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Transfer between anticipatory and consummatory tasks involving reward loss

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ABSTRACT

Does recovery from reward devaluation or partial reinforcement (PR) involve the counterconditioning of frustration? Transfer among tasks involving reward loss was used to uncover frustration counterconditioning. In Experiment 1, Phase 1 training in consummatory successive negative contrast (cSNC; 32-to-4% sucrose devaluation) eliminated Phase 2 iSNC in one-way avoidance (40-to-3 s safety-time reduction), but the opposite sequence generated no detectable transfer. In Experiment 2, transfer from Phase 1 cSNC to Phase 2 autoshaping extinction after continuous reinforcement increased lever pressing in previously downshifted animals relative to unshifted controls. However, Phase 1 training in autoshaping under partial reinforcement (PR) had no effect on Phase 2 cSNC. Transfer from PR to cSNC also failed when sucrose pellets were used in autoshaping (Experiment 3), when autoshaping acquisition was extended from 100 to 300 trials (Experiment 4), and when preshift training in cSNC was extended from 10 to 20 sessions (Experiment 5). In Experiment 6, Phase 1 training in PR for licking enhanced Phased 2 cSNC, also involving licking, and in Experiment 7 Phase 1 PR training in autoshaping enhanced Phase 2 cSNC after a 22-to-4% sucrose downshift. Whereas prior exposure to cSNC (consummatory task) increased resistance to extinction in autoshaped lever pressing, prior training in one-way avoidance, PR in autoshaping, or PR in taste conditioning (all anticipatory tasks) either had no effect or they enhanced the cSNC effect. Frustration counterconditioning developed during these tasks, but the type of transfer effect depends on task sequence.

1. Introduction

Animals tend to reject rewarding outcomes when their incentive value is lower than expected. This phenomenon, called successive negative contrast, occurs in anticipatory instrumental responses (iSNC) and in consummatory responses (cSNC), and with magnitude and quality reward devaluations (Flaherty, 1996). Rejection of the devalued, small reward is transient; when sufficient training is provided, behavior returns to the level of unshifted controls reinforced always with the small reward. A contributing factor to SNC is the aversive emotion resulting from the negative discrepancy between received and expected reward magnitudes (Papini, Fuchs, & Torres, 2015). This aversive emotion has been traditionally referred to as frustration—a hedonically aversive internal state that suppresses goal approach and induces drive or attention (Amsel, 1962, 1992). The transient nature of the SNC effect implies that frustration is reduced in the course of experience with the devalued reward, but by what mechanisms?

Fig. 1 shows the two hypothesized mechanisms of recovery from SNC: memory update and frustration counterconditioning (Papini, 2003). Reward devaluation combined with food deprivation generates an approach-avoidance conflict. The relatively low

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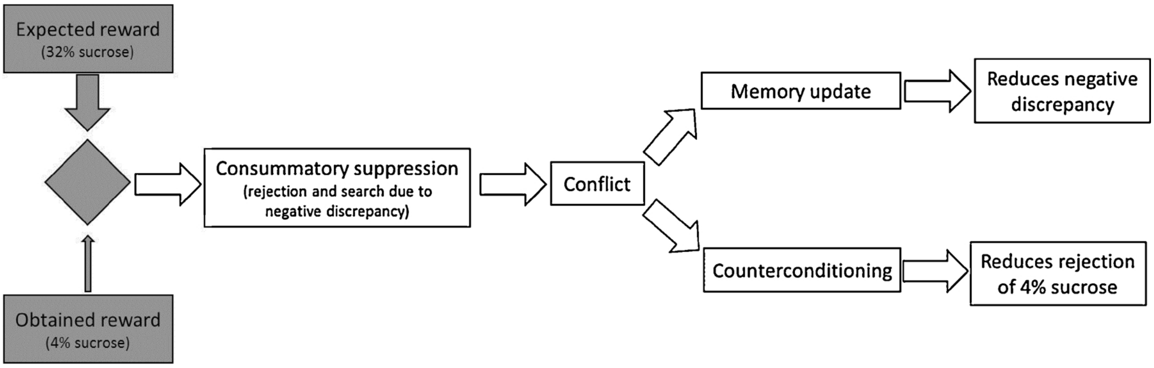

Fig. 1. Amsel's (1992) frustration theory applied to cSNC. When obtained rewards are less valued than expected rewards (represented by the thickness of the arrows converging on the comparator), then consummatory behavior is suppressed. The ensuing conflict involves approaching the devalued reward, which is still rewarding because of food deprivation, versus rejecting/avoiding the devalued reward because it is not as large as expected. Recovery from this conflict is hypothesized to involve two mechanisms (Papini, 2003). Memory update adjusts the reward expectation until it matches the obtained reward, thus eliminating the negative discrepancy. Counterconditioning resulting from pairings of anticipatory frustration with the devalued reward reduces rejection and avoidance.

incentive value of the devalued reward induced rejection and avoidance of the outcome, but food deprivation instigates approach to the outcome. Thus, presession feeding attenuates the approach response and prolongs cSNC (Cuenya et al., 2015). Moreover, presession anxiolytics (e.g., ethanol and benzodiazepines; Flaherty, Grigson, & Rowan, 1986; Kamenetzky, Mustaca, & Papini, 2008) and opioid agonists (Rowan & Flaherty, 1987; Wood, Daniel, & Papini, 2005; Wood, Norris, Daniel, & Papini, 2008) reduce cSNC by attenuating the rejection/avoidance response. According to this analysis, recovery from reward devaluation requires conflict resolution.

