 daily trials and were subsequently shifted to 1 pellet for 20 additional trials. Thus, the effect of a 15-to-1 downward shift was assessed in Group 15-1 by comparing the performance of Groups 1 and 15-1 on Trials 41 to 60. The effects of reward magnitude on extinction were assessed between Trials 61 and 100 in Groups 1 and 15.

## Results

In the pretraining phase, pigeons reached the performance criterion in 29.3 (range = 23–43), 53 (range = 28–92), and 48.6 (range = 27–110) sessions in Groups 1, 15, and 15-1, respectively. The main results are shown in Figure 3, where the performance of all groups is plotted as a function of four-trial blocks, in terms of the ln of the initial latency (left panel) and of the FR latency (right panel). Blocks 1 to 10 provide information about acquisition, Blocks 11 to 15 provide information about the effects of a downward shift in reward magnitude on instrumental key-pecking performance (the shift is marked by an arrow), and Blocks 16 to 25 provide information about extinction.

During the initial 10 blocks of acquisition, Groups 15 and 15-1, both receiving 15 pellets per trial, initiated the key-pecking sequence more quickly than the group trained with only 1 pellet. A statistical analysis indicated a significant effect of group,  $F(2, 12) = 4.08$ , and a significant acquisition effect across blocks,  $F(9, 108) = 6.25$ . The interaction between these factors was not significant,  $F(18, 108) = 1.14$ . A similar difference was observed in terms of the FR latency, but the statistical analysis yielded a significant effect only for blocks,  $F(9, 108) = 6.30$ ; the effects of group,  $F(2, 12) = 1.42$ , and the Group  $\times$  Block interaction ( $F < 1$ ) were not significant.

After the shift from 15 pellets to 1 (see arrow in Figure 3), both initial and FR latencies of Group 15-1 gradually approached the level of Group 1 and moved away from the level of Group 15 (this is particularly clear in the initial latency measure). There was, however, no indication of an SNCE, that is, the performance of Group 15-1 did not deteriorate beyond that of Group 1. Analyses of the performance of Groups 15-1 and 1 for both dependent measures

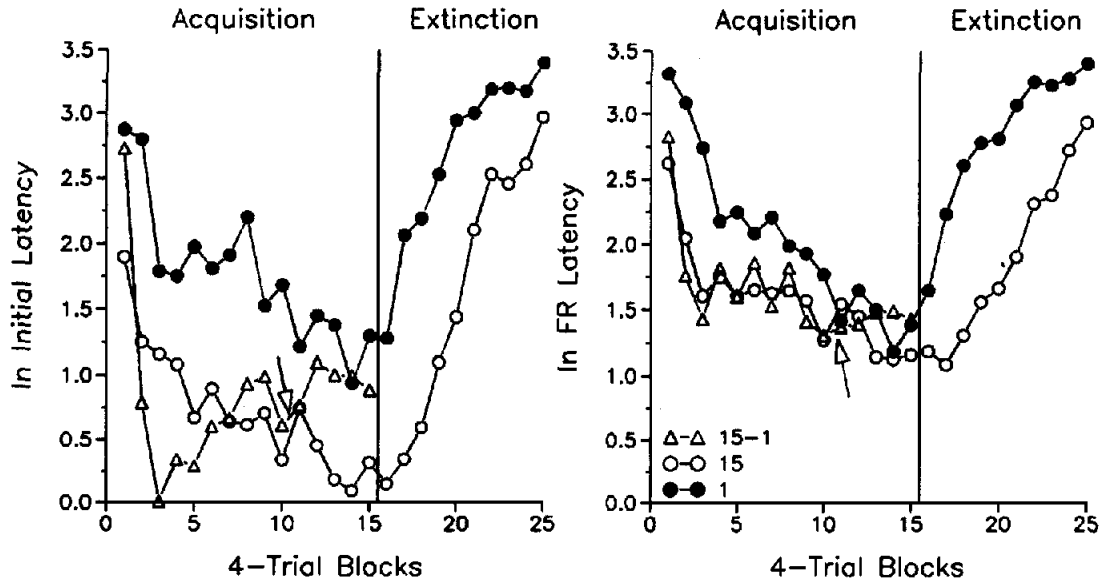


Figure 3. Initial and fixed-ratio (FR) latency (natural logarithm [ln]) results are presented in the left and right panels, respectively, for groups of pigeons reinforced with either 1 or 15 food pellets during acquisition and subsequently shifted to extinction. One of the groups (open triangles) was subjected to a downward shift in reward magnitude from 15 pellets to 1 pellet at the point marked by the arrow.

and during Blocks 11 to 15 indicated that none of the factors reached statistical significance ( $F_s < 1.01$ ). This lack of statistical significance is particularly informative in the case of the initial latencies, given that Groups 15-1 and 1 were performing at different levels before the shift. The 15-to-1 shift had a measurable effect on postshift performance, although it did not result in an SNCE but only in a gradual change in performance level.

