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Abstract:
This review focuses on reward-schedule effects, a family of learning phenomena involving surprising devaluations in reward quality or quantity (as in incentive contrast), and reward omissions (as in appetitive extinction), as studied in three taxonomic groups of vertebrates:

mammals, birds, and amphibians. The largest database of dependable data comes from research with mammals in general, and with rats in particular. These experiments show a variety of behavioral adjustments to situations involving reward downshifts. For example, rats show disruption of instrumental and consummatory behavior directed at a small reward after receiving a substantially larger reward (called successive negative contrast, SNC)—a *reward-schedule effect*. However, instrumental SNC does not seem to occur when animals work for sucrose solutions—a *reversed* reward-schedule effect. Similar modes of adjustment have been reported in analogous experiments with avian and amphibian species. A review of the evidence suggests that carry-over signals across successive trials can acquire control over behavior under massed practice, but emotional memory is required to account for reward-schedule effects observed under widely spaced practice. There is evidence for an emotional component to reward-schedule effects in mammals, but similar evidence for other vertebrates is scanty and inconsistent. Progress in the comparative analysis of reward-schedule effects will require the intense study of a set of selected species, in selected reward-downshift situations, and aiming at identifying underlying neural mechanisms.

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Diversity of Adjustments to Reward Downshifts in Vertebrates

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This review focuses on reward-schedule effects, a family of learning phenomena involving surprising devaluations in reward quality or quantity (as in incentive contrast), and reward omissions (as in appetitive extinction), as studied in three taxonomic groups of vertebrates: mammals, birds, and amphibians. The largest database of dependable data comes from research with mammals in general, and with rats in particular. These experiments show a variety of behavioral adjustments to situations involving reward downshifts. For example, rats show disruption of instrumental and consummatory behavior directed at a small reward after receiving a substantially larger reward (called successive negative contrast, SNC)—a *reward-schedule effect*. However, instrumental SNC does not seem to occur when animals work for sucrose solutions—a *reversed* reward-schedule effect. Similar modes of adjustment have been reported in analogous experiments with avian and amphibian species. A review of the evidence suggests that carry-over signals across successive trials can acquire control over behavior under massed practice, but emotional memory is required to account for reward-schedule effects observed under widely spaced practice. There is evidence for an emotional component to reward-schedule effects in mammals, but similar evidence for other vertebrates is scanty and inconsistent. Progress in the comparative analysis of reward-schedule effects will require the intense study of a set of selected species, in selected reward-downshift situations, and aiming at identifying underlying neural mechanisms.

Bitterman (1975) reviewed evidence suggesting discontinuities among vertebrates in the mechanisms underlying several sets of learning phenomena, including probability learning, discrimination reversal, and *reward-schedule effects* (*RSEs*). This article concentrates on the latter—a family of phenomena characterized by the adjustment to the unexpected devaluation or omission of rewards. These involve effects such as successive negative contrast (SNC), the magnitude of reinforcement extinction effect (MREE), and the partial reinforcement extinction effect (PREE), among others, most extensively studied in mammals (for a brief characterization, see Table 1 and references therein). These three effects illustrate the two basic *reward downshift* manipulations; in *reward devaluation* (e.g., SNC), the downshift is to a nonzero reward value, whereas in *reward omission* (e.g., MREE, PREE), the downshift is to a zero reward value. Bitterman (1975) summarized evidence from several nonmammalian species suggesting that these RSEs were not always found in analogous experiments. For example, goldfish (*Carassius auratus*) trained under either instrumental (Lowes & Bitterman, 1967) or consummatory (Couvillon & Bitterman, 1985) conditions showed a gradual adjustment or no adjustment whatsoever to reward devaluation, although they clearly differentiated reward types and magnitudes. A reward devaluation paradigm that yields evidence of quality or magnitude differentiation, but no evidence of SNC, will be qualified as *reversed*; for example, the behavioral outcome of the goldfish

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experiments just described is referred to as a *reversed SNC effect*. Mammals such as rats, however, exhibited an exaggerated response to the devaluation, with extensive (albeit transient) deterioration of either instrumental or consummatory behavior (see Flaherty, 1996). Bitterman (1975) emphasized the co-variation of RSEs in any given species, that is, they either occurred or did not occur, and derived two major hypotheses. First, that such co-variation suggested common underlying mechanisms among RSEs, and second, that reversed RSEs in fish suggested an evolutionary transition in learning processes which, in turn, implied that different theories of learning were required for different vertebrate taxa.

This review concentrates on research with representatives of three vertebrate classes: mammals, birds, and amphibians (RSEs are virtually unexplored in cartilaginous and jawless fish; for research with bony fish and reptiles, see Macphail, 1982; Papini, 2006). An analysis of RSEs requires many experimental manipulations performed under analogous conditions varying training factors that affect behavior. Isolated experiments in a single species may be informative, but, as in other research areas (e.g., fruit flies and mice in genetics), what is required are systematic variations in a relatively small number of selected species and situations. Based on this type of evidence, this review will show that there are several modes of adjustment to situations involving reward downshifts that resist a unitary theoretical treatment. Two possible mechanisms, *carry-over signals* and *emotional memory*, are described and considered in some detail in the final section. Moreover, some traditional categories provide little guidance to organize the literature. This is the case with the classic distinction between general-process and ecological views of the evolution of learning (Papini, 2002, 2008; Shettleworth, 2010; Thorndike, 1911). The general-process view maintains that learning processes are basically common to a wide variety of species otherwise divergent in their morphology and physiology. Indeed, there is remarkable constancy in basic learning phenomena across species, from simple acquisition and extinction, to compound conditioning effects and even seemingly cognitive processes. By contrast, the ecological view suggests that learning is closely tied to ecological pressures. It seems obvious that the relevance of perceptual, motivational, and motor capacities of any given species (i.e., contextual variables; Bitterman, 1960) for understanding their behavior in learning situations cannot be ignored—and is not actually ignored when designing apparatus and testing procedures (Timberlake & Lucas, 1989). But it turns out that it is rather difficult to demonstrate that ecological pressures affect behavior by shaping learning mechanisms, rather than by shaping these other contextual variables. Evidence consistent with this view comes from artificial selection studies based on learned behaviors (Brush, 1985; Torres & Sabariego, 2014). For example, rat strains originally selected for good vs. poor avoidance learning apparently diverged on the basis of differences in what might be loosely called *emotionality*, rather than in terms of evolving different associative processes. Conservation in the evolution of learning mechanisms is likely more the rule than the exception, as suggested by wide phylogenetic homologies in cell-molecular cascades involved in synaptic plasticity in mollusks, arthropods, and vertebrates (Lonze & Ginty, 2002; Sakamoto, Karelina, & Obrietan, 2011; Silva, Kogan, Frankland, & Kida, 1998).

One aspect of the terminology used in this review needs clarification. A description of experimental outcomes in terms of the presence or absence of a given RSE is insufficient because *absence* is ambiguous. There are two potential outcomes that might be described as the absence of a RSE: either because some other effect is present or because there are no differences between the experimental conditions throughout the experiment. Figure 1 shows the regular RSE and these two additional outcomes using idealized data in the PREE and SNC situations: the RSE (1A and 1D), the reversed RSE (1B and 1E), and a null result (1C and 1F). The phrase *reversed RSE*, as used above to describe the effect of reward devaluation in experiments with goldfish (Couvillon & Bitterman, 1985; Lowes & Bitterman, 1967), refers to reward conditions that can be shown to differentially control behavior, but that produce a gradual adjustment, rather that the abrupt changes in behavior typical of RSEs. In some experiments (e.g., the goldfish experiments just cited), different reward values generate differential preshift performance (i.e., they are discriminable), but following reward

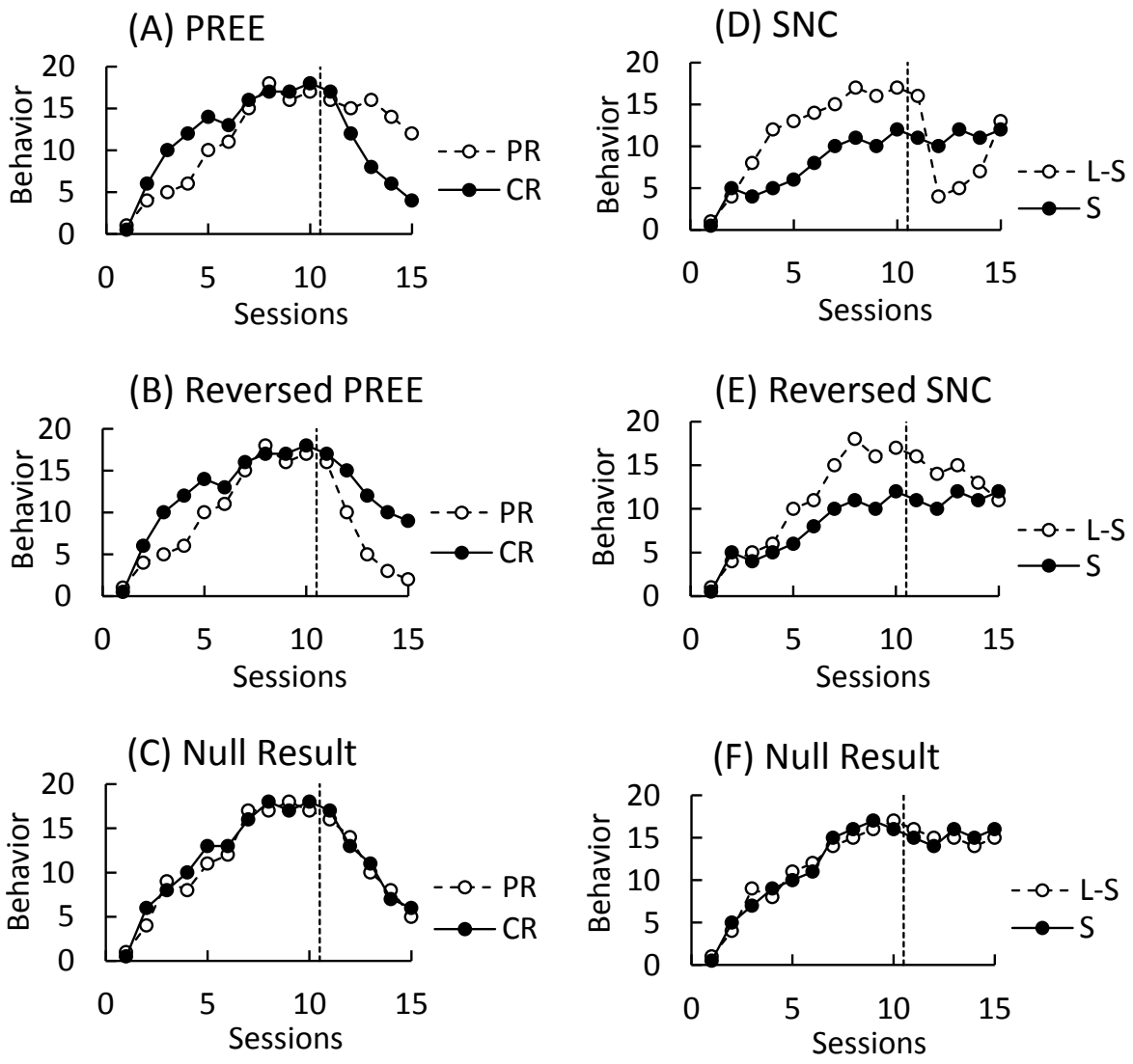

Figure 1. Idealized representation of three possible outcomes of RSEs illustrated in terms of the partial reinforcement extinction effect (PREE) and successive negative contrast (SNC). (A) The *PREE* varies across experiments in terms of the acquisition profile. Here partial reinforcement (PR) animals are slower to acquire than continuous reinforcement (CR) animals, but reach the same asymptote. In other cases, PR animals end at a lower or higher asymptote compared to CR animals. In extinction, however, the PREE involves higher responding or slower extinction rate in PR animals relative to CR animals. (B) The *reversed PREE* involves higher responding or slower extinction rate in CR animals, relative to PR animals, just the opposite. The effect is *reversed* because the difference between groups in extinction is statistically significant (either in terms of a main schedule effect or as a schedule by session interaction). (C) A *null PREE* occurs when neither the acquisition nor the extinction effects of schedule or of schedule by session interaction are significant. In this case, it is parsimonious to attribute the absence of the PREE to a failure of the animals to discriminate the schedules. (D) The regular *SNC effect* involves an exaggerated response of the downshifted animals (large to small reward: L-S) during postshift sessions, relative to animals always given access to the small reward (S). There may be or not behavioral differences in preshift sessions. (E) The *reversed SNC effect* occurs when groups differ during the postshift sessions, but without the exaggerated response by the downshifted animals. There may be an adjustment to the new reward, as shown in here, or downshifted animals may remain at their preshift behavioral level. In the latter case, it is assumed that given a sufficient number of sessions, downshifted animals would drop their behavior to the level of unshifted controls. There must be evidence of control by reward magnitude or quality before the shift. (F) A *null SNC effect* occurs when there are no differences between groups before and after the reward downshift. Again, the most parsimonious hypothesis is that the two chosen rewards did not control behavior differentially, so the reward downshift was not detected by the animals.

devaluation the behavior of downshifted animals exhibits no change. For simplicity it will be assumed that given a sufficient number of trials, a gradual adjustment would have been observed, so that this outcome is also characterized here as a reversed RSE. A null effect, however, can be dismissed on a purely procedural basis; the absence of group differences suggests the parsimonious (and uninteresting) alternative that the RSE failed to occur because the conditions of reinforcement were not discriminable to the animal.