As the animal experiences the devalued reward it is also learning to anticipate it—a memory-update process (Papini, 2003). Memory update reduces the negative discrepancy until eventually there is no basis for negative emotion because the obtained reward matches the expected reward. Memory update has been tested with postsession administration of chlordiazepoxide, a benzodiazepine that has memory-interfering effects (e.g., Silva & Frussa-Filho, 2000). Immediate, but not delayed, administration of chlordiazepoxide after the first downshift session prolongs the cSNC effect in subsequent sessions (Ortega, Glueck, Daniel, White, & Papini, 2014). Control experiments indicate that this drug effect requires reward devaluation to occur. A retardation of recovery from cSNC is consistent with interference with the acquisition of a new memory about the devalued reward. Thus, one way to reduce the conflict is to adjust the comparison memory to the new reward magnitude so as to reduce negative discrepancy. The experiments reported in this article relate to the second mechanism of recovery: the counterconditioning of frustration.

Counterconditioning was first described by Pavlov (1927) in an experiment in which a dog received pairings of an electric shock with food. Pavlov noticed that after a few pairings, defensive responses gave way to salivary secretion when the shock was administered. Similarly, Amsel (1992) argued that the pairing of anticipatory frustration with reward weakened the tendency to evoke outcome avoidance and replaced it with a tendency to induce outcome approach. In Amsel's (1992) theory, counterconditioning is a major mechanism to account for increased response persistence in extinction after training with partial reinforcement (PR) relative to continuous reinforcement (CR). In the SNC situation, counterconditioning would result from pairings between anticipatory frustration and the devalued reward. The devalued reward is still a reward given the high motivational state derived from food deprivation. A key property of counterconditioning is that it supports transfer across situations, responses, and motivational states. Ross (1964); see also Mellgren, Hoffman, Nation, Williams, & Wrather, 1979; Nation, Wrather, Mellgren, & Spivey, 1980) reported an experiment in which rats received training in three phases, under different conditions, that provided support for transfer across situations. In Ross' experiment, six groups of rats received training in either PR (3 groups) or CR (3 groups) during Phase 1. Pairs of PR−CR groups differed in the response requirement (running, climbing, or jumping), but were all food deprived, food reinforced, and trained in a short, black, wide box. In Phase 2, all animals received CR training for running in a long, narrow, white runway, while water deprived, and to collect water in the goal box. Finally, in Phase 3, all animals received extinction of the running response trained in the previous phase. Ross argued that the counterconditioning of frustration in Phase 1 would reinstate the associated response during extinction in Phase 3. Such reinstatement would either facilitate extinction when that response was incompatible with running (such as climbing), but it would induce persistence when the responses were compatible (such as with running and jumping). Ross confirmed these counterintuitive predictions. Animals exhibited transfer of counterconditioned frustration to a novel context, under a different motivational state, and working for a different reward. Such transfer occurred even if no opportunity for counterconditioning was provided in Phases 2–3 when only CR training was administered. Transfer was hypothesized to be based on anticipatory frustration induced during the extinction of running in Phase 3.

Recent experiments have used this strategy to determine whether transfer attributable to frustration counterconditioning could be detected with mixed results. Cuenya et al. (2015) investigated the role of transfer across cSNC and iSNC tasks in inbred Roman strains of rats. Roman rats have been selectively bred since the 1960 s to exhibit either fast (Roman high-avoidance strain, RHA) or slow (Roman low-avoidance strain, RLA) avoidance learning in the two-way active avoidance situation. Strains also differ in a variety of nonselected traits, including anxiety (see Torres & Sabariego, 2014) and SNC tasks (Gómez et al., 2009; Rosas et al., 2007; Torres et al., 2005). Because RLA animals demonstrate an increased sensitivity to reward devaluation in both cSNC and iSNC, Cuenya et al. (2015) hypothesized that RLA rats would demonstrate stronger evidence of transfer than RHA rats. The results revealed that RHA animals exhibited both effects with an equal duration whether in Phase 1 (with no prior experience) or in Phase 2 (with prior exposure to the alternative task), thus yielding no evidence of transfer. However, prior experience affected the performance of RLA rats in both tasks. Thus, in RLA rats, exposure to one SNC task during Phase 1 either shortened or eliminated the other SNC task during Phase 2. Therefore, RLA rats showed evidence of positive transfer and the effects were bidirectional (from iSNC to cSNC, and vice versa) and symmetrical (positive transfer in both directions).

Transfer was also sought in experiments involving iSNC and adjunctive wheel running induced by intermittent reinforcement (Rick, Donaire, Papini, Torres, & Pellón, 2018). Two experiments were designed to test the hypothesis that adjunctive behavior depends on frustration induced by periods of nonreinforcement during intermittent reinforcement training (Papini & Dudley, 1997). There was evidence that PR training in Phase 1 enhanced adjunctive wheel running, but no evidence that adjunctive wheel running influence extinction of running after CR training. Thus, transfer was unidirectional. Notice that unlike in Ross' (1964) experiment, these recent attempts at observing transfer have involved bidirectional exposure to the tasks (i.e., for tasks A and B, A→B and also B→A were tested). The present experiments also tested for bidirectional transfer between anticipatory response tasks and consummatory response tasks.

2. Experiment 1

One experiment involving transfer across situations cited above is procedurally similar to Experiment 1. Nation et al. (1980) trained four groups of rats in PR or CR and in either escape conditioning (aversive) or food-reinforced running (appetitive) in Phase 1. In Phase 2, groups were trained in the opposite situation (i.e., aversive to appetitive and vice versa) under CR and then exposed to extinction. They reported bidirectional transfer, that is, Phase 1 PR training in either task increased resistance to extinction in the other task during Phase 2.