Figure 3 also shows the acquisition and extinction results for Groups 1 and 15. The effect of reward magnitude on acquisition was clearer in initial latencies than in FR latencies. In both measures, however, extinction performance again provided evidence for an anti-MREE: lower response latencies after acquisition with a large reward than those after acquisition with a small reward. Statistical analyses of Blocks 1 to 15 showed significant acquisition effects in both measures,  $F_s(14, 112) > 3.57$ . The group effect for the initial latencies fell short of statistical significance,  $F(1, 8) = 5.08, p < .055$ . All the other effects were nonsignificant ( $F_s < 1.70$ ). Extinction performance of Group 15 was significantly better than that of Group 1 for both initial latencies,  $F(1, 8) = 10.23$ , and FR latencies,  $F(1, 8) = 8.98$ . There was also a significant block effect for both dependent measures,  $F_s(9, 72) > 8.68$ , but no significant Group  $\times$  Block interactions ( $F_s < 1.39$ ). Unlike subjects in Experiment 1, then, groups trained with different reward magnitudes did not differ in their extinction rate (nonsignificant interactions) but rather in their performance level.

### Experiment 3

Experiments 1 and 2 provided evidence that reward magnitude produced differential performance. Statistically

significant group differences were obtained either in terms of an overall simple main effect of group in the initial latency in acquisition (Experiment 2) or in both measures in extinction (Experiments 1 and 2). Experiment 3 sought evidence of differential control of key pecking by different reward magnitudes in a within-subject design. A group of pigeons was trained with two stimuli paired with either 1 or 15 pellets. Discrimination training was administered at a rate of a single trial per day. The design is thus very similar to a simultaneous negative contrast experiment, with the exception that these studies are usually carried out in sessions with multiple trials (for an example with pigeons, see Gonzalez & Champlin, 1974). Therefore, the design included a control group that received training with either one or the other stimulus, counterbalanced across subjects, but was reinforced consistently with a single pellet. A comparison of the performance of both groups in equivalent trials in which they were reinforced with 1 pellet would determine the presence of simultaneous negative contrast.

In addition, all the animals were eventually shifted to extinction. An interesting prediction follows from frustration theory when animals subjected to different conditions of reinforcement are shifted to extinction. Amsel (1992) suggested that common mediating expectancies (i.e., anticipatory frustration) can override the control exerted over behavior by external stimuli, thus leading to generalization across conditions. Some experiments show, for example, that rats trained in one runway under continuous reinforcement, and in a discriminably different runway under partial reinforcement, do not show differential persistence in extinction (i.e., no within-subject PREE; Amsel, Rashotte, & MacKinnon, 1966; Brown & Logan, 1965). If this explana-

tion is applied to the present situation, frustration theory predicts that the extinction performance of the stimuli previously paired with 1 and 15 pellets should rapidly converge to become nondifferential, even if acquisition performance was differential. This would be based on the common properties of a mediating internal response of anticipatory frustration, generated by the unexpected omission of the rewards in both types of extinction trials.

In contrast, the results obtained in Experiments 1 and 2 would be consistent with extinction rates that remain differential across the two stimuli trained with different reward magnitudes. This is so because key-pecking performance in the present training situation appears to be controlled in a simple, strengthening–weakening fashion, by reward magnitude (Couvillon & Bitterman, 1985a; Papini & Bitterman, 1991). If reward magnitude controls the strength of a particular stimulus and nonreward causes decrements in stimulus strength without inducing an emotional reaction (cf. Papini & Dudley, 1997), then extinction of the stimuli paired with different magnitudes should proceed independently.

### Method

**Subjects and apparatus.** The subjects were 10 naive pigeons obtained from a local dealer. They were all sexually mature, but their age and sex were not determined. The same conditions of housing and maintenance and the same apparatus described in Experiment 1 were used in Experiment 3.

**Procedure.** Subjects were pretrained following the same procedure described in Experiment 1 until they consistently responded

on an FR 10 schedule. Pigeons were subsequently assigned randomly to two groups.