This review aims at describing the diversity of behavioral adjustments to situations involving reward downshifts in vertebrates. It illustrates major trends, suggests areas requiring additional experimental attention, identifies brain processes engaged in these situations, and recognizes some factors that account for the spectrum of outcomes observed in vertebrates. I focus first on the mammalian model *par excellence*: the rat.

RSEs in Rats and Other Mammals

Several results inconsistent with Bitterman's (1975) co-variation of RSEs have emerged in experiments with rats. Whatever their comparative implications, these apparently inconsistent results demonstrate that even within a single species, several modes of adjustment are observed in situations involving the unexpected devaluations or omissions of rewards. This makes it difficult for a single set of mechanisms to account for the available evidence. Let's begin by asking what factors lead to apparent inconsistencies in the outcomes of reward-schedule experiments. Three factors are identified here: behavior, reward, and training procedure. Importantly, experiments differ in terms of the distribution of practice. *Massed practice* refers to the administration of sessions with multiple trials separated by intertrial intervals in the order of seconds to a few minutes, whereas *spaced practice* refers to sessions with trials separated by intervals ranging from one hour to days (e.g., one trial per day). A *trial* involves the presentation of one signal-outcome pairing (Pavlovian) or one response-outcome pairing (instrumental), in which the outcome could be reward (R) or nonreward (N).

Anticipatory vs. Consummatory Behavior

To be sure, rats do not always produce evidence of RSEs. Consider the two most typical behaviors engaged in animal learning experiments. In *anticipatory* behavior, the target response occurs before the animal reaches the reward, whereas in *consummatory* behavior, the response involves a direct interaction with the reward. Examples of anticipatory behavior include running in runways and lever pressing in Skinner boxes, whereas fluid consumption is typically used in experiments involving consummatory behavior.

A striking dissociation of RSEs has been demonstrated in the runway situation, using sucrose solutions as the reward. Flaherty and Caprio (1976) have shown, *in the same animals*, that reinforcing rats with sucrose in the goal box yields a reversed iSNC effect in running behavior (anticipatory), but a strong cSNC in licking behavior (consummatory). Thus, there are conditions that promote consummatory contrast, but fail to influence anticipatory behavior in the same direction. This dissociation between anticipatory and consummatory behavior is also present in terms of the effect of some neurobiological manipulations. Several experiments involving brain lesions show that whether an effect on behavior is observed depends critically on the type of behavior. For example (Leszczuk & Flaherty, 2000), electrolytic lesions of the nucleus accumbens had no detectable effect on cSNC or cANC (Table 1), whether at the level of overall consummatory behavior or in terms of lick microstructure (e.g., burst duration, number of licks per burst). However, the same lesions eliminated the iSNC effect in the section of the runway closest to the goal. A similar dissociation was reported after Ibotenic acid lesions of the hippocampus (Flaherty, Coppotelli, Hsu, & Otto, 1998). However, the

Table 1. *A brief characterization of some reward-schedule effects (RSEs) induced by unexpected reward devaluation or omission cited in the article*

Acronym	Behavior	Dependent Variable	Description
cANC	Consummatory	Lick frequency	Reduced consummatory behavior of a low-value incentive when followed by a high-value incentive (low→high), relative to one followed by a low-value incentive (low→low), in daily training trials.
iMREE **cMREE**	Anticipatory Consummatory	Latency, response rate Goal-tracking time	Faster extinction of anticipatory or consummatory behavior after acquisition with a large, rather than with a small incentive.
OEE	Anticipatory	Latency	Faster extinction after a greater amount of acquisition training than after a relatively shorter number of acquisition sessions.
ORE	Anticipatory	Latency	Faster reversal learning after greater amount of discrimination training than after a relatively small amount of discrimination training.
PPEE	Anticipatory	Latency	Faster extinction after continuous food reinforcement, than after partial punishment superimposed on a continuous food reinforcement schedule.
PRAE	Anticipatory	Latency	Higher acquisition performance in a group receiving partial reinforcement training than in one receiving continuous reinforcement training.
iPREE **cPREE**	Anticipatory Consummatory	Latency, response rate Goal-tracking time	Faster extinction of anticipatory or consummatory behavior after acquisition with continuous, rather than with partial incentive training.
iSNC **cSNC**	Anticipatory Consummatory	Latency, response rate Fluid intake, lick frequency, goal-tracking time	Greater deterioration of anticipatory (induced via instrumental or Pavlovian procedures) or consummatory behavior in animals downshifted from a large to a small incentive, relative to unshifted controls exposed to the small incentive.
SPC	Anticipatory	Latency	Increased responding for a large reward after training with a small reward, relative to an unshifted control always trained with the large reward.
VMREE	Anticipatory	Latency	Faster extinction after acquisition with small reward than with an unpredictable mixture of large and small rewards.

Note. Lower case prefixes stand for instrumental (i) and consummatory (c) procedures. ANC: anticipatory negative contrast. MREE: magnitude of reinforcement extinction effect. OEE: overtraining extinction effect. ORE: overtraining reversal effect. PPEE: partial punishment extinction effect. PRAE: partial reinforcement acquisition effect. PREE: partial reinforcement extinction effect. SNC: successive negative contrast. SPC: successive positive contrast. VMREE: variable magnitude of reinforcement extinction effect. The procedures to induce instrumental effects are in some cases Pavlovian (i.e., response-independent reward presentations). The word *anticipatory* is intended to encompass both instrumental and Pavlovian procedures since in both cases the target behavior is measured before the animal reaches the goal. In *consummatory* situations, the target behavior is the animal's interaction with (i.e., consumption of) the reward. The prefix *i* (*instrumental*, e.g., iSNC) is left in place, even when the procedure was Pavlovian, because it has become established in the literature, although perhaps *a* (*anticipatory*) would be more precise. Some key references (see text for additional references): Amsel (1992), Amsel and Stanton (1980), Bitterman (2000), Flaherty (1996), and Papini (2006).

opposite pattern of results was reported for excitotoxic lesions of the gustatory thalamus—impairment of cSNC, but not of iSNC (Sastre & Reilly, 2006).

There are also discrepancies between different RSEs when the task requires different types of behavior. For example, although rats readily yield the iPREE and iMREE in autoshaping after being reinforced with food pellets in acquisition (Boughner & Papini, 2006; Papini, Ludvigson, Honeycutt, & Boughner, 2001), they show reversed cPREE and cMREE during consummatory extinction, after being offered sucrose solutions for consumption (Mustaca, Freidin, & Papini, 2002). These reversed effects in consummatory extinction, cPREE and cMREE, also point to an inconsistency with cSNC, which is routinely observed in analogous experiments (e.g., Flaherty, 1996). In fact, consummatory extinction and cSNC sometimes yield opposite results for the same manipulation. For example, ethanol reduces cSNC (Kamenetzky, Mustaca, & Papini, 2008) and thus one would expect that it would also reduce consummatory extinction; in fact, ethanol enhances extinction after consummatory training (Kamenetzky, Mustaca, Pedron, Cuenya, & Papini, 2009). To the extent that these effects are based on the same mechanisms, they should obey Bitterman's (1975) co-variation prediction. In these cases, as in those reviewed above (i.e., iSNC vs. cSNC), requiring different responses also usually implies the administration of different rewards, which itself may be responsible for the inconsistency (see below).

Psychological-level concepts, such as expectancy, incentive comparisons, and frustration, may apply equally to situations involving similar procedures (e.g., reward downshift), but the actual implementation of the procedure can engage different brain mechanisms. Thus, when the reward downshift is implemented using anticipatory behaviors, the nucleus accumbens and the hippocampus are more critical than when the operation is implemented in a consummatory situation. One corollary of these results for comparative analyses of learning processes reminds us of the distinction between homology (similarity of characters by inheritance from a common ancestor) and homoplasy (similarity of characters by common selective pressures, but evolved from different ancestors) in evolutionary theory (Papini, 2002). Two different species may show very similar behavioral adjustments based on independently evolved mechanisms, just as two behaviorally similar tasks engage different mechanisms even in the same animal. Behavioral similarities do not demonstrate homology of mechanism; it is analysis at lower mechanistic levels (i.e., brain circuitry, neurochemical systems, and synaptic plasticity) that has the potential to distinguish between these possibilities (Papini, 2002, 2003).

Food Pellets vs. Sucrose Solutions as the Reward

As mentioned previously, rats trained to run down a runway or lever press for sucrose reinforcement usually yield evidence of a reversed iSNC (Barnes & Tombaugh, 1973; Flaherty & Caprio, 1976; Flaherty, Riley, & Spear, 1973; Goodrich & Zaretsky, 1962; Pellegrini & Papini, 2007; Rosen, 1966; Rosen & Ison, 1965; Sastre, Lin, & Reilly, 2005; Shanab, Domino, & Ralf, 1978; Spear & Hill, 1965). This is perhaps one of the most puzzling results in the entire field of incentive contrast, one that, to my knowledge, has not been clarified despite having been identified in the 1960s. Trained under these conditions, rats adjust their performance after the downshift but exhibit no contrast effect, much like nonmammalian vertebrates do in analogous experiments with solid or liquid reinforcers (e.g., Papini, 1997). There is some indication that iSNC also fails to occur when sucrose pellets are downshifted in terms of the sucrose concentration or in terms of the number of pellets (Burns, McCrary, McRae, & Lorig, 1984; Shanab et al., 1978). An apparent demonstration of iSNC with a downshift in sucrose concentration can be explained in terms of cSNC (Weinstein, 1970). In Weinstein's experiment, rats deprived of food and water received lever-pressing, free-operant training for access to either 16% or 4% sucrose. However, the lever and dipper were sufficiently close spatially for rats to operate the lever and drink the solution at the same time. After a downshift from 16% to 4% sucrose, rats exhibited a significant decrease in response rate below the level of the unshifted 4% controls. Although

technically a case of iSNC the close spatial proximity between lever and sucrose, the use of a free-operant procedure, and the continuous reinforcement schedule suggest that the reduction in lever pressing resulted from withdrawal from the reward area, a behavior observed in the cSNC situation (Pellegrini & Mustaca, 2000). This artifact is prevented in the runway situation, where the anticipatory response and the goal response are spatially segregated (Flaherty & Caprio, 1976).

As a reinforcer, however, sucrose exhibits standard properties. For example, both sucrose and food pellets support single alternation patterning (Burns, 1984), suggesting that their stimulus traces can acquire control over instrumental behavior. Rats can also anticipate the presentation of a 30% sucrose solution when R and N trials alternate regularly within a session (Burns & Wiley, 1984). In one experiment, rats trained with an R–N–N sequence exhibited lower performance on the second trial than rats trained with an R–N–R sequence, suggesting anticipation of the 30% sucrose reward in the latter group. In turn, this suggests that a representation of sucrose reward can be accessed in a cued-recall situation, something that would be required for animals to show evidence of the iSNC effect (Papini & Pellegrini, 2006). Notice, however, that unlike the single alternation of R and N trials, the iSNC effect requires a comparison between two different sucrose concentrations. Would rats show behavioral patterning when exposed to two different concentrations of sucrose solutions? A negative result would suggest that rats fail to produce the iSNC effect with sucrose solutions as rewards because they have a limited ability to anticipate the sweetness of a sucrose solution.

Successive vs. Anticipatory Contrast

One set of inconsistent results comes from different types of reward downshift situations. Consider cSNC and cANC (see Table 1). These two situations may be designed such that they involve the same rewards, but presented in different arrangements. For example, whereas in cSNC a rat may receive 32% sucrose for 10 daily trials followed by 4% sucrose for five additional trials (with a 4-to-4% sucrose unshifted control), in cANC rats may receive two trials per day, separated by a brief interval, in which the first provides access to 4% sucrose and the second to 32% sucrose (vs. a 4-to-4% sucrose each day). In cANC, consummatory behavior in the first trial is lower in the 4-to-32% sucrose condition than in the first trial of the 4-to-4% sucrose control (Flaherty, 1996).