Experiment 1 tested for bidirectional transfer across appetitive (cSNC) and aversive tasks (one-way avoidance, OWA). One task was consummatory, cSNC, and the other task was anticipatory, OWA. Both tasks involved reward downshift, similarly to Cuenya et al. (2015) study. Candido, Maldonado, Megias, and Catena (1992) reported that rats downshifted from 30 s to 1 s in the safety compartment during a OWA task exhibited a deterioration of avoidance behavior relative to animals always allowed 1 s in the safety compartment. This was interpreted as an SNC effect involving the unexpected reduction in the reward obtained by spending 1 s in the safety compartment—a prospective, incentive effect. An interpretation of this SNC effect in the OWA task in terms of Amsel's (1992) theory would suggest that the reduction in safety time is frustrating; anticipating that frustration increases the tendency to avoid the safety compartment, thus requiring additional trials to reach the acquisition criterion. Consistent with this interpretation, the effect of reward downshift in the OWA situation was attenuated by presession treatment with benzodiazepine and barbiturate anxiolytics (Morales, Torres, Megías, Cándido, & Maldonado, 1992; Torres, Morales, Cándido, & Maldonado, 1996). In the same vein, the effect was observed in RLA and Wistar rats, but not in RHA rats (Torres et al., 2005). Similar results with Roman strains were obtained with cSNC and appetitive iSNC tasks (Torres & Sabariego, 2014).

The goal of Experiment 1 was to determine whether exposure to reward devaluation in one task would attenuate the effects of reward devaluation in the other. Based on previous results (Cuenya et al., 2015; Nation et al., 1980), we predicted bidirectional transfer assuming that approaching the safety compartment in the OWA task and the goal box in the runway are analogous behaviors.

2.1. Method

2.1.1. Subjects

The subjects were 49 male Sprague-Dawley rats, approximately 90 days old at the start of training, and experimentally naïve. In this series of experiments, the strain and sex of the animals used were based on availability. The mean (± SEM) ad lib weight was 226.4 g (± 33.0 g). Animals were housed individually, kept on a 14:10-hr light:dark cycle, and maintained at 82% of their free-feeding weight. Animals were fed once daily, approximately 30 min after the end of each session. Water was continuously available in the home cage. Cages were housed in a colony room with constant temperature and humidity.

2.1.2. Apparatus

The cSNC task was carried out in four identical metal cages (24.5 × 17.5 × 18 cm). A 1-cm diameter hole was centered 7 mm above the floor on one side of the cage. A graduated cylinder was placed outside the cage so that the orifice of the drinking spout was centered in the hole flush with the outside wall of the cage. A contact-relay circuit was used to record licking responses.

The OWA task was carried out in a shuttle box (Coulbourn Instruments, Allentown, PA). The avoidance box consisted of two equal compartments (16 × 18 × 22 cm, W × L × H) separated by a wall with an opening 7-cm wide and 8-cm high as measured from the grid floor, and a removable gate to allow communication between compartments. The grid floor consisted of 24 stainless steel bars (diameter: 0.5 cm) connected in series to a module capable of delivering a continuous scrambled shock of 1 mA. The floors in both compartments were hinged to operate a microswitch when depressed; this allowed the control of apparatus and recording of responses by a computer. A speaker was placed in the middle of a lateral wall so that half of it was oriented toward the danger compartment and the other half toward the safe compartment. The warning signal was a 2.9-KHz tone, 88-dB SPL. The shuttle box was illuminated with a 12-W light bulb. The roof of the danger compartment consisted of a black glass panel, which was only

Table 1
Summary of Designs Used in this Series of Experiments.

Experiment	Figure	Phase	Training
1a	2	1	OWA, 40-3 s of safety vs. 3-3 s of safety
		2	cSNC, 32-4% sucrose vs. 4-4% sucrose
1b	3	1	cSNC, 32-4% sucrose vs. 4-4% sucrose
		2	OWA, 40-3 s of safety vs. 3-3 s of safety
2a	4	1	AS with CR vs. PR, 5 food pellets/trial, 100 acquisition trials
		2	cSNC, 32-4% sucrose vs. 4-4% sucrose
2b	5	1	cSNC, 32-4% sucrose vs. 4-4% sucrose
		2	AS with CR vs. PR, 5 food pellets/trial, 100 acquisition trials, extinction
3	6	1	AS with CR vs. PR, 5 sucrose pellets/trial, 100 acquisition trials
		2	cSNC, 32-4% sucrose vs. 4-4% sucrose
4	7	1	AS with CR vs. PR, 5 food pellets/trial, 300 acquisition trials
		2	cSNC, 32-4% sucrose vs. 4-4% sucrose
5	8	1	AS with CR vs. PR, 5 food pellets/trial, 100 acquisition trials
		2	cSNC, 32-4% sucrose vs. 4-4% sucrose, 20 preshift sessions
6	9	1	Taste with CR vs. PR, chocolate milk, 100 acquisition trials
		2	cSNC, 32-4% sucrose vs. 4-4% sucrose
7	10	1	AS with CR vs. PR, 5 food pellets/trial, 200 acquisition trials
		2	cSNC, 22-4% sucrose vs. 4-4% sucrose
		3	AS with CR, 5 food pellets/trial, 50 reacquisition trials, extinction

Note: AS, autoshaping. CR, continuous reinforcement. cSNC, consummatory successive negative contrast. OWA, one-way avoidance. PR, partial reinforcement.

removed to place the subject into the chamber. A rigid, nontransparent white plastic transportation box, 11 × 15 × 12 cm (W × L × H), was placed in the safe compartment in contact with the communication hole. This box was used as the safe compartment and to move the rat when safe time was completed. The transportation box had no wall on the side in contact with the partition of the avoidance chamber and, therefore, with the communication hole and gate. The floor, ceiling, and walls of this box were made of the same material. The chamber was enclosed in a fan-ventilated, sound- and light-attenuating isolation cubicle.