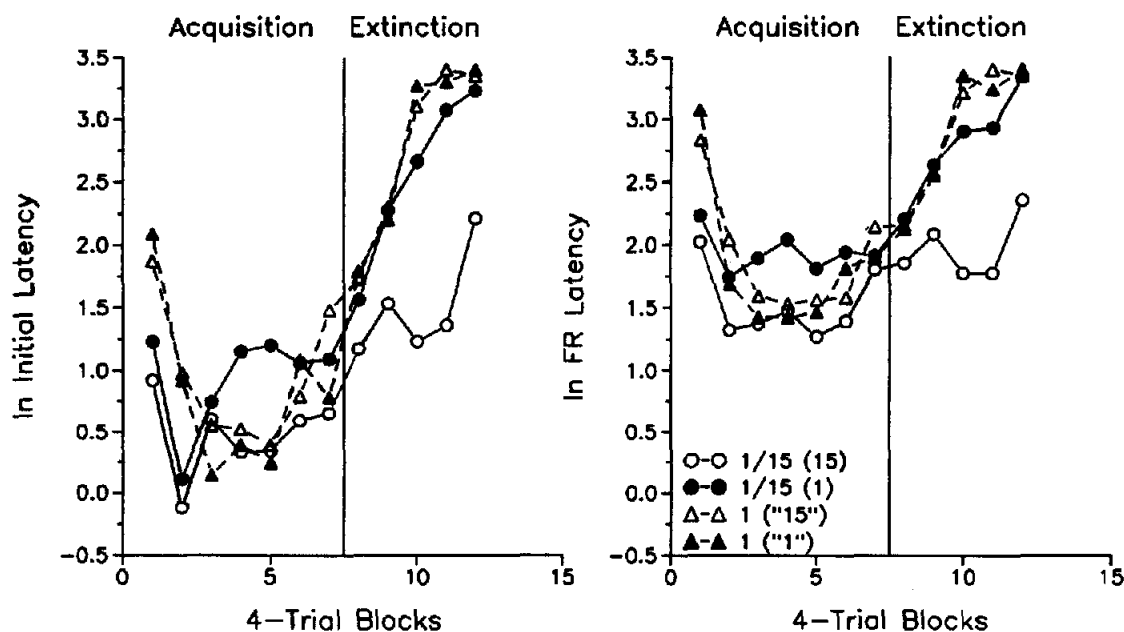
Group 1/15 ( $n = 6$ ) received training with two stimuli (the plus sign and a green key light) paired with either 1 or 15 pellets. Three pigeons received plus–1 and green–15 trials, whereas the rest received plus–15 and green–1 trials. The trials were administered in Gellermann order. In all other respects, training trials were as described in Experiment 1. There were 56 daily trials of acquisition, of which 28 trials were administered with each stimulus, followed by 40 extinction trials, 20 with each stimulus.

Two of the pigeons assigned to Group 1 ( $n = 4$ ) were trained with the plus sign stimulus, whereas the other 2 were trained with the green stimulus. In all cases, trials ended with the administration of a single food pellet. In all other respects, the procedure was equal to that described in Experiments 1 and 2.

### Results

Pigeons achieved the pretraining criterion in 32.3 (range = 29–37) and 33.7 (range = 30–40) sessions for Groups 1 and 1/15, respectively. The main results of this experiment are presented in Figure 4, again in terms of the  $\ln$  of initial (left panel) and FR latencies (right panel). The performance of Group 1 was segregated according to trials that corresponded, in their order, to those reinforced with 1 and 15 pellets in Group 1/15. However, all the trials in Group 1 ended with the delivery of 1 food pellet.

During the acquisition phase, Group 1/15 exhibited clear evidence of differential performance in both latency measures, responding more quickly to the stimulus paired with 15 pellets than to the stimulus paired with 1 pellet. In Blocks 3–5, the average latencies to the stimulus paired with 1 pellet



**Figure 4.** Initial and fixed-ratio (FR) latency (natural logarithm [ $\ln$ ]) results are presented in the left and right panels, respectively. In Group 1/15 key pecking was reinforced with 1 or 15 food pellets, depending on the stimulus present in a particular trial. Group 1 received the same stimuli but responding was reinforced with 1 pellet. The functions labeled "1" and "15" in Group 1 correspond to trials that matched, in terms of their order, the trials reinforced with 1 and 15 pellets in Group 1/15.

increased above the level of Group 1, thus suggesting simultaneous negative contrast, but this difference was only transient. Separate analyses of variance were performed on various pairwise combinations. An analysis of Group 1/15's latencies indicated a significant effect of reward magnitude for both the initial latency,  $F(1, 65) = 8.23$ , and the FR latency,  $F(1, 65) = 14.09$ . The acquisition effect was significant for the initial latency,  $F(6, 65) = 2.44$ , and only marginally significant for the FR latency,  $F(6, 65) = 2.15$ ,  $p < .06$ . The Trial  $\times$  Block interactions did not achieve a significant level in any of the measures ( $F_s < 1$ ). A similar analysis for Group 1 yielded a significant acquisition effect for the two measures,  $F_s(6, 39) > 8.34$ ; all the other effects were nonsignificant ( $F_s < 1$ ).