Although a priori one could apply the same psychological mechanisms to both situations (e.g., an explanation based on Amsel's, 1992, frustration theory), psychopharmacological evidence suggests that these two situations engage different neurochemical mechanisms (Flaherty, 1996). For example, whereas cSNC is attenuated by benzodiazepine anxiolytics such as diazepam and chlordiazepoxide (e.g., Flaherty, Grigson, & Rowan, 1986; Mustaca, Bentosela, & Papini, 2000; Ortega, Glueck, et al., 2014), there is no evidence that cANC is influenced by these drugs (Flaherty & Rowan, 1988). Similarly, whereas corticosterone administration immediately after the first downshift experience impairs subsequent consummatory behavior in the cSNC situation, the same treatment has no measurable effect on cANC (Ruetti, Justel, Mustaca, & Papini, 2009).

Thus, even under generally similar conditions of training, with the same rewards (albeit presented in different arrangements), dissimilar brain mechanisms are engaged in the same species.

Generality of RSEs Among Mammals

Although the largest amount of systematic data comes from experiments with rats, there have been a handful of additional experiments on RSEs and related situations with other mammalian species. SNC is the

situation that has attracted most attention using mammals other than rats, but, occasionally, the effects of unexpected reward omissions in other situations have also been reported. For example, appetitive extinction has been shown to be accompanied by increased pituitary and adrenal hormonal activity in pigs, Alpine goats, squirrel monkeys, and rats (Carbonaro, Friend, Dellmeier, & Nuti, 1992; Coe, Stanton, & Levine, 1983; Davis, Memmott, MacFadden, & Levine, 1976; Lyons, Fong, Schrieken, & Levine, 2000), and increased aggressive behavior in pigs and rats (Dantzer, Arnone, & Mormede, 1980; Thompson & Bloom, 1966; for the opposite result, see Mustaca, Martinez, & Papini, 2000). Preventing access to food has also been shown to induce goal-avoidance behavior and reduce activity in the prefrontal cortex measured by functional near-infrared spectroscopy in dwarf goats (Gygax, Reefmann, Wolf, & Langbein, 2013). This evidence is consistent with the view that reward loss can have emotional significance for mammalian species, as is further shown by experiments on SNC reviewed below.

One drawback of isolated experiments is that they can tell us relatively little about the conditions that enhance and reduce the size of RSEs. Additionally, until reversed RSEs were recognized as providing positive information, the absence of a regular RSE was often taken as a null result (e.g., compare Figure 1E vs. 1F); such conclusions probably resulted in the editorial rejection of the submission. A null result unworthy of publication is one in which the behavior of animals in groups treated with different reward magnitudes or schedules does not differ before and after the critical downshift (see Figure 1C and 1F; e.g., Bergvall, Rautio, Luotola, & Leimar, 2007). In a case like this, the most parsimonious explanation for the absence of a RSE after the downshift is that the two reward conditions failed to differentially control behavior. However, if there is evidence of control by reward magnitude or schedule before the downshift, then the absence of a RSE in postshift behavior is informative (i.e., a reversed RSE; see Figure 1B and 1E). Thus, for example, the lack of iSNC with sucrose rewards (see above) represents a reversed iSNC effect, rather than a null result (Sastre et al., 2005). Therefore, we cannot be sure that we have a reasonably full list of conditions that promote reversed RSEs in mammals. With this caveat in mind, what do analogous SNC experiments with mammalian species other than rats show?

Papini, Mustaca, and Bitterman (1988) reported significant cSNC effects in experiments with two species of didelphid marsupials (*Lutreolina crassicaudata, Didelphis albiventris)*. These animals were exposed to conditions similar to those used with rats: 32% and 4% sucrose solutions, one 5-min trial per day, and consummatory behavior as the dependent variable. In addition, they received four successive 32-to-4% sucrose downshifts. In rats, repeated downshifts cause no measurable changes in the size of the cSNC effect (Flaherty, Clarke, & Coppotelli, 1996), but in didelphid marsupials, the cSNC effect actually increased in size across the four downshift events. The reasons for this discrepancy and its significance are not known. Red opossums (*L. crassicaudata*) also showed an increase in running speed during appetitive extinction (Papini & Ramallo, 1990); this effect is reminiscent of the extinction burst or spike also observed in rats under a variety of situations (e.g., Dudley & Papini, 1995; Stout, Boughner, & Papini, 2003; Thomas & Papini, 2001).

Similar SNC effects have been reported in a variety of mammalian species. In one of the first demonstrations, Tinklepaugh (1928; Watanabe, 1996) trained rhesus monkeys (*Macacca* sp.) to choose one of two cups for rewards that could be either highly preferred (a piece of banana) or not very appealing, but acceptable (a leaf of lettuce). The monkeys first saw the experimenter depositing the reward under one of the cups and then, after a short retention interval with a screen preventing the monkey from accessing the cups, the monkeys could choose a cup and consume the reward. On some probe trials, the monkey saw the experimenter depositing a piece of banana under the cup, but it did not see the experimenter replacing the banana for lettuce during the retention interval. When the screen was raised and the monkey could choose, the banana-to-lettuce downshift often resulted in the animal refusing to consume the food and behaving aggressively toward the experimenter. This can be understood as a special case of cSNC with repeated qualitative downshifts and relatively massed conditions of training. Similar cSNC effects have been reported in

human babies (Kobre & Lipsitt, 1972) and mice (*Mus musculus*; Mustaca, Bentosela, & Papini, 2000) using more conventional procedures with sucrose solutions. Human babies also demonstrate a variety of behavioral changes in instrumental situations (Lewis, Alessandri, & Sullivan, 1990; Mast, Fagen, Rovee-Collier, & Sullivan, 1980). For example, 82-112-day old infants who could move a mobile attached to their legs by kicking exhibited increased kicking and negative vocalizations (e.g., crying, fuzzing) when the number of pieces in the mobile was reduced from 10 to 2. The increased kicking may seem puzzling, but rats also increase the rate of anticipatory behavior after reward devaluations or omissions (e.g., Dudley & Papini, 1995; Stout et al., 2003). These instrumental effects with human babies were observed under relatively massed conditions of training. Similar results were observed under massed-training conditions with dogs (*Canis familiaris*) in reward devaluation (Bentosela, Jakovcevic, Elgier, Mustaca, & Papini, 2009) and reward omission paradigms (Bentosela, Barrera, Jakovcevic, Elgier, & Mustaca, 2008). In one experiment (Bentosela et al., 2009), dogs exposed to a qualitative downshift in food availability (from dry liver to dog pellets) rejected the reward more than unshifted controls, and also withdrew from the experimenter and exhibited a reduction in gaze duration.

Thus, it seems that mammalian species trained under conditions of reward devaluation tend to exhibit changes in behavior that are congruent with SNC effects. The conditions of training vary across species and the actual behaviors measured are also adjusted to the peculiar repertoire of the animal. The phenomenon is there in these mammalian species, but what is lacking in these cases is a detailed analysis of the underlying mechanisms, something that has only been done with some degree of depth for rats.

RSEs in Mammals: Conclusions

Several conclusions can be reached from the research reviewed in this section. Despite being well-represented in published articles, there are still several outstanding issues that remain to be resolved. First, RSEs can be dissociated in rats behaviorally (e.g., cSNC and reversed iSNC, cSNC and reversed cPREE), in terms of brain lesions (e.g., hippocampal damage affects iSNC, but not cSNC), and pharmacologically (e.g., ethanol affects cE and iE in opposite directions). What brain processes are responsible for these behavioral dissociations? Second, why do rats show a reversed iSNC in the runway with a downshift in sucrose concentration? Third, there are entire mammalian orders that have not been studied in terms of the RSEs. Especially intriguing is the status of RSEs in evolutionarily conservative species: Would these effects be observed in experiments with monotremes (egg-laying mammals), marsupials, edentates (e.g., armadillos), and insectivores (e.g., hedgehogs)? Do RSEs reflect the operation of a brain circuit common to all mammals?

RSEs in Birds

As with rats and other mammals, the research on RSEs using birds also yields outcomes that are inconsistent with Bitterman's (1975) co-variation hypothesis. The picture is most complete for pigeons (*Columba livia*), which are used extensively in animal learning experiments based on instrumental conditioning procedures. Papini (1997) reported evidence of a reversed iSNC using a key-pecking procedure with pigeon-formula food pellets as the reward. A single trial per day was used and 10 responses were required to receive the reward, either 1 pellet or 15 pellets. Although pigeons acquired the pecking response faster when reinforced with 15 pellets than with 1 pellet, thus showing control of behavior by reward magnitude, a 15-to-1 pellet reward downshift only yielded evidence of adjustment, without contrast—a reversed iSNC. Further experiments based on the same procedure showed that extinction of key-pecking was faster after acquisition with a small reward than with a large reward—a reversed iMREE (Papini, 1997; Papini & Thomas, 1997).

A similar reversed iMREE effect was obtained with male quail (*Coturnix japonica*) using copulation with females as the reinforcer (Baquero, Puerta, & Gutierrez, 2009). Males were trained to run to the goal box of a runway for access to either 8 females or just 1 female (i.e., a magnitude of sexual reinforcement manipulation). Although running latencies were very similar during acquisition, the large-reward group continued to run for a larger number of trials in extinction (when no females were available in the goal box) than the small-reward group. A second experiment showed that males preferred access to 8 females rather than one, suggesting that they differentiated the two magnitudes. This is where the agreement with Bitterman's (1975) co-variation hypothesis stops. There are two exceptions to the co-variation hypothesis, one involving a demonstration of cSNC with starlings (*Sturnus vulgaris*) and the other involving demonstrations of the iPREE in pigeons and quail.

Freidin, Cuello, and Kacelnik (2009) reported evidence of cSNC in starlings, using solid food and a qualitative downshift in reward from mealworms to turkey crumbs. Starlings in the downshift condition received access to mealworms in one of three cups for 15 trials, at a rate of 3 trials per daily session separated by a fixed 90-min intertrial interval; these were followed by 9 trials with the same temporal spacing (3 trials/session) in which they had access to turkey crumbs in all three cups. The amount of food consumed was measured. Downshifted starlings consume more food than unshifted controls (receiving turkey crumbs throughout training) during preshift trials, but they consumed less food during postshift trials, thus exhibiting a cSNC effect. In addition, downshifted animals switched between feeders more than unshifted controls during postshift trials, when all three cups contained turkey crumbs for all the animals. Because these measures (food consumption and feeder switching) occurred after contact with the reward, they can be both considered consummatory measures. A third measure, probing the target feeder cup (i.e., the one containing mealworms on preshift trials), possibly an instrumental response, did not yield group differences. Experiments with rats in which both cSNC and iSNC are studied simultaneously generally show that conditions that fail to promote contrast in anticipatory behavior, can produce evidence of contrast in consummatory behavior (e.g., with sucrose solutions as the reward; Flaherty & Caprio, 1976). Because demonstrations of reverse SNC effects in birds are instrumental (e.g., Papini, 1997), it is possible that the cSNC procedure would be more sensitive to the behavioral effects of reward devaluation with avian species, as shown by this experiment with starlings. This remains to be seen.

The second source of variance with respect to Bitterman's (1975) co-variation hypothesis comes from experiments involving spaced-trial outcome uncertainty. Pigeons reinforced with solid food either to peck a localized light (Papini, Thomas, & McVicar, 2002) or to run down a runway (Roberts, Bullock, & Bitterman, 1963; Thomas & Papini, 2003) demonstrated stronger resistance to extinction after 50% partial reinforcement training than after continuous reinforcement. Extinction was also retarded after training with variable magnitudes of reinforcement (the VMREE; see Table 1), using the same reward amounts that yield evidence of a reversed iMREE (Thomas & Papini, 2003). A similar iPREE was obtained in a spaced-trial runway experiment with solid food using quail as subjects (Butiricá, Ortega, Papini, & Gutierrez, 2013). Thus, there seems to be no co-variation of RSEs in pigeons, which show reverse iSNC and iMREE, but regular iPREE and VMREE under spaced practice.