2.1.3. Procedure

The results will be presented separately for each of the two sequences of training. The designs of both experiments are described in Table 1. In Experiment 1a, Phase 1 involved training in the OWA task whereas Phase 2 involved training in the cSNC task. Since the two tasks involve a downshifted condition and unshifted control, and since the goal was to determine whether a downshift experience in one task affects the adjustment to reward downshift in the other task, the incentive conditions remain constant. Thus, animals assigned to the downshift condition in the OWA task were also assigned to the downshift condition in the subsequent cSNC task. Similarly, unshifted controls in Phase 1 were also assigned to the unshifted control group in Phase 2.

For each session of the OWA task, rats were put into the shuttle box and allowed 5 min to explore both compartments without interference, in the presence of the background noise. Thereafter, the communication gate was closed, shutting the rat in the danger compartment, and then the trial began. Each trial consisted of a warning signal followed after 5 s by a 1-mA electric shock. Both the warning signal and the shock continued until the animal moved into the safe compartment or until 30 s had elapsed. The gate between the two compartments was opened as soon as the warning signal sounded and closed when the rat entered the safe compartment. Time in the danger compartment before the onset of the warning signal was the same for all experimental conditions: 15 s. Once the safe time ended (signaled by an on/off light located in the danger compartment), the transportation box was lifted over the apparatus and the rat was placed in the danger compartment; this took about 1–2 s. The box was then replaced in the safe compartment of the shuttle box. All rats were trained until they emitted five consecutive avoidance responses in the preshift phase and ten consecutive avoidance responses in the postshift phase. The avoidance response was considered to have taken place when the animal moved into the safe compartment with its four limbs within 5 s of the onset of the warning signal. The postshift phase began once five consecutive avoidance responses were emitted. This involved the same procedure used in the preshift phase, except that the time in the safe compartment was downshifted or not depending on the experimental condition. The postshift phase continued until rats emitted ten consecutive avoidance responses. Animals in the downshifted condition (Group 40/32) were then left in the safety compartment for 40 s in each preshift trial, before being returned to their home cage. During postshift sessions, the trial proceeded as described, except that animals were confined in the safety compartment for 3 s, rather than 40 s as during preshift sessions. For unshifted controls (Group 3/4), trials with a successful avoidance response (entering the safety compartment) were rewarded with 3 s in the safety compartment throughout the entire experiment. Learning was assessed by recording the number of trials to reach

5 successive avoidance responses (preshift criterion) and the number of trials to reach 5, 8, and 10 successive avoidance responses (postshift criteria). Because behavioral criteria were used to assess avoidance learning, the number of preshift and postshift trials was not necessarily the same for all animals.

During the preshift phase of the cSNC task (10 daily sessions), half of the subjects (Group 40/32) received daily access (5 min per day) to 32% sucrose (w/w, 32 g sucrose for every 68 g of tap water), whereas half (Group 3/4) were given daily access to 4% sucrose (w/w, 4 g sucrose for every 96 g of tap water). During the postshift phase (4 daily sessions), Group 40/32 was downshifted to 4% sucrose, whereas Group 3/4 was maintained on 4% sucrose. Animals were assigned to a given squad and trained around the same time each day; the order of squads was varied across sessions.

In Experiment 1b, Phase 1 involved training in the cSNC task whereas Phase 2 involved training in the OWA task. The procedures were identical to those described above for Experiment 1a, except that the order in which the tasks were administered was the opposite.

All the experiments in this series were analyzed using nonparametric tests. Whenever repeated measures are encountered, the analyses were based on a mean of a specified number of sessions. In Experiments 1a and 1b, cSNC data (lick frequency) were averaged for the 10 preshift sessions in groups receiving access to either 32% or 4% sucrose, and for postsessions 11–14 in groups receiving a 32-to-4% sucrose downshift or for unshifted, 4% sucrose controls. Mann-Whitney tests were applied to these data. OWA data (trials to criterion) were analyzed with separate Mann-Whitney tests for preshift and for each of the three criteria used during postshift sessions. An alpha level equal or lower than 0.05, two-tailed, was used in all tests. All analyses were conducted on IBM SPSS Statistics 24 software.

2.2. Results

2.2.1. Experiment 1a: from OWA to cSNC

The results of this experiment are presented in Fig. 2. The top panel (Phase 1, OWA task) shows that animals receiving 40 s of safety achieved the preshift acquisition criterion faster than animals kept in safety for only 3 s, $U(12, 12) = 0$, $p < 0.001$. During postshift trials, however, animals downshifted from 40 to 3 s in the safety compartment exhibited a deterioration of performance, achieving the successive criteria in a progressively larger number of trials than unshifted controls. Groups did not differ in terms of the less demanding criterion (5-trial criterion), $U(12, 12) = 49.5$, $p > 0.10$, but Group 40/32 took significantly more trials to reach the 8- and 10-trial criteria than Group 3/4, $Us(12, 12) < 32$, $ps < 0.02$. This difference confirms the presence of an iSNC effect in the