An analysis of the performance on trials reinforced with 1 pellet in Group 1/15 and the equivalent trials in Group 1 provided no evidence of simultaneous negative contrast in terms of group effects ( $F_s < 1$ ). The acquisition effect was significant in both dependent variables,  $F_s(6, 48) > 2.29$ . Whereas the Group  $\times$  Block interaction was not significant in the case of the initial latency,  $F(6, 48) = 1.88$ , it did achieve a significant level in the case of the FR latency,  $F(6, 48) = 2.43$ . Because the two functions under analysis cross over in Block 2 (see Figure 4, right panel), it is not clear whether the interaction effect is due to this crossing over or to a significant simultaneous contrast in Blocks 3–5. Pairwise comparisons were therefore computed on these blocks and on the basis of the overall analysis, according to Howell's (1990) method. Groups 1 and 1/15 did not differ in their performance on the 1 pellet trials, in Blocks 3–5, and in terms of their FR latency,  $F_s(1, 17) < 1.51$ . There was no evidence for simultaneous contrast in these data.

Figure 4 also shows the extinction results. For both dependent measures, extinction was mainly a function of the magnitude of reinforcement experienced during acquisition. Particularly important is the differential resistance to extinction observed in Group 1/15 for each type of trial; extinction proceeded more slowly for the signal paired with 1 pellet than for the signal paired with 15 pellets during discrimination training. Trial  $\times$  Block analyses for Group 1/15 and for both dependent measures indicated a significant extinction effect,  $F_s(4, 45) > 2.87$ , and significantly shorter latencies for the stimulus associated with the large reward than for the stimulus associated with the small reward,  $F_s(1, 45) > 25.95$ . The Trial  $\times$  Block interaction was not significant in any of the measures,  $F_s(4, 45) < 1.12$ . A similar set of analyses for Group 1 yielded significant extinction effects for only the two dependent variables,  $F_s(4, 27) > 6.50$ ; all other simple and interaction effects were nonsignificant ( $F_s < 1$ ). Finally, an analysis of the performance of both groups in the trials with the stimulus previously paired with 1 pellet indicated, for both types of latency, a significant extinction effect,  $F_s(4, 32) > 5.58$ , but nonsignificant group or Group  $\times$  Block effects ( $F_s < 1$ ). Contrary to a prediction derived from frustration theory, the difference in key-pecking performance maintained by the two reward magnitudes persisted during extinction.

## General Discussion

These experiments provide evidence of the behavioral adjustment of an avian species to shifts in reward magnitude under widely spaced training conditions. A shift from a large to a small (or zero) magnitude produces clear evidence of nonparadoxical behavior. Extinction performance is better or faster after training with large rewards than after training with small rewards, and a shift from a large to a small reward produces an adjustment of performance without contrast. These results have been obtained with different large magnitudes (10 and 15 pellets), different amounts of training before extinction (40 and 60 trials), and different dependent measures (initial and FR latencies). The absence of paradoxical behavior cannot be attributed to an insufficient number of training sessions, either in acquisition or in extinction, or to performance ceilings. These results cannot be attributed either to a failure by the pigeons to notice the different reward magnitudes; discrimination of reward magnitude was observed in both between- and within-subject designs. Experiment 3 provided clear evidence of magnitude discrimination and, at the same time, no evidence of a spaced-trial simultaneous negative contrast effect. Under the present conditions, extinction performance depended on the magnitude of the reward experienced during acquisition trials. Moreover, when a single animal experienced the extinction of stimuli paired with different reward magnitudes, extinction rates depended mostly on the individual stimulus' history of reinforcement. In sum, there was no indication of paradoxical behavior in these results.

These findings have implications at both the mechanistic and evolutionary levels. At the level of the underlying mechanisms, the present results were unexpected for several reasons. First, there is a demonstration of the spaced-trial PREE in pigeons (Roberts et al., 1963) that led to the expectation that similar paradoxical performance would be obtained under the present training conditions. This prediction was based on the all-or-none nature of the spaced-trial paradoxical phenomena in rats. Moreover, the PREE, MREE, and SNCE are thought to be determined by a set of related processes (Amsel, 1992). There is also evidence of emotional reactions akin to primary frustration in pigeons that could be taken as prerequisite for the paradoxical performance dependent on the anticipation of such frustrative reactions (see Papini & Dudley, 1997). For example, pigeons react aggressively during the presentation of signals for nonreward, particularly early in discrimination training (Terrace, 1971), and also during the early portions of extinction (Azrin, Hutchinson, & Hake, 1966). Pigeons also learn a new response that has as its only consequence the elimination of a stimulus paired with nonreward or with a lower reward density (Rilling, Askew, Ahlskog, & Kramer, 1969; Terrace, 1971). These results strongly suggest that pigeons find unexpected reinforcer omissions frustrating or aversive. It is less clear whether pigeons can actually learn to anticipate such emotional responses based on the unexpected omission of rewards, which is precisely the implication that follows from Roberts et al.'s (1963) demonstration of the PREE.