To avoid the potentially unreliable comparison across experiments, Thomas and Papini (2003) trained pigeons in a four-group experiment designed to test the iMREE and iPREE within the same conditions of training. The performance of a 50% partial reinforcement group receiving 5 g of mixed grain on R trials and nothing on N trials (for a total of 48 daily trials) was compared to the performance of three groups receiving continuous reinforcement. The iPREE was assessed against continuous groups also reinforced with 5 g of mixed grain and matched either in terms of total trials (48; but then receiving twice as many rewards) or R trials (24; but then receiving half as many trials). Importantly, the continuous group matched for rewards was

trained on days in which partial animals were scheduled to receive an R trial; thus, these groups were matched in the number and temporal distribution of R trials. The iMREE was assessed by adding a fourth group receiving 1 g of mixed grain in a continuous reinforcement schedule for 48 daily trials. All animals received one trial per day. Across twenty extinction trials, the performance of these groups showed the following effects: (1) iPREE: there was hardly any change in runway behavior for pigeons trained under partial reinforcement, which extinguished more slowly in comparison to continuous reinforcement groups matched in terms of trials or rewards. (2) Reversed iMREE: continuous reinforcement with 5 g of mixed grain extinguished more slowly than with 1 g of mixed grain. (3) Reversed overtraining extinction effect (OEE; see Table 1): pigeons receiving 24 acquisition trials extinguished faster than pigeons receiving 48 acquisition trials, all under continuous reinforcement. In the OEE, greater amount of acquisition training leads to faster extinction. This RSE has been shown in rats (e.g., Ison, 1962) and in turtles (*Geoclemys reevesii*; Ishida & Papini, 1997), but the reversed version was observed with pigeons and amphibians (see below). Using a similar design, Gonzalez and Bitterman (1969) reported both iPREE and iMREE under spaced practice (1-h intertrial interval) in rats. To complicate matters further, Papini et al. (2002) showed that pigeons did show co-variation of reversed iPREE and reversed iMREE in a spaced-trial (24-h intertrial interval), key-pecking experiment based on a within-subject design. Thus, pigeons extinguished fastest to a key light paired with continuous/small reward, intermediate to another key light paired with partial/large reward, and slowest to yet another key light paired with continuous/large reward.

How is this dissociation of iPREE and iMREE in pigeons to be understood? One possibility is that there is something inadequate about the training parameters leading to dissociated outcomes. This seems unlikely because the adjustment to reward magnitude and schedule in pigeons before the shift to extinction shows nothing unusual. Moreover, as noted above, the same reward magnitudes that produce a reversed iMREE also yield a regular VMREE. A second possibility is that the similarities among the spaced-practice iPREEs observed in birds (pigeons and quail) and mammals (rats) are the result of different underlying mechanisms. Direct comparisons between pigeons and rats suggest different underlying mechanisms. For example, in reward devaluation tasks, the behavior of rats in downshifted trials in consummatory and instrumental tasks, and whether SNC is induced or not, is controlled by the ratio of the reward magnitudes obtained in postshift and those expected from preshift sessions, rather than by their absolute magnitude (Papini & Pellegrini, 2006; Pellegrini & Papini, 2007; Pellegrini, Lopez-Seal, & Papini, 2008). In pigeons, however, postshift key-pecking performance is controlled by the absolute magnitude of the preshift reward (Pellegrini et al., 2008). Using a spatial discrimination reversal task in which successive reversals occurred in the middle of the session, Rayburn-Reeves, Stagner, Kirk, and Zentall (2013) reported that pigeons adjusted to the reversal by making anticipatory errors (before the reversal) and then perseverative errors (after the reversal). Unlike pigeons, the discriminative behavior of rats was more closely controlled by the response-outcome contingencies of previous trials. Tight control of behavior by the long-term memory of a preshift reward magnitude connects seemingly disparate findings from reward devaluation (Papini, 1997; Pellegrini et al., 2008), reward omission (Papini & Thomas 1997; Thomas & Papini, 2003), and perseverative errors in successive reversals (Rayburn-Reeves et al., 2013). There is a component of flexibility in the behavior of rats under shifting reward conditions that seems to be attenuated or missing in pigeons. Negative emotions such as anticipatory frustration induced by prior experience with surprising nonreward may accelerate the detachment from a signal or location previously paired with reward. This process, termed *incentive disengagement* (Papini, 2003), may induce escape behavior and facilitate a switch to a searching mode or to an alternative previously paired with reward.

There is surprisingly little evidence involving manipulations of brain processes during appetitive extinction in birds that produce known effects in mammals. For example, Lengersdorf, Stüttgen, Uengoer, and Güntürkün (2014) infused the sodium channel blocker tetrodotoxin into the pigeon hippocampus during contextual appetitive extinction to produce a temporary inactivation of neural activity. They reported that, as

in rats, hippocampal inactivation impaired the retrieval of the extinction memory in pigeons, thus leading to higher levels of spontaneous recovery. Although suggestive, the effects of hippocampal inactivation in pigeons were not tested in relation to reward schedule or magnitude, thus bearing less relevance to the issue under discussion. Using a pharmacological approach, Thomas and Papini (2003) tested three different drugs in the iPREE runway situation with pigeons. The drugs were chosen according to known effects on the iPREE in rats: chlordiazepoxide (a benzodiazepine anxiolytic that eliminates the rat iPREE), nicotine (a cholinergic drug that increases the rat iPREE), and haloperidol (a dopamine antagonist that has no detectable effect on the rat iPREE). In pigeons, however, the effects of these drugs were different. Chlordiazepoxide retarded the pigeon iPREE, but did not eliminate it, whereas nicotine and haloperidol did eliminate the pigeon iPREE. The possibility that the iPREE is based on GABAergic transmission in mammals, but on dopaminergic transmission in birds needs careful examination. These experiments illustrate the type of approach needed to resolve the issue of the behavioral similarity in the spaced-trial iPREE among pigeons and rats.

RSEs in Birds: Conclusions

As shown in this review, birds have provided the best evidence against Bitterman's (1975) co-variation hypothesis. Pigeons readily show reversed iSNC and reversed iMREE, while simultaneously exhibiting the iPREE. This dissociation could provide insights into the differences in brain processes underlying RSEs and reversed RSEs in the same animals. The intriguing results with starlings in the cSNC situation merit further evaluation of consummatory procedures with avian species.

RSEs in Amphibians

There is a slowly emerging literature on learning in toads in situations involving reward devaluation and omission that takes advantage of the adaptive significance of water balance for these animals. The toad *Rhinella arenarum* (formerly *Bufo arenarum*) is a terrestrial anuran that, like most amphibians, returns to water ponds daily for rehydration (Wells, 2007). In the lab, these animals can be maintained for months in good conditions and show excellent motivation to work for an opportunity to sit on a bowl containing distilled water (toads *drink* by absorption through a patch of ventral skin). Reward magnitude can be manipulated by allowing animals to sit on different amounts of water or for different amounts of time in a water container. The consequences of consumption can be assessed by measuring the change in weight before and after a given trial, to ascertain whether indeed different amounts of water were absorbed. Using these procedures, toads were shown to acquire and extinguish an approach response in a runway, and to acquire a spatial discrimination in a Y-maze followed by a discrimination reversal, all under massed practice (Schmajuk, Segura, & Reboreda, 1980). These learning effects were supported by a 2-min of access to water in each of five trials per session (1-min intertrial intervals). In a subsequent experiment, different groups were given five trials per session (30-s intertrial intervals) ending with access to the goal box of a runway for 3.5 min where they found different amount of water. These amounts resulted in 0.5 or 5 g of weight gain per session on average. These two reward magnitudes produced different acquisition functions, but a downshift from the large to the small magnitude led to an adjustment without contrast—a reversed iSNC effect (Schmajuk, Segura, & Ruidiaz, 1981). Similar reversed iSNC effects were observed under spaced practice (one trial per day) in animals given access to water for either 1,280 s or 80 s (Papini, Muzio, & Segura, 1995). In this case, water uptake was measured for each trial thus yielding data on the effects of the reward devaluation in a consummatory measure. There was no evidence of cSNC; rather, the amount of water uptake was essentially dependent on the absolute value of the current reward magnitude. This experiment had two unshifted controls which were then trained in extinction, after 24 daily acquisition trials. The performance of both groups converged during extinction without yielding any evidence of the iMREE. In another spaced-practice

experiment (Muzio, Segura, & Papini, 1992), independent groups of toads received reward magnitudes of 20, 80, 320, or 1280 s of access to water, yielding differential gains in body weight, except for the two lowest magnitudes, and differential terminal performance in acquisition for each of the four magnitudes. In extinction, however, there was again a convergence of performance among all groups with no evidence of an iMREE.

The toad's skin can also detect the salinity of the water and react accordingly depending on whether they are hydrating or dehydrating. Thus, by varying the concentration of sodium in the water offered to the toads, one can manipulate the hedonic value of the solution. For example, a 300 mM (slightly hypertonic) sodium solution is a neutral solution that leads neither to gain nor loss of water, whereas an 800 mM strongly hypertonic solution results in dehydration. Toads exposed to an inescapable immersion (Pavlovian) in an 800 mM solution or to an immersion that can be avoided (instrumental) respond, respectively, with an anticipatory increase in heart rate and avoidance of the goal compartment in a one-way active avoidance task (Daneri, Papini, & Muzio, 2007). Response latency in a runway also varies with the degree of hydration: Toads learn to approach the goal for distilled water, show a mild tendency to approach for a 300 mM solution, and one trial of immersion in an 800 mM solution is enough for them to stay away from the goal (i.e., passive or inhibitory avoidance) during 17 subsequent daily trials (Muzio et al, 2011). Using this runway procedure with the neutral, 300 mM solution, Muzio et al. (2011) also found reversed MREE, SNC, and SPC effects (i.e., an upshift from 300 mM to distilled water; see Table 1) in several dependent variables, including running latency, consummatory behavior, changes in coloration of the ventral skin where water uptake occurs, contact time with the reward, and rubbing behavior during water uptake (Muzio et al., 2011). Moreover, a downshift from distilled water to three molarities slightly more appetitive than the neutral (225, 212, and 200 mM solutions) all yielded reversed iSNC and cSNC, with one caveat. Albeit nonsignificant, the mean consummatory behavior of these downshifted groups fell below that of unshifted controls, providing a hint of a cSNC effect (Muzio et al., 2011). Given that cSNC seems more sensitive than iSNC in rats and possibly in birds (see above), this hint deserves further exploration.

Additional studies have dealt with appetitive extinction in amphibians in relation to partial reinforcement and amount of acquisition training. Comparisons between partial vs. continuous reinforcement have produced reversed iPREEs in two species of toads, *R. arenarum* and *Bombina orientalis*. Experiments with *R. arenarum* using the water-reinforced runway procedure described above, spaced practice (24-h intertrial intervals), and runway response have uniformly shown slower extinction after continuous than 50% partial reinforcement with trials equated and, thus, with a different number and temporal distribution of reinforcements (Muzio et al., 1992, 1994). Similarly, an experiment involving solid food (crickets), spaced practice (48-h intertrial intervals), and tongue-snapping responses with *B. orientalis* produced evidence of a reversed iPREE after either 6 or 12 acquisition trials, with a single-alternation schedule of partial reinforcement and conditions matched by trials (Ramsay, Ikura, & Laberge, 2013). In this experiment there was also a continuously reinforced group that received twice the amount of food for six trials; a comparison with the small reward condition yielded evidence of a reversed iMREE. Muzio et al. (2011) reported an additional experiment that combined access to distilled water (positive reinforcer) with access to a hypertonic 800 mM solution (negative reinforcer) in randomly presented daily trials. This design was intended to mimic the partial punishment procedure used by Brown and Wagner (1964), in which rats were reinforced with food in every trial, but with the addition of electric shock in the goal box in a random half of the trials. Rats developed persistence in extinction compared to animals given only food reward—a PPEE (see Table 1). Toads, however, showed no acquisition of runway performance when half the trials involved access to the hypertonic solution. Additionally, a group receiving the neutral 300 mM solution (mimicking a nonreinforced trial) showed a reversed iPREE (Muzio et al., 2011).

What exactly determines resistance to extinction in amphibians? Because experiments involving partial reinforcement usually match the number of trials and the intertrial interval, 50% partial reinforcement groups received half the number of reinforcements with twice the length of the interreinforcement interval compared to continuously reinforced groups. Experiments varying the number of reinforced trials provide evidence of a direct relationship between the number of acquisition trials and the strength of the response during extinction. Such reversed OEEs were reported in toads (Muzio, Ruetti, & Papini, 2006; Ramsay et al., 2013) and newts (*Cynops pyrrhogaster*; Shibasaki & Ishida, 2012). Interestingly, a continuously reinforced group receiving R trials only on days when the partial reinforcement group also received R trials, thus matching the number of reinforcements and their temporal distribution, yielded an extinction performance analogous to that of a regular 50% partial reinforcement group (Muzio et al., 2006; for a similar result in pigeons, see Thomas & Papini, 2003). This last result suggests that reversed iPREEs in toads may result not so much from the schedule of partial reinforcement as from the distribution of R trials in time, as if the reward memory were to weaken in time. To test this memory-decay hypothesis, Puddington, Papini, and Muzio (2013) interpolated retention intervals of 1, 4, 8, 16, 32, or 64 days between the last acquisition and first extinction trials using the runway procedure and found that extinction performance weakened as the retention interval increased. An additional experiment showed that a large reward (600 s of access to distilled water) led to increased responding in extinction compared to a small reward (30 s) with an 8-day retention interval, a result also consistent with the memory-decay hypothesis. Thus, although toads, like most (if not all) animals tested in conditioning experiments, exhibit a reduction in the strength of an acquired response during extinction, thus implying control of instrumental behavior by nonreinforcement, memory decay and limited amounts of acquisition training also weaken extinction performance.