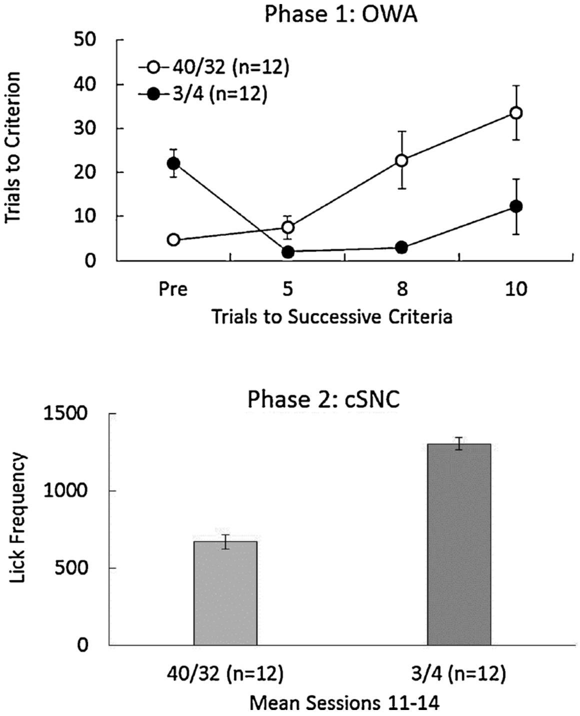

Fig. 2. The top figure (Phase 1) shows the performance of rats in the OWA task in terms of meeting successively more demanding acquisition criteria. The group downshifted from 40 to 3 s in safety (Group 40/32) exhibited behavioral deterioration relative to the unshifted control (Group 3/4). The bottom figure (Phase 2) shows the postshift performance averaged for the initial three downshift sessions. The group downshifted from 32 to 4% sucrose, which had also been previously downshifted in the OWA task (Group 40/32), exhibited significant consummatory suppression relative to unshifted controls (Group 3/4). Both effects were statistically significant, which implies that OWA experience did not eliminate the cSNC effect. Means and SEMs are plotted in all figures. Results from Experiment 1a.

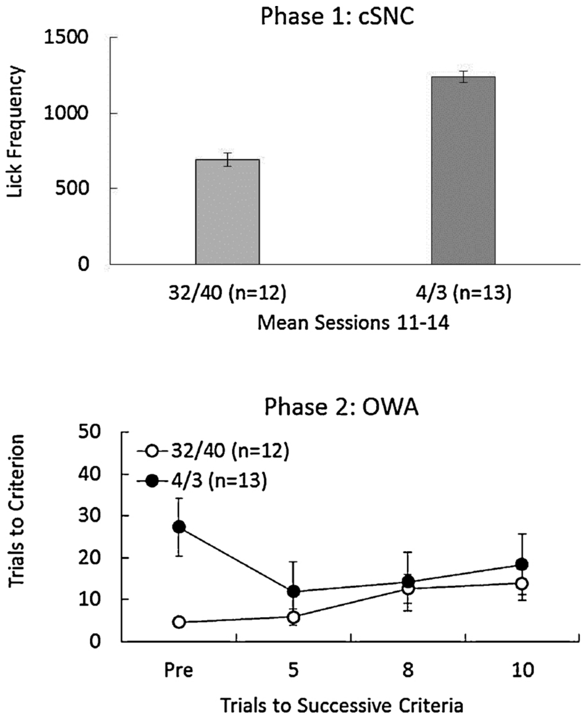

Fig. 3. cSNC (top) followed by OWA (bottom). See legend to Fig. 2 for details. Whereas the cSNC effect was statistically significant, the iSNC effect in OWA was nonsignificant. The implication is that prior cSNC experience eliminated the iSNC effect in OWA. Results from Experiment 1b.

OWA task after a downshift in the length of the safety period.

As for the cSNC task, lick frequency during the 10 preshift sessions averaged (± SEM) 1075.9 (± 76.8) and 830.3 (± 32.1) for Groups 40/32 and 3/4, respectively, and the difference was significant, $U(12, 12) = 15, p < 0.002$. Average lick frequency during the initial four postshift trials (Fig. 2, bottom panel, Phase 2) was significantly lower in downshifted animals compared to unshifted controls, $U(12, 12) = 0, p < 0.001$. Thus, there was a clear cSNC effect during Phase 1 in this experiment.

2.2.2. *Experiment 1b: from cSNC to OWA*

Fig. 3 shows the results of Experiment 1b. In the cSNC task, the means (± SEM) for lick frequency over the 10 preshift sessions were 1013.0 (± 44.7) and 856.7 (± 48.3) for Groups 32/40 and 4/3, respectively. This differential lick frequency across groups was significant, $U(12, 12) = 42, p = 0.050$. As for postshift performance (Fig. 3, top panel, Phase 1), there was significant lick suppression in Group 32/40 relative to Group 4/3, $U(12, 12) = 8, p < 0.001$. Thus, there was a clear cSNC effect.

Interestingly, as shown in the bottom panel of Fig. 3, animals that had experienced a 32-to-4% sucrose downshift in the consummatory situation did not express iSNC in the OWA task. The avoidance performance was different during the preshift phase, $U(12, 12) = 0.5, p < 0.001$, but the avoidance performance of downshifted and unshifted animals converged during the successive criteria of the postshift phase, $Us(12, 12) > 70, ps > 0.67$. Thus, prior experience in the cSNC task eliminated the iSNC effect in the OWA task.

2.3. *Discussion*

Previous studies testing for bidirectional transfer (Cuenya et al., 2015; Nation et al., 1980) reported just such a result using cSNC and iSNC tasks or escape and food-reinforced extinction. Unlike those experiments, the present results showed unidirectional transfer in that the cSNC task reduced iSNC in the OWA task, but the opposite was not observed. Because the effect observed in Phase 1 involved a reduced iSNC effect in Phase 2, we understand it as a case of positive transfer (negative transfer would involve an enhancement of a Phase 2 effect produced by a Phase 1 experience with reward loss). In terms of Amsel's (1992; Ross, 1964) theory, positive transfer implies a degree of compatibility between the responses in both phases. In this case, the assumption is that consummatory behavior in Phase 1 transferred into approach behavior in Phase 2, a result consistent with a role of counterconditioning in recovery from reward devaluation. However, the lack of evidence for transfer in the opposite direction, from OWA to cSNC, is difficult to accommodate for frustration theory. According to this theory (Amsel, 1992), pairings between anticipatory frustration and reward, as would happen during the postshift phase of a SNC experiment, should lead to the counterconditioning of anticipatory frustration. Counterconditioning implies that anticipatory frustration become associated to a form of approach behavior, rather than eliciting withdrawal or avoidance of the goal object, as it does initially. Thus, frustration theory assumes a habitual associative

Table 2
Comparison of tasks used in the present experiments.