A comparison of the training procedures used by Roberts et al. (1963) and those used in the present experiments indicates many potentially important differences that might account for the discrepancy in the results. First, the responses were different: running in a runway versus pecking at a key. Although it is not typical for the outcome of spaced-trial experiments to depend critically on the selected response, there are many documented cases of response bias in other learning situations (e.g., LoLordo & Droungas, 1989). It has even been argued, on the basis of foraging considerations, that running and key pecking (or lever pressing in rats) correspond to food searching and procurement and, therefore, may depend on different underlying mechanisms (Mellgren & Elsmore, 1991). This does not appear to be a factor in rats, which show the spaced-trial PREE in both runway and lever-pressing situations (McNaughton, 1984; Weinstock, 1954). Additional research needs to be done, in particular with manipulations of reward magnitude, to replicate and extend both Roberts et al.'s runway results with pigeons and McNaughton's lever-pressing results with rats. Along the same line, it would be informative to extend the analysis of the effects of reward schedule and magnitude in birds to include other responses (e.g., treadle pressing), response requirements (e.g., higher ratio requirements), and rewards (e.g., grain, water, sexual reinforcement).

A second procedural difference concerns the manner in which the reinforcement contingencies were enforced in these experiments. For example, consider how Roberts et al. (1963) handled the trials in which pigeons failed to respond in comparison with the present procedure. In the former case, pigeons were gently guided toward the goal box of the runway where they received the scheduled outcome. In the latter case, the cue was maintained for a maximum amount of time and, if the pigeon failed to peck at the key, the scheduled outcome was administered. One critical difference is that whereas in the runway the outcome was contingent with a response similar to the regular running response, in the key-pecking situation the outcome was probably rarely, if ever, administered while the pigeon was pecking (although in some cases the pigeons might have been engaging in weak pecking responses that did not result in the operation of the pellet delivery mechanism). Whereas both procedures ensured the scheduled outcome, independently of whether or not the pigeon completed the required response, the procedure used in the present experiments might have had a significant Pavlovian component (i.e., response-independent outcomes). The magnitude of this potential problem can be directly estimated by calculating the number of training trials in which the pigeons failed to respond. This information is presented in Table 1. There were consistently more sessions without responding in the small magnitude conditions than in the large magnitude conditions, although the percentage of trials without responding was generally low (except for Group 1, Experiment 2, which failed to respond in one third of the acquisition trials). More important, despite a more than fourfold degree of disruption (e.g., from 7.5 to 33.4%) exhibited by the various groups trained with 1 pellet, they consistently showed

Table 1  
*Mean Percentage of Trials  
in Which Pigeons Failed to Respond*

Group	Failure (%)	Trials
Experiment 1		
1	7.5	40
10	0.4	40
Experiment 2		
1	33.4	60
15	9.7	60
15-1	14.0	40
Experiment 3		
1/15, 1 pellet	16.1	28
1/15, 15 pellets	2.4	28
1	9.4	56

poorer extinction performance than did the groups receiving large magnitudes. Furthermore, unpublished results of an experiment in which purely instrumental training contingencies were used during both pretraining and spaced-trial acquisition also showed poorer extinction performance after acquisition with 1 pellet than after acquisition with 15 pellets. It is unlikely, therefore, that the present results depend critically on this procedural feature.

Another procedural difference between these experiments concerns the amount of pretraining. Roberts et al. (1963) provided no pretraining; pigeons readily engaged in food searching in the runway situation. In contrast, in the key-pecking situation, pigeons had to be extensively pre-trained to find food and to habituate to the noise produced by the pellet dispenser. Judging from the similar levels of performance obtained early in acquisition and late in extinction (e.g., Figure 3), it would appear that there was little positive transfer from pretraining to acquisition; positive transfer would have resulted in a lower response level early in acquisition than it would have later in extinction. The different stimuli used in each of these phases (a white light and a plus sign) may have contributed to disrupt performance early in acquisition. It would be interesting to determine if one-trial-per-day performance can be shaped when only magazine training is provided.