A few experiments have explored the effects of medial pallium lesions on reward devaluation and omission in toads. Based on afferent/efferent connections, the amphibian medial pallium has been hypothesized to be the homolog of the subiculum and CA fields of the mammalian hippocampal formation (Northcutt & Ronan, 1992). Hippocampal lesions in rats eliminate the iSNC even when relatively short intertrial intervals are used (e.g., 5-8 min; Flaherty et al., 1998; Franchina & Brown, 1971). However, hippocampal lesions eliminate the iPREE with spaced practice (Rawlins, Feldon, & Gray, 1980), but not with very short (1-2 s) intertrial intervals (Rawlins, Feldon, Ursin, & Gray, 1985). These effects are eliminated because lesions of the hippocampus *increase* resistance to change, whether in extinction after continuous reinforcement or in contrast after reward downshift; however, these lesions *reduce* persistence in extinction after partial reinforcement. *Increased* resistance to extinction after continuous reinforcement or reward downshift was also observed in toads with medial pallium lesions (Muzio et al., 1993, 1994; Papini et al., 1995), thus showing results consistent with analogous experiments with rats. However, unlike in hippocampectomized rats, medial pallium lesions also *increase* persistence in extinction after partial reinforcement in toads (Muzio et al., 1994). Thus, hippocampal lesions produce opposite effects on extinction after continuous vs. partial reinforcement in rats, suggesting that these situations engage different neural processes; however, hippocampal lesions produce the same effects on extinction after continuous vs. partial reinforcement in toads, suggesting that learning in these two situations engages the same mechanisms.

Like pigeons, amphibians tested in situations involving reward devaluations and omissions show a type of behavioral adjustment that one might label as lacking in flexibility when compared to mammalian behavior. Is this true in other situations? Toads can learn a discrimination reversal based on appetitive reinforcement (Jenkin & Laberge, 2010), but it is unclear what type of adjustment they would exhibit in midsession reversal procedures of the type explored with rats and pigeons (Rayburn-Reeves et al., 2013). Reversals are also observed in toads trained to solve spatial problems in a T-maze, where they tend to show a response strategy in probe trials in which the spatial and response strategies are pit against each other (Daneri, Casanave, & Muzio, 2011). The decay of the reward memory, N trials, reward magnitude, and amount of training are some of the acquisition parameters that determine the reverse RSEs observed in amphibians.

RSEs in Amphibians: Conclusions

Unlike birds, research with amphibians provides support for Bitterman's (1975) co-variation hypothesis. However, additional processes have been identified. There are indications that memory decay for R episodes plays an important role in amphibians, something that is also apparent in analogous experiments with pigeons, as shown above. The relevance of this potential mechanism needs careful attention. Moreover, consummatory situations may prove valuable in uncovering the capacity to show RSEs in amphibians, just as it is suggested above for birds.

Further Comments

This review of RSEs in vertebrates brings to the foreground the diversity of behavioral adjustments that have been discovered in analogous experiments sharing reward devaluation and reward omission as their common procedural denominator. RSEs and reversed RSEs have been described in the three taxonomic groups covered in this review. In mammals, for example, reward devaluations lead to iSNC with solid rewards, but reversed iSNC with sucrose solutions (see references above). Because sucrose solutions yield cSNC effects, it seems likely that the reversed iSNC is the result of a peculiar interaction of the instrumental procedure and sucrose solutions as stimuli, rather than resulting from the engagement of different learning mechanisms. One possibility that needs examination suggests that rats find it difficult to anticipate specific sucrose concentrations. This could be tested by exposing rats to specific sequences of reinforcements in the runway, with short intertrial intervals, and with solutions of different sucrose concentrations. For example, a group trained with 32%-4%-32% exhibiting a shorter latency in the second trial than a group trained with 32%-4%-4% would provide evidence inconsistent with this hypothesis.

In birds, RSEs and reversed RSEs have been observed within the same experiment (Thomas & Papini, 2003). For example, in a runway situation, pigeons exhibit both the iPREE and a reversed iMREE. Moreover, using the same reward magnitudes that yield a reversed iMREE, pigeons showed the VMREE also in the runway. Across-species discrepancies were also noted: a reversed iSNC in pigeons (Papini, 1997), but a cSNC effect in starlings (Freidin et al., 2009). A similar situation has also been observed in experiments with amphibians. I mentioned above a hint of a cSNC effect with downshifts in the sodium concentration of drinking water (Muzio et al., 2011). There was also direct evidence within a single experiment of a dissociation of RSEs: Toads produce an iPREE with 15-s intertrial intervals, but a reversed iPREE with 300-s intertrial intervals (Muzio et al., 1992). Toads also exhibited a performance resembling that of a partially-reinforced group when given training with continuous reinforcement, but with the spacing of rewards equal to that of a partially reinforced condition (Muzio et al., 2006).

As far as I know, there is currently no single learning theory that could accommodate these inconsistencies across species. They challenge two seminal ideas suggested by Bitterman (1975), namely, that RSEs such as the PREE, MREE, and SNC are produced by a common set of underlying mechanisms (e.g., Amsel, 1992), and that their co-variation across species, with RSEs in mammalian and reversed RSEs in nonmammalian vertebrates, suggests the evolution of novel learning mechanisms in mammalian ancestors not present in other vertebrates (e.g., Papini, 2002, 2003, 2006). The first hypothesis, that RSEs are the result of a common set of learning mechanisms, has been challenged independently of the comparative research reviewed here. For example, rats produced an iPREE when trained under either spaced (24-h intertrial intervals) or massed practice (intervals of a few seconds), but the same brain lesion (e.g., hippocampal ablation) disrupts the

spaced-practice iPREE (Jarrard, Isaacson, & Wickelgren, 1964; Rawlins et al., 1980), but not the massed-practice PREE (Rawlins et al., 1985).

Practice spacing has, in fact, been used to account for the dissociation of RSEs observed in comparative research, including the toad's iPREE/reversed-iPREE results mentioned above (Muzio et al., 1992). Massed-practice iPREEs have been reported in bony fish (*Carassius auratus*, *Tilapia macrocephala*) and turtles (*G. reevesii*, *Pseudemys scripta*, *Chrysemys picta*) trained in runway situations (Gonzalez & Bitterman, 1967; Gonzalez, Eskin, & Bitterman, 1963; Ishida & Kitamura, 1988; Murillo, Diercks, & Capaldi, 1961; Wise & Gallagher, 1964), although spaced-practice analogues result in reversed iPREEs in bony fish and turtles (Ishida & Papini, 1993; Pert & Bitterman, 1970). It is conceivable that a short intertrial interval may allow the aftereffects (e.g., sensory or short-term memory aftereffects) of one trial to control behavior in the subsequent trial, a mechanism known as *signal carry over* first suggested by Sheffield (1949). Such signal carry-over mechanism was specifically tested in goldfish under training conditions that yield the massed-practice iPREE (Gonzalez & Bitterman, 1967). Couvillon (1984) showed that massed practice produced a reversed iPREE when nontarget trials were interpolated between trials with a target stimulus trained either under partial or continuous reinforcement. This result suggests that goldfish relay on carry-over signals to produce the massed-practice iPREE, a result also consistent with reversed iPREE under spaced-practice conditions (Schutz & Bitterman, 1969). The rationale behind such procedure was to interfere with carry-over signals by interpolating nontarget trials. Using the same procedure, but with pigeons, interpolated trials did not eliminate the iPREE (Couvillon, Brandon, Woodard, & Bitterman, 1980), suggesting that pigeons do not relay on carry-over signals to develop this effect, a result consistent with the spaced-trial iPREE reported in these animals (Roberts et al., 1963; Thomas & Papini, 2003). Thus, there is support for the hypothesis that carry-over signals across trials can produce RSEs under relatively massed-practice conditions (with intertrial intervals from seconds to a few minutes) in all vertebrates studied thus far. However, such a mechanism cannot account for RSEs produced under spaced practice (with intervals in the order of hours to days) because carry-over signals would decay in time during the interval, thus not being available to control behavior in the following trial.

There is substantial evidence of an *emotional memory* component contributing to the spaced-practice RSEs in rats (Papini, Fuchs, & Torres, submitted; Papini, Wood, Daniel, & Norris, 2006). First, behavioral manipulations thought to reduce the impact of negative emotions on behavior, such as counterconditioning resulting from partial reinforcement training (pseudo random alternation of 32% sucrose and water trials), ameliorate the impact of reward devaluation in the cSNC situation (Cuenya et al., 2012; Pellegrini, Muzio, Mustaca, & Papini, 2004). Furthermore, administration of the benzodiazepine anxiolytic chlordiazepoxide before each N trial (i.e., water only) during the preshift period eliminates the effects of partial reinforcement during the 32-to-4% downshift period (Pellegrini et al., 2004). There are also several behavioral tests yielding results consistent with an emotional component to reward downshift. For example, aggressive behavior (Mustaca, Martinez, & Papini, 2000) and male sexual behavior (Freidin & Mustaca, 2004) are impaired, and pain sensitivity heightened (Mustaca & Papini, 2005) immediately after a downshift in the consummatory situation. Furthermore, presession induction of peripheral pain by a subcutaneous injection of formalin in a hind foot (Ortega, Daniel, Davis, Fuchs, & Papini, 2011) or by restraint stress (Ortega, Prado-Rivera et al., 2013) enhance the cSNC effect.

Second, pharmacological manipulations with drugs that affect emotion and mood modulate RSEs. Presession administration of benzodiazepine anxiolytics (Flaherty et al., 1986; Iwahara, Nagamura, & Iwasaki, 1967; Mustaca et al., 2000; Rosen & Tessel, 1970), ethanol (Becker & Flaherty, 1982; Kamenetzky et al., 2008), opioid agonists (Le Moal, Koob, & Bloom, 1979; Rowan & Flaherty, 1987; Wood, Daniel, & Papini, 2005; Wood, Norris, Daniel, & Papini, 2008), and cannabinoid agonists (Genn, Tucci, Parikh, & File, 2004) reduce RSEs in rats. The effects of benzodiazepine anxiolytics on cSNC are mediated by the amygdala, since

infusions of diazepam there, but not in the hippocampus, also reduce the cSNC effect (Liao & Chuang, 2003). In the case of opioid receptors, there is evidence that antagonists like naloxone and naltrindole produce the opposite effect, enhancing the cSNC, instrumental extinction, and consummatory extinction (Norris, Daniel, & Papini, 2008; Norris, Perez-Acosta, Ortega, & Papini, 2009; Pellegrini, Wood, Daniel, & Papini, 2005). Antidepressants such as imipramine and citalopram also modulate instrumental appetitive extinction (Huston, van den Brink, Komorowski, Huq, & Topic, 2012) and testosterone has an anxiolytic-like effect ameliorating cSNC (Justel, Ruetti, Mustaca, & Papini, 2012; Justel, Ruetti, Bentosela, Mustaca, & Papini, 2012).

Third, reward devaluation and omission lead to hypothalamic-pituitary-adrenal axis activation. In the cSNC situation, reward devaluation is accompanied by release of stress hormones like the adrenocorticotropic hormone and corticosterone (Flaherty, Becker, & Pohorecky, 1985; Mitchell & Flaherty, 1998; Pecoraro, de Jong, & Dallman, 2009). Reward omission also induces the release of stress hormones in both Skinner box and runway situations (Coe et al., 1983; Coover, Goldman, & Levine, 1971; Romero, Levine, & Sapolsky, 1995). Corticosterone release in appetitive extinction was also higher after acquisition with a large reward than with a small reward (Kawasaki & Iwasaki, 1997). Corticosterone administered immediately after the first devaluation session also enhances cSNC (Bentosela, Ruetti, Muzio, Mustaca, & Papini, 2006; Ruetti et al., 2009), a memory effect that might be mediated by N-methyl-D-aspartate receptors (Norris, Ortega, & Papini, 2011).