Feature	cSNC	iSNC (OWA)	AS
Response	Licking	Approach to safety, escape from fear	Lever pressing, goal entry
Reward	Sucrose solutions	Time in safety after shock	Food or sucrose pellets
Signal present	Context	Tone	Lever presentation
Response type	Consummatory	Anticipatory	Anticipatory
Trials/session	1	Variable (training to a behavioral criterion)	10 (30 in Experiment 4)

structure (i.e., a stimulus-response association, S-R) involving anticipatory frustration and a form of approach. However, the actual form of that approach response depends on the conditions of training. Two different approach responses may be compatible or incompatible, giving rise to positive or negative transfer, respectively. Thus, when approach responses are compatible, counterconditioning in Phase 1 should reduce the impact of reward loss in Phase 2 because anticipatory frustration would induce a form of the approach response that would attenuate the disruption otherwise caused by an avoidance response. However, when approach responses are incompatible, counterconditioning in Phase 1 would induce a form of the approach response that will interfere with the target approach response, thus increasing the effects of reward loss in Phase 2.

The tasks used in the present experiments make different demands on the organism, as described in Table 2. In particular, we cannot predict with certainty whether licking (in the cSNC task) and approaching safety (in the OWA task) are compatible. However, based on Cuenya et al.'s Cuenya et al. (2015b) experiment involving licking (cSNC) and running (iSNC in a runway), we hypothesized that these two responses would be compatible and, therefore, we expected bidirectional transfer. Contrary to this prediction, transfer in the present experiment was unidirectional. The aim of the remaining set of experiments was to identify factors that would allow for bidirectional transfer between autoshaping (AS; an anticipatory response task) and cSNC (a consummatory response task). Like licking, lever pressing and goal entry during AS training are activities carried out in a specific location rather than walking or running toward a place, as in instrumental procedures. The animal, of course, must approach the lever, but this is also true of the sipper tube in the cSNC task. As before, we predicted bidirectional transfer between cSNC and AS tasks.

3. Experiment 2

In this experiment, the cSNC task was the same as that used in Experiment 1 and also used by Cuenya et al. (2015b). However, the second task involved continuous or partial reinforcement (CR, PR) followed by extinction in the rat AS situation. The AS task used here (see Ortega, Norris, Lopez-Seal, Ramos, & Papini, 2014) involved response-independent pairings of a retractable lever (the conditioned stimulus, CS) and pellets (the unconditioned stimulus, US). After a few pairings and despite not being strictly required, rats approach and press the lever, a behavior that can be recorded and quantified. In addition to lever pressing, most of these experiments report goal entries, that is, insertions of the head in the magazine hole during CS presentations. Two experiments carried out at different times are presented separately. Experiment 2a involved AS acquisition under PR or CR in Phase 1 followed by cSNC training in Phase 2. Experiment 2b involved cSNC training in Phase 1 followed by AS acquisition (under PR or CR) and extinction in Phase 2. In the AS, the way to induce anticipatory frustration was different depending on whether AS was scheduled in Phase 1 (Experiment 2a) or in Phase 2 (Experiment 2b). In Experiment 2a, Phase 1, reward loss was implemented in terms of a PR schedule of lever-food pairings. Rats trained under PR in the AS situation tend to lever press at a higher rate than rats receiving CR training—the partial reinforcement acquisition effect (PRAE; Anselme, 2016; Ortega et al., 2014; Torres, Glueck, Conrad, Morón, & Papini, 2016). The presence of a PRAE provides evidence that the PR vs. CR manipulation affected behavior. If PR training led to the counterconditioning of frustration in Phase 1, then this should either attenuate (positive transfer) or enhance (negative transfer) the cSNC effect in Phase 2 depending on the interaction between the responses emerging in each phase (Ross, 1964). Notice that we are not arguing that frustration counterconditioning leads to the PRAE; for an explanation of this phenomenon one could turn to Amsel's (1992) drive induction or Anselme's (2016) incentive hope. In Experiment 2b, Phase 1, animals were exposed to reward downshift in the cSNC situation. If recovery from reward downshift involves counterconditioning, then this should not affect AS acquisition under CR in Phase 2, but it should lead to either slow extinction (positive transfer) or rapid extinction (negative transfer) when the animal experiences frustration as a result of reward omission in extinction trials. Moreover, extinction performance was expected to exhibit the partial reinforcement extinction effect (PREE) among animals exposed to unshifted, 4% sucrose conditions in Phase 1. However, a reduced or absent PREE in animals exposed to a 32-to-4% sucrose downshift in Phase 1 would be consistent with the development of counterconditioning during recovery from reward downshift.

3.1. Method

3.1.1. Subjects

A total of 77 female Wistar rats, experimentally naïve, and approximately 90 days old at the start of the experiments were used as subjects. Forty rats were assigned to Experiment 2a (Mean weight: 243.3 g, SEM: ± 3.6 g) and 37 to Experiment 2b (Mean weight: 282.4 g, SEM: ± 3.3 g). All rats were deprived to 81–84% of their ad libitum weight and kept stable by providing the appropriate amount of food each day, at least 15 min after the end of the daily training session. Animals were housed under a 12-h light/12-h dark cycle (lights on at 07:00 h) in a room that controlled for noise, and had constant temperature (22–23 ∘C) and humidity (40–65%).