These results also have implications at the evolutionary level. As anticipated, nonparadoxical performance in the present key-pecking situation is consistent with an independent-origin hypothesis (see 2 and 2' in Figure 1). According to this hypothesis, because paradoxical performance in birds and mammals is based on different mechanisms as a result of convergent evolution, different types of interactions between training parameters and the behavioral adjustments they induce would be expected. For example, the choice of an operant or an instrumental response could be more critical for pigeons than it appears to be for rats. The experiments proposed earlier should clarify this issue. It is also possible that the paradoxical phenomena are dissociable in some species, just as they seem to be for developing rats. For example, whereas 12–14-day-old rats show clear evidence of the PREE, they show neither the MREE nor the SNCE,

both of which appear after 20 days (Amsel, 1992). Daly (1991) has successfully simulated this developmental dissociation by assuming that the PREE requires a weaker emotional reaction to unexpected nonreward than that required by the MREE and SNCE. It is possible that paradoxical performance in pigeons could be restricted to situations involving partial reinforcement, which, after all, have produced some evidence of paradoxical behavior that cannot be attributed to stimulus aftereffects from prior trials (Couvillon, Brandon, Woodard, & Bitterman, 1980; Roberts et al., 1963). Finally, it is possible too that the conclusion that pigeons in particular, and birds in general, show paradoxical performance is simply incorrect. Based, as it is, on the results of a single spaced-trial experiment (Roberts et al., 1963), it is not a particularly strong generalization. It is still possible, therefore, that paradoxical mechanisms are uniquely mammalian.

It would seem premature to try to outline a theory of the evolution of paradoxical mechanisms in vertebrates given a rather limited taxonomic database. There is a need for behavioral and neurobiological analyses of paradoxical and nonparadoxical behavior in a variety of groups. Entire classes of vertebrates (e.g., jawless and cartilaginous fishes) and some major taxonomic groups (e.g., salamanders, snakes, monotremes) are still completely absent from this data base. I am hopeful that the refutability of the evolutionary hypotheses discussed in this article will provide the theoretical impetus for additional comparative research in this area.