Fourth, several areas in the prefrontal cortex known to be implicated in emotion regulation have also been shown to modulate cSNC in rats. For example, lesions of the anterior cingulate cortex retard recovery from reward downshift (Ortega, Uhelski, Fuchs, & Papini, 2011), whereas lesions of the insular cortex eliminate the cSNC effect (Lin, Roman, & Reilly, 2009). Moreover, the ventrolateral orbital cortex seems to control the level of drive during reward devaluation (Ortega, Glueck, Uhelski, Fuchs, & Papini, 2013). These results are potentially relevant to an understanding of RSEs from a comparative perspective. Although precursor cells from all brain areas, including the neocortex, are present in most, if not all, vertebrates, the layered architecture of the mammalian neocortex is unique among the vertebrates (Butler, & Hodos, 2005). It is possible that the functional properties of cortical circuits are necessary for the RSEs observed in mammals, a possibility that has not yet received appropriate attention.

Finally, there is extensive data from selective breeding studies. Roman rat strains selected for high vs. low performance in a two-way active avoidance task exhibit correlated changes in RSE situations. The high-avoidance strain, which shows resilience in a variety of anxiety-inducing situations (Torres & Sabariego, 2014), also demonstrates reduced cSNC (Gomez, Escarabajal et al., 2009), impaired appetitive and aversive iSNC (Rosas et al., 2007; Torres et al., 2005), increased resistance to appetitive extinction (Gomez, de la Torre et al., 2009), and no evidence of iPREE (Gómez et al., 2008) relative to the low-avoidance strain. In another study, Long-Evans rats selected for fast vs. slow recovery from reward devaluation responded differentially to selective breeding (Ortega, Norris, Lopez-Seal, Ramos, & Papini, 2014). Whereas slow-recovery rats were no different form randomly selected controls, fast-recovery rats evolved reduced cSNC effects across seven generations. Interestingly, fast-recovery rats also showed no evidence of PRAE (see Table1) and iPREE, both of which were present in slow-recovery and random rats.

Compelling evidence for an emotional component in reward devaluation and omission comes from studies in which rats are allowed access to anxiolytics after the training session. In one study (Manzo et al., 2014), low-avoidance Roman rats (but not high-avoidance Roman rats) increased their voluntary oral consumption of ethanol immediately after consummatory and instrumental extinction sessions. These rats did not consume more ethanol after acquisition sessions. Moreover, control groups with postsession access to water did not show elevated levels of consumption, thus showing that this effect was driven by ethanol intake, rather than just drinking behavior. Increased oral consumption of the benzodiazepine anxiolytic

chlordiazepoxide, as well as ethanol, was also observed after reward devaluation in the cSNC runway situation in Wistar rats (Manzo, Sabariego, Donaire, Papini, & Torres, submitted). These effects were interpreted as anti-anxiety self-medication since these particular drugs have been shown to have anxiolytic properties in reward devaluation and omission situations (see references above).

The evidence for an emotional memory component in RSE experiments with mammals is persuasive, but, one could ask, is there similar evidence in experiments with nonmammalian vertebrates? In this case, the data are scanty and inconsistent. In agreement with an emotional component in RSEs, pigeons exhibit aggressive behavior toward signals of reward omission (Terrace, 1972) and toward another pigeon present during appetitive extinction (Azrin, Hutchinson, & Hake, 1966; Rilling, Askew, Ahlskog, & Kramer, 1969; Rilling & Caplan, 1973). Fowls (*Gallus gallus*) also exhibit aggressive responses when exposed to inaccessible food (Duncan & Wood-Gusch, 1971) and during appetitive extinction (Kuhne, Sauerbrey, & Adler, 2013). Pigeons also learn to turn off a visual stimulus signaling nonreinforcement (Terrace, 1971). These aggressive and escape behaviors are similar to what has been described in several mammalian species exposed to analogous conditions (see Papini & Dudley, 1997). However, an emotional component is inconsistent with some results that show qualitative differences in behavior between mammals and birds. For example, procedures that increase responding after surprising nonreward in rats (Stout et al., 2003) do not invigorate key pecking in pigeons (Papini & Hollingsworth, 1998; Stout, Muzio, Boughner, & Papini, 2002). As already mentioned, chlordiazepoxide eliminates the iPREE in rats (Rosen & Tessel, 1970), but it delays its emergence without eliminating it in pigeons (Thomas & Papini, 2003). There are no comparable data from other nonmammalian vertebrates. Still, what is needed is a systematic study of the mechanisms underlying extinction-induced aggression, escape from signals and contexts associated to nonreinforcement, and behavioral invigoration following surprising nonreward in mammals and birds to determine whether these behavioral similarities are homologous or homoplasic.

Although there seems to be no theoretical framework that can account for the diversity of adjustments to situations involving reward devaluations and omissions in vertebrates, two mechanisms stand out as relatively well tested: carry-over signals and emotional memory. The former mechanism is especially well suited to deal with the results of experiments based on massed practice and is possibly common to all vertebrates, whereas the latter mechanism deals best with spaced-practice experiments and could be unique to mammals. None of these mechanisms can account for RSEs in species that otherwise show reversed RSEs, such as the iPREE in pigeons (Thomas & Papini, 2003) and the OEE and ORE (see Table 1) in turtles (Ishida & Papini, 1997) because they should lead to co-variation of RSEs. But they offer a good starting point for an analysis of neural processes underlying the behavioral adjustments of a few selected vertebrates in a few selected testing conditions aimed at identifying common and divergent mechanisms engaged by surprising changes in reward conditions. As Bitterman (1975) put it:

> The learning processes that we now are able to infer from performance in learning situations are far removed, of course, from learning mechanisms. […] At the present stage of the inquiry, the question whether the processes of learning are the same in all animals reduces to the question whether the performance of all animals can be deduced from a common set of principles or whether different principles are necessary. It should be evident that the answer to this question must come not from casual work with a large assortment of animals but from intensive work with a small number of widely divergent forms. (pp. 706-707)

References

Amsel, A. (1992). *Frustration theory*. Cambridge, UK: Cambridge University Press.

Amsel, A., & Stanton, M. (1980). Ontogeny and phylogeny of paradoxical reward effects. In J. S. Rosenblatt, R. A. Hinde, C. Beer, & M. Busnel (Eds.), *Advances in the study of behavior* (pp. 227-274). New York, NY: Academic Press.

Azrin, N. H., Hutchinson, R. R., & Hake, D. F. (1966). Extinction-induced aggression. *Journal of the Experimental Analysis of Behavior, 9*, 191-204.

Baquero, A., Puerta, A., & Gutiérrez, G. (2009). Magnitude effects of sexual reinforcement in Japanese quail (*Coturnix japonica)*. *International Journal of Comparative Psychology, 22*, 113-126.

Barnes, W., & Tombaugh, T. N. (1973). Another failure to obtain negative incentive contrast following reductions in sucrose reward. *Psychological Reports, 33*, 801–802.

Becker, H. C., & Flaherty, C. F. (1982). Influence of ethanol on contrast in consummatory behavior. *Psychopharmacology*, *77*, 253-258.

Bentosela, M., Barrera, G., Jakovcevic, A., Elgier, A. M., & Mustaca, A. E. (2008). Effect of reinforcement, reinforcer omission and extinction on a communicative response in domestic dogs (*Canis familiaris*). *Behavioural Processes, 78,* 464–469.

Bentosela, M., Jakovcevic, A., Elgier, A. M., Mustaca, A. E., & Papini, M. R. (2009). Incentive contrast in domestic dogs (*Canis familiaris*). *Journal of Comparative Psychology, 123*, 125-130.

Bentosela, M., Ruetti, E., Muzio, R. N., Mustaca, A. E., & Papini, M. R. (2006). Administration of corticosterone after the first downshift trial enhances consummatory successive negative contrast. *Behavioral Neuroscience, 120,* 371–376.

Bergvall, U. A., Rautio, P., Luotola, T., & Leimar, O. (2007). A test of simultaneous and successive negative contrast in fallow deer foraging behaviour. *Animal Behaviour, 74*, 395-402.

Bitterman, M. E. (1960). Toward a comparative psychology of learning. *American Psychologist, 15*, 704-712.

Bitterman, M. E. (1975). The comparative analysis of learning. *Science, 188*, 699-709.

Bitterman, M. E. (2000). Cognitive evolution: A psychological perspective. In C. Heyes & L. Huber (Eds), *The evolution of cognition* (pp. 61-79). Cambridge, MA: Bradford Press.

Boughner, R. L., & Papini, M. R. (2006). Survival of the partial reinforcement extinction effect after contextual shifts. *Learning and Motivation*, *37*, 304-323.

Brown, R. T., & Wagner, A. R. (1964). Resistance to punishment and extinction following training with shock or nonreinforcement. *Journal of Experimental Psychology, 68*, 503–507.

Brush, F. R. (1985). Genetic determinants of avoidance learning: Mediation by emotionality? In F. R. Brush & J. B. Overmier (Eds.), A*ffect, conditioning, and cognition: Essays on the determinants of behavior* (pp. 27–42). Hillsdale, NJ: Erlbaum.

Burns, R. A. (1984). The goal units dimension in negative contrast failures with sucrose. *Journal of General Psychology, 111*, 9–23.

Burns, R. A., McCrary, M. D., McRae, H. L., & Lorig, T. S. (1984). Sucrose pellet reduction and runway performance. *Journal of General Psychology, 111*, 25–30.

Burns, R. A., & Wiley, L. P. (1984). Interevent anticipation of liquid and solid sucrose rewards. *Bulletin of the Psychonomic Society, 22*, 571–573.

Buriticá, J., Ortega, L. A., Papini, M. R., & Gutiérrez, G. (2013). Extinction of food-reinforced instrumental behavior in Japanese quail (*Coturnix japonica*). *Journal of Comparative Psychology, 127*, 33-39.

Butler, A. B., & Hodos, W. (2005). Co*mparative vertebrate neuroanatomy: Evolution and adaptation*. 2nd Edition. New York, NY: Wiley.

Carbonaro, D. A., Friend, T. H., Dellmeier, G. R., & Nuti, L. C. (1992). Behavioral and physiological responses of dairy goats to food thwarting. *Physiology & Behavior, 51*, 303–308.

Coe, C. L., Stanton, M. E., & Levine, S. (1983). Adrenal responses to reinforcement and extinction: Role of expectancy versus instrumental responding. *Behavioral Neuroscience, 97*, 654-657.
Couvillon, P. A. (1984). Performance of goldfish (*Carassius auratus*) in patterned sequences of rewarded and nonrewarded trials. *Journal of Comparative Psychology, 98*, 333-344.
Couvillon, P. A., & Bitterman, M. E. (1985). Effect of experience with a preferred food on consummatory responding for a less preferred food in goldfish. *Animal Learning & 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.
Cuenya, L., Sabariego, M., Donaire, R., Fernández-Teruel, A., Tobeña, A., Gómez, M. J., Mustaca, A. E., & Torres, C. (2012). The effect of partial reinforcement on instrumental successive negative contrast in inbred Roman High- (RHA-I) and Low- (RLA-I) Avoidance rats. *Physiology & Behavior, 105*, 1112-1116.
Coover, G. D., Goldman, L., & Levine, S. (1971). Plasma corticosterone increases produced by extinction of operant behavior in rats. *Physiology & Behavior, 6*, 261-263.
Daneri, M. R., Casanave, E., & Muzio, R. N. (2011). Control of spatial orientation in terrestrial toads (*Rhinella arenarum*). *Journal of Comparative Psychology, 125*, 296–307.
Daneri, M. F., Papini, M. R., & Muzio, R. N. (2007). Common toads (*Bufo arenarum*) learn to anticipate and avoid hypertonic saline solutions. *Journal of Comparative Psychology, 121*, 419-427.
Dantzer, R., Arnone, M., & Mormede, P. (1980). Effects of frustration on behaviour and plasma corticosteroid levels in pigs. *Physiology & Behavior, 24*, 1-4.
Davis, H., Memmott, J., MacFadden, L., & Levine, S. (1976). Pituitary-adrenal activity under different appetitive extinction procedures. *Physiology & Behavior, 17*, 687–690.
Dudley, R. T., & Papini, M. R. (1995). Pavlovian performance of rats following unexpected reward omissions. *Learning & Motivation, 26*, 63–82.
Duncan, I. J. H., & Wood-Gush, D. G. M. (1971). Frustration and aggression in the domestic fowl. *Animal Behaviour, 19*, 500-504.
Flaherty, C. F. (1996). *Incentive relativity.* Cambridge, UK: Cambridge University Press.
Flaherty, C. F., Becker, H. C., & Pohorecky, L. (1985). Correlation of corticosterone elevation and negative contrast varies as a function of postshift day. *Animal Learning & Behavior, 13*, 309-314.
Flaherty, C. F., & Caprio, M. (1976). Dissociation between instrumental and consummatory measures of incentive contrast. *American Journal of Psychology, 89*, 485-498.
Flaherty, C. F., Clarke, S., & Coppotelli, C. (1996). Lack of tolerance to contrast-reducing actions of chlordiazepoxide with repeated reward reductions. *Physiology & Behavior, 60*, 645-652.
Flaherty, C. F., Coppotelli, C., Hsu, D., & Otto, T. (1998). Excitotoxic lesions of the hippocampus disrupt runway but not consummatory contrast. *Behavioural Brain Research, 93*, 1-9.
Flaherty, C. F., Grigson, P. S., & Rowan, G. A. (1986). Chlordiazepoxide and the determinants of contrast. *Animal Learning & Behavior, 14*, 315-321.
Flaherty, C. F., Riley, E. P., & Spear, N. E. (1973). Effect of sucrose concentration and goal units on runway behavior in the rat. *Learning & Motivation, 4*, 163-175.
Flaherty, C. F., & Rowan, G. A. (1988). Effect of intersolution interval, chlordiazepoxide, and amphetamine on anticipatory contrast. *Animal Learning & Behavior, 16*, 47-52.
Franchina, J. J., & Brown, T. S. (1971). Reward magnitude shift effects in rats with hippocampal lesions. *Journal of Comparative & Physiological Psychology, 76*, 365–370.
Freidin, E., Cuello, M. I., & Kacelnik, A. (2009). Successive negative contrast in a bird: Starlings' behaviour after unpredictable negative changes in food quality. *Animal Behaviour, 77*, 857-865.
Freidin, E., & Mustaca, A. E. (2004). Frustration and sexual behavior in male rats. *Learning & Behavior, 32*, 311-320.