3.1.2. Apparatus

cSNC training took place in eight conditioning boxes (MED Associates, St. Albans, VT) constructed of aluminum and Plexiglas, and measuring 29.4 × 28.9 × 24.7 cm (L × H × W). The floor was made of steel rods 0.5 cm in diameter and 1.2 cm apart (from center to center) running perpendicular to the feeder wall. A tray filled with corncob bedding was placed below the floor to collect fecal pellets and urine. Against the feeder wall were two elliptical holes 1 × 2 cm (W × H), 3.5 cm from the floor, separated by 6.5 cm. A sipper tube, 1 cm in diameter, was inserted through the middle hole (the lateral hole for a second sipper tube was not used in this experiment). When fully inserted, the sipper tubes were flush against the outer wall of the apparatus, such that the rats could only reach the tubes with their tongues. A computer located in an adjacent room controlled the presentation and retraction of the sipper tube, and detected contact with the sipper tube via a circuit involving the steel rods in the floor. Such circuit was used to record the cumulative time in contact with the sipper tube (called goal-tracking time). Each conditioning box was placed inside a sound-attenuating chamber that contained a house light (GE 1820), a speaker that delivered white noise, and a fan for ventilation. Together, the speaker and fan produced noise with an intensity of 80.1 dB (SPL, Scale C).

Four standard operant chambers (MED Associates, St. Albans, VT) each enclosed in a sound-attenuating chamber were used during AS training. Each box was 20.1 × 28 x 20.5 cm (W x L x H), with a grid floor consisting of stainless steel bars 0.4 cm in diameter and spaced 1.6 cm apart (from center to center). Underneath the grid floor was a pan filled with corncob bedding. The food cup was located on the front wall of the chamber, 2 cm above the floor. Two retractable levers were located 1 cm to the right and left of the feeder, and 6 cm above the floor. Only one lever, located to the left of the magazine hole, was used in this experiment. This lever was 4.8 cm wide and when fully inserted protruded 1.9 cm into the chamber. The lever was set to be displaced by the lowest possible force. It took 0.2 s for the lever to be fully inserted or retracted. Pellet dispensers delivered 45-mg food pellets (Bio-Serv, Frenchtown, NJ). Each food pellet contained protein (18.8%), fat (5.0%), carbohydrate (61.5%), fiber (4.6%), ash (4.4%), and moisture (5.0%), and provided 3.68 kcal/g. The sound-attenuating chambers were equipped with a light (GE 1820) that provided diffuse illumination, a speaker that administered white noise, and a fan for air circulation. Background masking noise (speaker and fan) registered 80.1 dB (SPL, Scale C).

3.1.3. Procedure

The procedure will be described separately for each training sequence. The designs of both experiments are described in Table 1. In Experiment 2a, Phase 1 involved AS training whereas Phase 2 involved training in the cSNC task. Training in the AS task started when animals reached the target deprivation level, which typically occurred at about 96 days of age. Animals were matched for weight and randomly assigned to one of four groups ($n = 10$): Group CR/32, CR/4, PR/32, and PR/4. Group labels correspond to their training in Phase 1 (CR: 100% reinforcement, PR: 50% reinforcement) and Phase 2 (32% sucrose, 4% sucrose in preshift sessions). There were 10 sessions of acquisition, 1 session/day, each with 10 trials. In each trial, the lever was presented for 10 s. Trials were separated by variable intervals averaging 90 s (range: 60–120 s). During acquisition, each trial ended with the delivery of five 45-mg precision food pellets for CR groups, but only a random 50% of the trials ended with food delivery for the PR groups. During nonreinforced trials, pellets were not administered. A computer located in an adjacent room recorded lever presses. Although the computer was set to also record goal entries, we have technical failures that prevent the use of these data. Similar failures occurred in other experiments of this series, so goal entry data are presented only in a subset of the experiments reported here.

cSNC training started a day after the last AS session. During preshift trials, animals received 10 daily sessions of access to either 32% sucrose (w/w, 32 g sucrose for every 68 g of deionized water) or 4% sucrose (w/w, 4 g sucrose for every 96 g of deionized water), depending on the contrast condition. This was followed by 5 daily postshift sessions in which all animals received 4% sucrose. Each session lasted 5 min from the first detected contact with the drinking spout. The amount of time the animal was in contact with the sipper tube (in 0.01-s units; called goal-tracking time) was recorded by a computer located in an adjacent room. Animals were assigned to a given squad and trained around the same time each day, although the order of the squads was varied across sessions.

In Experiment 2b, the conditions of training were the same as described above, except for the following aspects related to AS training in Phase 2. After cSNC training, all animals received 10 sessions of AS training under CR or PR, followed by 10 sessions of extinction. Extinction sessions were identical to acquisition sessions, except that no food was delivered at the end of each trial. Thus, four groups were formed: 32/CR ($n = 8$), 4/CR ($n = 10$), 32/PR ($n = 9$), and 4/PR ($n = 10$). The target manipulations involved reward loss in acquisition (in the PR groups) and in extinction. Moreover, goal entry data were recorded in this experiment. PR training was as described in Experiment 2a. Other procedural aspects were as described in Experiment 1.

Data from the cSNC task were analyzed as described in Experiment 1. The results of the AS procedure were analyzed in terms of lever pressing per minute and goal entries per trial. Goal entry data were lost due to equipment malfunction in Experiment 2a, but were available for Experiment 2b. In all the experiments reported in this article, AS data were averaged over all the acquisition and all the extinction sessions. These averages were subjected to nonparametric analyses with the Mann-Whitney test, as described in Experiment 1.