## References

- Amsel, A. (1992). *Frustration theory*. Cambridge, England: Cambridge University Press.
- Amsel, A., Rashotte, M. E., & MacKinnon, J. R. (1966). Partial reinforcement effects within subjects and between subjects. *Psychological Monographs*, *80* (Whole No. 628).
- Avers, C. J. (1989). *Process and pattern in evolution*. New York: Oxford University Press.
- Azrin, N. H., Hutchinson, R. R., & Hake, D. F. (1966). Extinction-induced aggression. *Journal of the Experimental Analysis of Behavior*, *9*, 191–204.
- Benton, M. J. (1990). Phylogeny of the major tetrapod groups: Morphological data and divergence dates. *Journal of Molecular Evolution*, *30*, 409–424.
- Bitterman, M. E. (1960). Toward a comparative psychology of learning. *American Psychologist*, *15*, 704–712.
- Bitterman, M. E. (1975, May 16). The comparative analysis of learning. *Science*, *188*, 699–709.
- Boitano, J. J., & Foskett, M. D. (1968). Effects of partial reinforcement on speed of approach responses in goldfish (*Carassius auratus*). *Psychological Reports*, *22*, 741–744.
- Bonner, J. T. (1988). *The evolution of complexity by means of natural selection*. Princeton, NJ: Princeton University Press.
- Brown, R. T., & Logan, F. A. (1965). Generalized partial reinforcement effect. *Journal of Comparative and Physiological Psychology*, *60*, 64–69.
- Bullock, T. H. (1993). How are more complex brains different? *Brain, Behavior and Evolution*, *41*, 88–96.
- Burghardt, G. M. (1988). Precocity, play, and the ectotherm-therm transition. In E. M. Blass (Ed.), *Developmental psychobiology and behavioral ecology* (pp. 107–148). New York: Plenum.
- Butler, A. B. (1994). The evolution of the dorsal pallium in the telencephalon of amniotes: Cladistic analysis and a new hypothesis. *Brain Research Reviews*, *19*, 66–101.
- Cai, Z. (1991). The functions of sleep: Further analysis. *Physiology and Behavior*, *50*, 53–60.
- Couvillon, P. A., & Bitterman, M. E. (1985a). Analysis of choice in honeybees. *Animal Learning and Behavior*, *13*, 246–252.
- Couvillon, P. A., & Bitterman, M. E. (1985b). Effect of experience with a preferred food on consummatory responding for a less preferred food in goldfish. *Animal Learning and Behavior*, *13*, 433–438.
- Couvillon, P. A., Brandon, S. E., Woodard, W. T., & Bitterman, M. E. (1980). Performance of pigeons in patterned sequences of rewarded and nonrewarded trials. *Journal of Experimental Psychology: Animal Behavior Processes*, *6*, 137–154.
- Crespi, L. P. (1942). Quantitative variation of incentive and performance in the white rat. *American Journal of Psychology*, *55*, 467–517.
- Daly, H. B. (1991). Changes in learning about aversive nonreward accounts for ontogeny of paradoxical appetitive reward effects in the rat pup: A mathematical model (DMOD) integrates results. *Psychological Bulletin*, *109*, 325–339.
- DiLollo, V. (1964). Runway performance in relation to runway-goal-box similarity and changes in incentive amount. *Journal of Comparative and Physiological Psychology*, *55*, 578–581.
- DiLollo, V., & Beez, V. (1966). Negative contrast effect as a function of magnitude of reward decrement. *Psychonomic Science*, *5*, 99–100.
- Eisenberger, R. (1992). Learned industriousness. *Psychological Review*, *99*, 248–267.
- Elliott, M. H. (1928). The effect of change of reward on the maze performance of rats. *University of California Publications in Psychology*, *4*, 19–30.
- Gonzalez, R. C., Behrend, E. R., & Bitterman, M. E. (1965). Partial reinforcement in the fish: Experiments with spaced trials and partial delay. *American Journal of Psychology*, *78*, 198–207.
- Gonzalez, R. C., & Bitterman, M. E. (1962). A further study of partial reinforcement in the turtle. *Quarterly Journal of Experimental Psychology*, *14*, 109–112.
- Gonzalez, R. C., & Champlin, G. (1974). Positive behavioral contrast, negative simultaneous contrast, and their relation to frustration in pigeons. *Journal of Comparative and Physiological Psychology*, *87*, 173–187.
- Gonzalez, R. C., Holmes, N. K., & Bitterman, M. E. (1967). Resistance to extinction in the goldfish as a function of frequency and amount of reward. *American Journal of Psychology*, *80*, 269–275.
- Gonzalez, R. C., Potts, A., Pitcoff, K., & Bitterman, M. E. (1972). Runway performance of goldfish as a function of complete and incomplete reduction in amount of reward. *Psychonomic Science*, *27*, 305–307.
- Graf, C. L. (1972). Spaced-trial partial reward in the lizard. *Psychonomic Science*, *27*, 153–154.
- Howell, D. C. (1990). *Statistical methods for psychology* (3rd ed.). Boston: PWS-KENT.
- Hulse, S. H., Jr. (1958). Amount and percentage of reinforcement and duration of goal confinement in conditioning and extinction. *Journal of Experimental Psychology*, *56*, 48–57.
- Ishida, M., & Papini, M. R. (1993). Spaced training and instrumental performance in the turtle (*Geoclemys reevesii*). *Memoirs of Osaka Kyoiku University*, *41*, 153–161.