Genn, R. F., Tucci, S., Parikh, S., & File, S. E. (2004). Effects of nicotine and a cannabinoid receptor agonist on negative contrast: Distinction between anxiety and disappointment? *Psychopharmacology, 177*, 93-99.

Gómez, M. J., de la Torre, L., Callejas-Aguilera, J. E., Lerma-Cabrera, J. M., Rosas, J. M., Escarabajal, M. D., Agüero, A., Tobena, A., Fernandez-Teruel, A., & Torres, C. (2008). The partial reinforcement extinction effect (PREE) in female Roman high- (RHA-I) and low-avoidance (RLA-I) rats. *Behavioural Brain Research, 194*, 187-192.

Gómez, M. J., de la Torre, L., Callejas-Aguilera, J. E., Rosas, J. M., Escarabajal, M. D., Agüero, Á., Tobena, A., Fernandez-Teruel, A., & Torres, C. (2009). Differences in extinction of an appetitive instrumental response in female inbred Roman high- (RHA-I) and low- (RLA-I) avoidance rats. *Psicológica, 30*, 181-188.

Gómez, M. J., Escarabajal, M. D., de la Torre, L., Tobeña, A., Fernández-Teruel, A., & Torres, C. (2009). Consummatory successive negative and anticipatory contrast effects in inbred Roman rats. *Physiology & Behavior, 97*, 374-380.

Gonzalez, R. C., & Bitterman, M. E. (1967). Partial reinforcement effect in the goldfish as a function of amount of reward. *Journal of Comparative & Physiological Psychology*, *64*, 163-167.

Gonzalez, R. C., & Bitterman, M. E. (1969). Spaced-trials partial reinforcement effect as a function of contrast. *Journal of Comparative & Physiological Psychology*, *69*, 94-103.

Gonzalez, R. C., Eskin, R. M., & Bitterman, M. E. (1963). Further experiments on partial reinforcement in the fish. *American Journal of Psychology*, *76*, 366-375.

Goodrich, K. P., & Zaretsky, H. (1962). Running speed as a function of concentration of sucrose during pretraining. *Psychological Reports, 11*, 463–468.

Gygax, L., Reefmann, N., Wolf, M., & Langbein, J. (2013). Pefrontal cortex activity, sympatho-vagal reaction and behaviour distinguish between situations of feed reward and frustration in dwarf goats. *Behavioural Brain Research*, *239*, 104-114.

Huston, J. P., van den Brink, J., Komorowski, M., Huq, Y., & Topic, B. (2012). Antidepressants reduce extinction-induced withdrawal and biting behaviors: A model for depressive-like behavior. *Neuroscience, 210*, 249-257.

Ishida, M., & Kitamura, G. (1988). Partial reinforcement and its extinction in the turtle, *Geoclemys reevesii*. *Memoirs of Osaka Kyoiku University*, *37*, 29-34.

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 in turtles (*Geoclemys reevesii*). *Quarterly Journal of Experimental Psychology*, *50B*, 1-16.

Ison, J. R. (1962). Experimental extinction as a function of number of reinforcements. *Journal of Experimental Psychology, 64*, 314-317.

Iwahara, S., Nagamura, N., & Iwasaki, T. (1967). Effect of chlordiazepoxide upon experimental extinction in the straight runway as a function of partial reinforcement in the rat. *Japanese Psychological Research, 9*, 128-134.

Jarrard, L. E., Isaacson, R. L., & Wickelgren, W. O. (1964). Effects of hippocampal ablation and intertrial interval on runway acquisition and extinction. *Journal of Comparative & Physiological Psychology*, *57*, 442-444.

Jenkin, S. E. M., & Laberge, F. (2010). Visual discrimination learning in the fire-bellied toad *Bombina orientalis*. *Learning & Behavior, 38*, 418-425.

Justel, N., Ruetti, E., Mustaca, A. E., & Papini, M. R. (2012). Effects of pretraining treatment with testosterone on successive and anticipatory negative contrast. *Physiology & Behavior, 105*, 933-937.

Justel, N., Ruetti, E., Bentosela, M., Mustaca, A. E., & Papini, M. R. (2012). Effects of testosterone administration and gonadectomy on incentive downshift and open field activity in rats. *Physiology & Behavior, 106*, 657-663.

Kamenetzky, G. V., Mustaca, A. E., & Papini, M. R. (2008). An analysis of the anxiolytic effects of ethanol on consummatory successive negative contrast. *Advances in Latin American Psychology, 26*, 135-144.
Kamenetzky, G. V., Mustaca, A. E., Pedron, V. T., Cuenya, L., & Papini, M. R. (2009). Ethanol facilitates consummatory extinction. *Behavioural Processes 82*, 352-354.
Kawasaki, K., & Iwasaki, T. (1997). Corticosterone levels during extinction of runway response in rats. *Life Sciences, 61*, 1721-1728.
Kobre, K. R., & Lipsitt, L. P. (1972). A negative contrast effect in newborns. *Journal of Experimental Child Psychology, 14*, 81–91.
Kuhne, F., Sauerbrey, A. F. C., & Adler, S. (2013). The discrimination-learning task determines the kind of frustration-related behaviours in laying hens (*Gallus gallus domesticus*). *Applied Animal Behaviour Science*, 148, 192-200.
Le Moal, M., Koob, G. F., & Bloom, F. E. (1979). Endorphins and extinction: Differential actions on appetitive and aversive tasks. *Life Sciences, 24*, 1631-1636.
Lengersdorf, D., Stüttgen, M. C., Uengoer, M., & Güntürkün, O. (2014). Transient inactivation of the pigeon hippocampus or the nidopallium caudolaterale during extinction learning impairs extinction retrieval in an appetitive conditioning paradigm. *Behavioural Brain Research, 265*, 93-100.
Leszczuk, M. H., & Flaherty, C. F. (2000). Lesions of nucleus accumbens reduce instrumental but not consummatory negative contrast in rats. *Behavioural Brain Research, 116*, 61-79.
Lewis, M., Alessandri, S. M., & Sullivan, M. W. (1990). Violation of expectancy, loss of control, and anger expressions in young infants. *Developmental Psychology, 26*, 745–751.
Liao, R. M., & Chuang, F. J. (2003). Differential effects of diazepam infused into the amygdala and hippocampus on negative contrast. *Pharmacology, Biochemistry & Behavior, 74*, 953-960.
Lin, J., Roman, C., & Reilly, S. (2009). Insular cortex and consummatory successive negative contrast in the rat. *Behavioral Neuroscience, 123,* 810–814.
Lonze, B. E., & Ginty, D. D. (2002). Function and regulation of CREB family transcription factors in the nervous system. *Neuron, 35*, 605-623.
Lowes, G., & Bitterman, M. E. (1967) Reward and learning in the goldfish. *Science¸ 157*, 455-457.
Lyons, D. M., Fong, K. D., Schrieken, N., & Levine, S. (2000). Frustrative nonreward and pituitary-adrenal activity in squirrel monkeys. *Physiology & Behavior, 71*, 559-563.
Macphail, E. M. (1982). *Brain and intelligence in vertebrates*. Oxford, UK: Clarendon Press.
Manzo, L., Gómez, M. J., Callejas-Aguilera, J. E., Fernández-Teruel, A., Papini, M. R., & Torres, C. (2014). Anti-anxiety self-medication induced by incentive loss in rats. *Physiology & Behavior, 123*, 86-92.
Mast, V. K., Fagen, J. W., Rovee-Collier, C. K., & Sullivan, M. W. (1980). Immediate and long-term memory for reinforcement context: The development of learned expectancies in early infancy. *Child Development, 51*, 700-707.
Mitchell, C., & Flaherty, C. F. (1998). Temporal dynamics of corticosterone elevation in successive negative contrast. *Physiology & Behavior, 64*, 287-292.
Murillo, N. R., Diercks, J. K., & Capaldi, E. J. (1961). Performance of the turtle, *Pseudemys scripta troostii*, in a partial-reinforcement situation. *Journal of Comparative & Physiological Psychology*, *54*, 204-206.
Mustaca, A. E., Bentosela, M., & Papini, M. R. (2000). Consummatory successive negative contrast in mice. *Learning & Motivation, 31*, 272-282.
Mustaca, A. E., Freidin, E., & Papini, M. R. (2002). Extinction of consummatory behavior in rats. *International Journal of Comparative Psychology*, *15*, 1-10.
Mustaca, A. E., Martínez, C., & Papini, M. R. (2000). Surprising nonreward reduces aggressive behavior in rats. *International Journal of Comparative Psychology*, *13*, 91-100.
Mustaca, A. E., & Papini, M. R. (2005). Consummatory successive negative contrast induces hypoalgesia. *International Journal of Comparative Psychology*, *18*, 255-262.
Muzio, R. N., Pistone-Creydt, V., Iurman, M., Rinaldi, M. A., Sirani, B., & Papini, M. R. (2011). Incentive or habit learning in amphibians? *PLoS ONE, 6*, 1-12.

Muzio, R. N., Ruetti, E., & Papini, M. R. (2006). Determinants of instrumental extinction in terrestrial toads (*Bufo arenarum*). *Learning & Motivation, 37*, 346-356.
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 & Motivation*, *23*, 406-429.
Muzio, R. N., Segura, E. T., & Papini, M. R. (1993). Effects of lesions in the medial pallium on instrumental learning in the toad (*Bufo arenarum*). *Physiology & 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 & Neural Biology, 61*, 36–46.
Norris, J. N., Daniel, A. M., & Papini, M. R. (2008). Spontaneous recovery of consummatory behavior, but not of consummatory successive negative contrast. *Learning & Motivation, 39*, 296-312.
Norris, J. N., Ortega, L. A., & Papini, M. R. (2011). Posttrial D-cycloserine enhances the emotional memory of an incentive downshift event. *Behavioural Brain Research, 223*, 348-355.
Norris, J. N., Pérez-Acosta, A. M., Ortega, L. A., & Papini, M. R. (2009). Naloxone facilitates appetitive extinction and eliminates escape from frustration. *Pharmacology, Biochemistry & Behavior, 94*, 81-87.
Northcutt, R. G., & Ronan, M. (1992). Afferent and efferent connections of the bullfrog medial pallium. *Brain, Behavior & Evolution, 40*, 1-16.
Ortega, L. A., Daniel, A. M., Davis, J. B., Fuchs, P. N., & Papini, M. R. (2011). Peripheral pain enhances the effects of incentive downshifts. *Learning & Motivation, 42*, 203-209.
Ortega, L. A., Glueck, A. C., Daniel, A. M., Prado-Rivera, M. A., White, M. M., & Papini, M. R. (2014). Memory interfering effects of chlordiazepoxide on consummatory successive negative contrast. *Pharmacology Biochemistry & Behavior, 116*, 96-106.
Ortega, L. A., Glueck, A. C., Uhelski, M., Fuchs, P. N., & Papini, M. R. (2013). Role of the ventrolateral orbital cortex and medial prefrontal cortex in incentive downshift situations. *Behavioural Brain Research, 244*, 120-129.
Ortega, L. A., Norris, J. N., Lopez-Seal, M. F., Ramos, T., & Papini, M. R. (2014). Correlates of recovery from incentive downshift: A preliminary selective breeding study. *International Journal of Comparative Psychology, 27*, 18-44.
Ortega, L. A., Prado-Rivera, M. A., Cárdenas-Poveda, D. C., McLinden, K. A., Glueck, A. C., Gutiérrez, G., Lamprea, M. R., & Papini, M. R. (2013). Tests of the aversive summation hypothesis in rats: Effects of restraint stress on consummatory successive negative contrast and extinction in the Barnes maze. *Learning & Motivation*, *44*, 159-173.
Ortega, L. A., Uhelski, M., Fuchs, P. N., & Papini, M. R. (2011). Impairment of recovery from incentive downshift after lesions of the anterior cingulate cortex: Emotional or cognitive deficits? *Behavioral Neuroscience, 125*, 988-995.
Papini, M. R. (1997). Role of reinforcement in spaced-trial operant learning in pigeons (*Columba livia*). *Journal of Comparative Psychology, 111*, 275–285.
Papini, M. R. (2002). Pattern and process in the evolution of learning. *Psychological Review*, *109*, 186-201.
Papini, M. R. (2003). Comparative psychology of surprising nonreward. *Brain, Behavior & Evolution, 62*, 83-95.
Papini, M. R. (2006). Role of surprising nonreward in associative learning. *Japanese Journal of Animal Psychology, 56*, 35-54.
Papini, M. R. (2008). *Comparative psychology: Evolution and development of behavior. 2nd Edition.* New York: Psychology Press.
Papini, M. R., & Dudley, R. T. (1997). Consequences of surprising reward omissions. *Review of General Psychology, 1*, 175-197.
Papini, M. R., & Hollingsworth, P. R. (1998). Role of nonreinforcement in the fixed-interval performance of pigeons. *Psychonomic Bulletin & Review, 5*, 84-90.
Papini, M. R., Ludvigson, H. W., Huneycutt, D., & Boughner, R. L. (2001). Apparent contrast effects in autoshaping with rats. *Learning & Motivation*, *32*, 434-456.