- Ishida, M., & Papini, M. R. (1997). Massed-trial overtraining effects on extinction and reversal performance of turtles (*Geoclemys reevesii*). *Quarterly Journal of Experimental Psychology*, *50B*, 1-16.
- Kennedy, M., Spencer, H. G., & Gray, R. D. (1996). Hop, step and gape: Do the social displays of the Pelecaniformes reflect phylogeny? *Animal Behaviour*, *51*, 273-291.
- Lawrence, D. H., & Festinger, L. (1962). *Deterrents and reinforcement: The psychology of insufficient reward*. Stanford, CA: Stanford University Press.
- LoLordo, V. M., & Droungas, A. (1989). Selective associations and adaptive specializations: Taste aversions and phobias. In S. B. Klein & R. R. Mowrer (Eds.), *Contemporary learning theories: Instrumental conditioning theory and the impact of biological constraints on learning* (pp. 145-179). Hillsdale, NJ: Erlbaum.
- Longo, N., & Bitterman, M. E. (1960). The effect of partial reinforcement with spaced practice on resistance to extinction in the fish. *Journal of Comparative and Physiological Psychology*, *53*, 169-172.
- Lowes, G., & Bitterman, M. E. (1967, July 28). Reward and learning in the goldfish. *Science*, *157*, 455-457.
- Macphail, E. M. (1982). *Brain and intelligence in vertebrates*. Oxford, England: Clarendon Press.
- McNaughton, N. (1984). Effects of anxiolytic drugs on the partial reinforcement effect in runway and Skinner box. *Quarterly Journal of Experimental Psychology*, *36B*, 319-330.
- McShea, D. W. (1996). Metazoan complexity and evolution: Is there a trend? *Evolution*, *50*, 477-492.
- Mellgren, R. L., & Elsmore, T. F. (1991). Extinction of operant behavior: An analysis based on foraging considerations. *Animal Learning and Behavior*, *19*, 317-325.
- Muzio, R. N., Segura, E. T., & Papini, M. R. (1992). Effect of schedule and magnitude of reinforcement on instrumental learning in the toad, *Bufo arenarum*. *Learning and Motivation*, *23*, 406-429.
- Muzio, R. N., Segura, E. T., & Papini, M. R. (1993). Effect of lesions in the medial pallium on instrumental learning in the toad (*Bufo arenarum*). *Physiology and Behavior*, *54*, 185-188.
- Muzio, R. N., Segura, E. T., & Papini, M. R. (1994). Learning under partial reinforcement in the toad (*Bufo arenarum*): Effects of lesions in the medial pallium. *Behavioral and Neural Biology*, *61*, 36-46.
- Northcutt, R. G. (1987). Evolution of the vertebrate brain. In G. Adelman (Ed.), *Encyclopedia of neuroscience* (Vol. 1, pp. 415-418). Boston: Birkhauser.
- Northcutt, R. G., & Kaas, J. H. (1995). The emergence and evolution of mammalian neocortex. *Trends in Neurosciences*, *18*, 373-379.
- Papini, M. R. (1987). The quest for divergent mechanisms in vertebrate learning. *Behavioral and Brain Sciences*, *10*, 676-677.
- Papini, M. R., & Bitterman, M. E. (1991). Appetitive conditioning in *Octopus cyanea*. *Journal of Comparative Psychology*, *105*, 107-114.
- Papini, M. R., & Dudley, R. T. (1997). Consequences of surprising reward omissions. *Review of General Psychology*, *1*, 175-197.
- Papini, M. R., & Ishida, M. (1994). Role of magnitude of reinforcement in spaced-trial instrumental learning in turtles (*Geoclemys reevesii*). *Quarterly Journal of Experimental Psychology*, *47B*, 1-13.
- Papini, M. R., Mustaca, A. E., & Bitterman, M. E. (1988). Successive negative contrast in the consummatory responding of didelphid marsupials. *Animal Learning and Behavior*, *16*, 53-57.
- Papini, M. R., Muzio, R. N., & Segura, E. T. (1995). Instrumental learning in toads (*Bufo arenarum*): Reinforcer magnitude and the medial pallium. *Brain, Behavior and Evolution*, *46*, 61-71.
- Pert, A., & Bitterman, M. E. (1970). Reward and learning in the turtle. *Learning and Motivation*, *1*, 121-128.
- Rashotte, M. E., & Surridge, C. T. (1969). Partial reinforcement and partial delay of reinforcement effects with 72-hour intertrial intervals and interpolated continuous reinforcement. *Quarterly Journal of Experimental Psychology*, *21*, 156-161.
- Rilling, M., Askew, H. R., Ahlskog, J. E., & Kramer, T. J. (1969). Aversive properties of the negative stimulus in a successive discrimination. *Journal of the Experimental Analysis of Behavior*, *12*, 917-932.
- Roberts, W. A., Bullock, D. H., & Bitterman, M. E. (1963). Resistance to extinction in the pigeon after partially reinforced instrumental training under discrete-trials conditions. *American Journal of Psychology*, *76*, 353-365.
- Ruben, J. (1995). The evolution of endothermy in mammals and birds: From physiology to fossils. *Annual Review of Physiology*, *57*, 69-95.
- Schutz, S. L., & Bitterman, M. E. (1969). Spaced-trials partial reinforcement and resistance to extinction in the goldfish. *Journal of Comparative and Physiological Psychology*, *68*, 126-128.
- Spence, K. W. (1956). *Behavior theory and conditioning*. New Haven, CT: Yale University Press.
- Terrace, H. S. (1971). Escape from S-. *Learning and Motivation*, *2*, 148-163.
- Thorndike, E. L. (1911). *Animal intelligence: Experimental studies*. New York: Macmillan.
- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, *20*, 410-433.
- Tinklepaugh, O. (1928). An experimental study of representative factors in monkeys. *Journal of Comparative Psychology*, *8*, 197-236.
- Weinstock, S. (1954). Resistance to extinction of a running response following partial reinforcement under widely spaced trials. *Journal of Comparative and Physiological Psychology*, *47*, 318-322.
- Wyles, J. S., Kunkel, J. G., & Wilson, A. C. (1983). Birds, behavior, and anatomical evolution. *Proceedings of the National Academy of Sciences, USA*, *80*, 4394-4397.

Received August 8, 1996

Revision received November 21, 1996

Accepted January 30, 1997 ■