Papini, M. R., Mustaca, A. E., & Bitterman, M. B. (1988). Successive negative contrast in the consummatory responding of didelphid marsupials. *Animal Learning & 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, & Evolution, 46*, 61–71.
Papini, M. R., & Pellegrini, S. (2006). Scaling relative incentive value in consummatory behavior. *Learning & Motivation*, *37*, 357-378.
Papini, M. R., & Ramallo, P. (1990). Primary frustration in the red opossum, *Lutreolina crassicaudata*. *International Journal of Comparative Psychology, 3*, 235–242.
Papini, M. R., & Thomas, B. (1997). Spaced-trial learning with purely instrumental contingencies in pigeons (*Columba livia*). *International Journal of Comparative Psychology, 10*, 128–136.
Papini, M. R., Thomas, B., & McVicar, D. G. (2002). Between-subject PREE and within-subject reversed PREE spaced-trial extinction with pigeons. *Learning & Motivation¸ 33*, 485-509.
Papini, M. R., Wood, M., Daniel, A. M., & Norris, J. N. (2006). Reward loss as psychological pain. *International Journal of Psychology & Psychological Therapy*, *6*, 189-213.
Pecoraro, N., de Jong, H., & Dallman, M. R. (2009). An unexpected reduction in sucrose concentration activates the HPA axis on successive post shift days without attenuation by discriminative contextual stimuli. *Physiology & Behavior, 96*, 651-661.
Pellegrini, S., Lopez-Seal, M. F., & Papini, M. R. (2008). Scaling relative incentive value: Different adjustments to incentive downshift in pigeons and rats. *Behavioural Processes*, *79*, 182-188.
Pellegrini, S., & Mustaca, A. E. (2000). Consummatory successive negative contrast with solid food. *Learning & Motivation*, *31*, 200-209.
Pellegrini, S., Muzio, R. N., Mustaca, A. E., & Papini, M. R. (2004). Successive negative contrast after partial reinforcement in the consummatory behavior of rats. *Learning and Motivation*, *35*, 303-321.
Pellegrini, S., & Papini, M. R. (2007). Scaling relative incentive value in anticipatory behavior. *Learning & Motivation*, *38*, 128-154.
Pellegrini, S., Wood, M., Daniel, A. M., & Papini, M. R. (2005). Opioid receptors modulate recovery from consummatory successive negative contrast. *Behavioural Brain Research, 164*, 239-249.
Pert, A., & Bitterman, M. E. (1970). Reward and learning in the turtle. *Learning & Motivation*, *1*, 121-128.
Puddington, M. M., Papini, M. R., & Muzio, R. N. (2013). Vulnerability of long-term memory to temporal delays in amphibians. *Behavioural Processes, 99*, 7-11.
Ramsay, Z. J., Ikura, J., & Laberge, F. (2013). Modification of a prey catching response and the development of behavioral persistence in the fire-bellied toad (*Bombina orientalis*). *Journal of Comparative Psychology, 127*, 399-411.
Rayburn–Reeves, R. M., Stagner, J. P., Kirk, C. R., & Zentall, T. R. (2013). Reversal learning in rats (*Rattus norvegicus*) and pigeons (*Columba livia*): Qualitative differences in behavioral flexibility. *Journal of Comparative Psychology, 127*, 202-211.
Rawlins, J. N. P., Feldon, J, & Gray J. A. (1980). The effects of hippocampectomy and of fimbria section upon the partial reinforcement extinction effect in rats. *Experimental Brain Research, 38*, 273-283.
Rawlins, J. N. P., Feldon, J., Ursin, H., & Gray, J. A. (1985). Resistance to extinction after schedules of partial delay or partial reinforcement in rats with hippocampal lesions. *Experimental Brain Research, 59,* 273-281.
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.
Rilling, M., & Caplan, H. J. (1973). Extinction-induced aggression during errorless discrimination learning. *Journal of the Experimental Analysis of Behavior, 20*, 85-92.
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.

Romero, L. M., Levine, S., & Sapolsky, R. M. (1995). Adrenocorticotropin secretagog release: stimulation by frustration and paradoxically by reward presentation. *Brain Research, 676*, 151-156.

Rosas, J. M., Callejas-Aguilera, J. E., Escarabajal, M. D., Gómez, M. J., de la Torre, L., Agüero, Á., Tobena, A., Fernandez-Teruel, A., & Torres, C. (2007). Successive negative contrast effect in instrumental runway behaviour: A study with Roman high- (RHA) and Roman low- (RLA) avoidance rats. *Behavioural Brain Research, 185,* 1-8.

Rosen, A. J. (1966). Incentive-shift performance as a function of magnitude and number of sucrose rewards. *Journal of Comparative and Physiological Psychology, 62*, 487–490.

Rosen, A. J., & Ison, J. R. (1965). Runway performance following changes in sucrose rewards. *Psychonomic Science, 2*, 335–336.

Rosen, A. J., & Tessel, R. E. (1970). Chlorpromazine, chlordiazepoxide and incentive shift performance in the rat. *Journal of Comparative & Physiological Psychology, 72*, 257-262.

Rowan, G. A., & Flaherty, C. F. (1987). The effects of morphine in the consummatory contrast paradigm. *Psychopharmacology, 93*, 51-58.

Ruetti, E., Justel, N., Mustaca, A. E., & Papini, M. R. (2009). Posttrial corticosterone administration enhances the effects of incentive downshift: Exploring the boundaries of this effect. *Behavioral Neuroscience, 123*, 137-144.

Sakamoto, K., Karelina, K., & Obrietan, K. (2011). CREB: A multifaceted regulator of neuronal plasticity and protection. *Journal of Neurochemistry, 116*, 1-9.

Sastre, A., & Reilly, S. (2006). Excitotoxic lesions of the gustatory thalamus eliminate consummatory but not instrumental successive negative contrast in rats. *Behavioural Brain Research, 170*, 34-40.

Sastre, A., Lin, J.-Y., & Reilly, S. (2005). Failure to obtain instrumental successive negative contrast in tasks that support consummatory successive negative contrast. *International Journal of Comparative Psychology, 18*, 307-319.

Schmajuk, N. A., Segura, E. T., & Reboreda, J. C. (1980). Appetitive conditioning and discriminatory learning in toads. *Behavioral & Neural Biology, 28*, 392-397.

Schmajuk, N. A., Segura, E. T., & Ruidiaz, A. C. (1981). Reward downshift in the toad. *Behavioral & Neural Biology, 33*, 519-523.

Schutz, S. L., & Bitterman, M. E. (1969). Spaced trials partial reinforcement and resistance to extinction in the goldfish. *Journal of Comparative & Physiological Psychology, 68,*126-128.

Shanab, M. E., Domino, J., & Ralf, L. (1978). The effects of repeated shifts in magnitude of food reward upon the barpress rate in the rat. *Bulletin of the Psychonomic Society, 12*, 29–31.

Sheffield, V. F. (1949). Extinction as a function of partial reinforcement and distribution of practice. *Journal of Experimental Psychology*, *39*, 511-526.

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior*. (2nd ed.). New York, NY: Oxford University Press.

Shibasaki, M., & Ishida, M. (2012). Effects of overtraining on extinction in newts (*Cynops pyrrhogaster*). *Journal of Comparative Psychology, 126*, 368-371.

Silva, A. J., Kogan, J. H., Frankland, P. W., & Kida, S. (1998). CREB and memory. *Annual Review of Neuroscience, 21*, 127-148.

Spear, N. E., & Hill, W. F. (1965). Adjustment to new reward: Simultaneous- and successive-contrast effects. *Journal of Experimental Psychology, 70*, 510–519.

Stout, S. C., Boughner, R. L., & Papini, M. R. (2003). Reexamining the frustration effect in rats: Aftereffects of surprising reinforcement and nonreinforcement. *Learning & Motivation*, *34*, 437-456.

Stout, S. C., Muzio, R. N., Boughner, R. L., & Papini, M. R. (2002). Aftereffects of the surprising presentation and omission of appetitive reinforcers on key pecking performance in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *28*, 242-256.

Terrace, H. S. (1971). Escape from S-. *Learning & Motivation, 2*, 148-163.

Terrace, H. S. (1972). By-products of discrimination learning. *Psychology of Learning & Motivation, 5*, 195-265.
Thomas, B., & Papini, M. R. (2001). Adrenalectomy eliminates the extinction spike in autoshaping with rats. *Physiology & Behavior*, *62*, 543-547.
Thomas, B., & Papini, M. R. (2003). Mechanism of spaced-trial runway extinction in pigeons. *Learning & Motivation*, *34*, 104-126.
Thompson, T., & Bloom, W. (1966). Aggressive behavior and extinction-induced response-rate increase. *Psychonomic Science, 5*, 335-336.
Thorndike, E. L. (1911). *Animal intelligence: Experimental studies*. New York, NY: Macmillan.
Timberlake, W., & Lucas, G. A. (1989). Behavior systems and learning: From misbehavior to general principles. In S. B. Klein & R. R. Mowrer (Eds.), *Contemporary learning theories. Instrumental conditioning and the impact of biological contraints on learning* (pp. 237-275). Hillsdale, NJ: Erlbaum.
Tinklepaugh, O. L. (1928). An experimental study of representative factors in monkeys. *Journal of Comparative Psychology, 8*, 197-236.
Torres, C., Cándido, A., Escarabajal, M. D., de la Torre, L., Maldonado, A., Tobeña, A., & Fernández-Teruel, A. (2005). Successive negative contrast in one-way avoidance learning in female Roman rats. *Physiology & Behavior, 85*, 377-382.
Torres, C., & Sabariego, M. (2014). Incentive relativity: Gene-environment interactions. *International Journal of Comparative Psychology*, *27*, 446-458.
Watanabe, M. (1996). Reward expectancy in primate prefrontal neurons. *Nature, 382*, 629-632.
Weinstein, L. U. (1970). Negative incentive contrast effects with saccharin vs. sucrose and partial reinforcement. *Psychonomic Science, 21*, 276–278.
Wells, K. D. (2007). *The ecology and behavior of amphibians*. Chicago, IL: University of Chicago Press.
Wood, M. D., Daniel, A. M., & Papini, M. R. (2005). Selective effects of the delta opioid receptor agonist DPDPE on consummatory successive negative contrast. *Behavioral Neuroscience*, *119*, 446-454.
Wood, M. D., Norris, J. N., Daniel, A. M., & Papini, M. R. (2008). Trial-selective effects of U50,488H, a kappa-opioid receptor agonist, on consummatory successive negative contrast. *Behavioural Brain Sciences, 193*, 28-36.
Wise, L. M., & Gallagher, D. P. (1964). Partial reinforcement of a discriminative response in the turtle. *Journal of Comparative & Physiological Psychology*, *57*, 311-313.

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