3.2. Results

3.2.1. Experiment 2a: from AS to cSNC

As shown in Fig. 4, top panel, PR training tended to induce a higher response level than CR during acquisition in Phase 1—the PRAE. A comparison between groups receiving CR and PR training during Phase 1 (CR/32 vs. PR/32 and CR/4 vs. PR/4) yielded a significant PRAE, $U(20, 20) = 89.5$, $p < 0.004$. Groups receiving either CR (CR/32 vs. CR/4) or PR (PR/32 vs. PR/4) did not differ from each other during AS acquisition (Fig. 4, top, Phase 1), $Us(10, 10) > 41$, $ps > 0.54$. This confirms that assignment to the

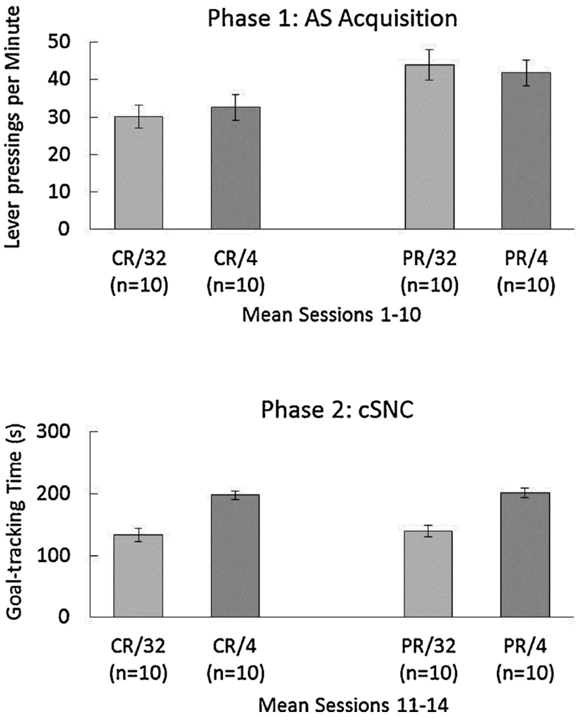

Fig. 4. AS acquisition under either PR or CR in Phase 1 (top) followed by consummatory performance after a 32-to-4% sucrose devaluation in Phase 2 (bottom). There was a PRAE in Phase 1 followed by significant cSNC effects in Phase 2. Therefore, prior PR training did not influence the cSNC effect. Results from Experiment 2a.

conditions enforced in Phase 2 was not biased in terms of the behavior in Phase 1.

The main results are plotted in Fig. 4, bottom panel. The cSNC effect was significant in groups that had received prior training in either CR (CR/32 vs. CR/4) or PR (PR/32 vs. PR/4), $Us(10, 10) = 4$, $ps < 0.002$. A comparison between cSNC groups exposed to a 32-to-4% sucrose downshift during Phase 2 (CR/32 vs. PR/32) and to the unshifted, 4% sucrose condition (CR/4 vs. PR/4) indicated nonsignificant differences, $Us(10, 10) > 45$, $ps > 0.76$. Thus, there was no detectable evidence that prior PR vs. CR training affected performance in the cSNC task.

As for preshift performance in the cSNC task (not shown), the averages (± SEM) over sessions 1–10 were 149.5 (± 10.5), 138.4 (± 6.9), 128.5 (± 4.4), and 153.8 (± 9.8) for Groups CR/32, CR/4, PR/32, and PR/4, respectively. The only significant difference was observed between Groups PR/32 and PR/4, with the former performing below the latter, $U(10, 10) = 23$, $p < 0.05$. Thus, there was evidence that prior PR experience in the AS situation suppressed consummatory performance for 32% sucrose in the cSNC task.

3.2.2. Experiment 2b: from cSNC to AS

The consummatory performance during preshift sessions (Phase 1) of animals receiving access to 32% and 4% sucrose, segregated according to their treatment in the following AS phase was not significant. The mean (± SEM) goal-tracking times (s) over the 10 preshift sessions (not shown) were 119.3 (± 8.6), 116.6 (± 17.0), 89.6 (± 12.6), and 127.8 (± 9.6) for Groups CR/32, CR/4, PR/32, and PR/4, respectively. Comparisons between groups receiving 32% vs. 4% sucrose later assigned to either CR or PR indicated nonsignificant differences during preshift sessions, $Us > 32$, $ps > 0.53$. Goal-tracking times during postshift sessions are shown in Fig. 5, top panel. Groups later assigned to either CR or PR during Phase 2 exhibited the cSNC effect in Phase 1, $Us < 13$, $ps < 0.02$. Thus, there was no evidence that the groups established for Phase 2 were different in terms of Phase 1 performance.

The middle panels in Fig. 5 show the performance of the four groups in acquisition and extinction in terms of lever pressing (Phase 2). Lever pressing did not differ during acquisition whether in CR or PR groups as a function of previous downshifted vs. unshifted experience, $Us > 30$, $ps > 0.23$. There was also no evidence of a PRAE effect in AS acquisition, whether in groups previously exposed to reward downshift or to the unshifted condition, $Us > 25$, $ps > 0.06$. However, in extinction, animals in Group 32/CR (previously downshifted) lever pressed significantly more than animals in Group 4/CR (previously unshifted), $U(8, 10) = 17$, $p < 0.05$. This extinction effect was not present in the comparison between Groups 32/PR vs. 4/PR, $U(9, 10) = 26$, $p > 0.12$. Interestingly, the PREE failed to emerged in groups that had experienced reward downshift, Groups 32/CR vs. 32/PR, $U(8, 9) = 23.5$, $p > 0.22$, but the PREE was detected in unshifted Groups 4/CR vs. 4/PR, $U(10, 10) = 15$, $p < 0.009$. This pattern is consistent with the development of counterconditioning during recovery from the 32-to-4% sucrose downshift in Phase 1. Such counterconditioning should reduce the difference in extinction performance between groups that received PR vs. CR training in acquisition.

The bottom panels in Fig. 5 show AS performance in terms of goal entries (Phase 2). None of the comparisons across groups were significant, $Us > 23$, $ps > 0.24$.

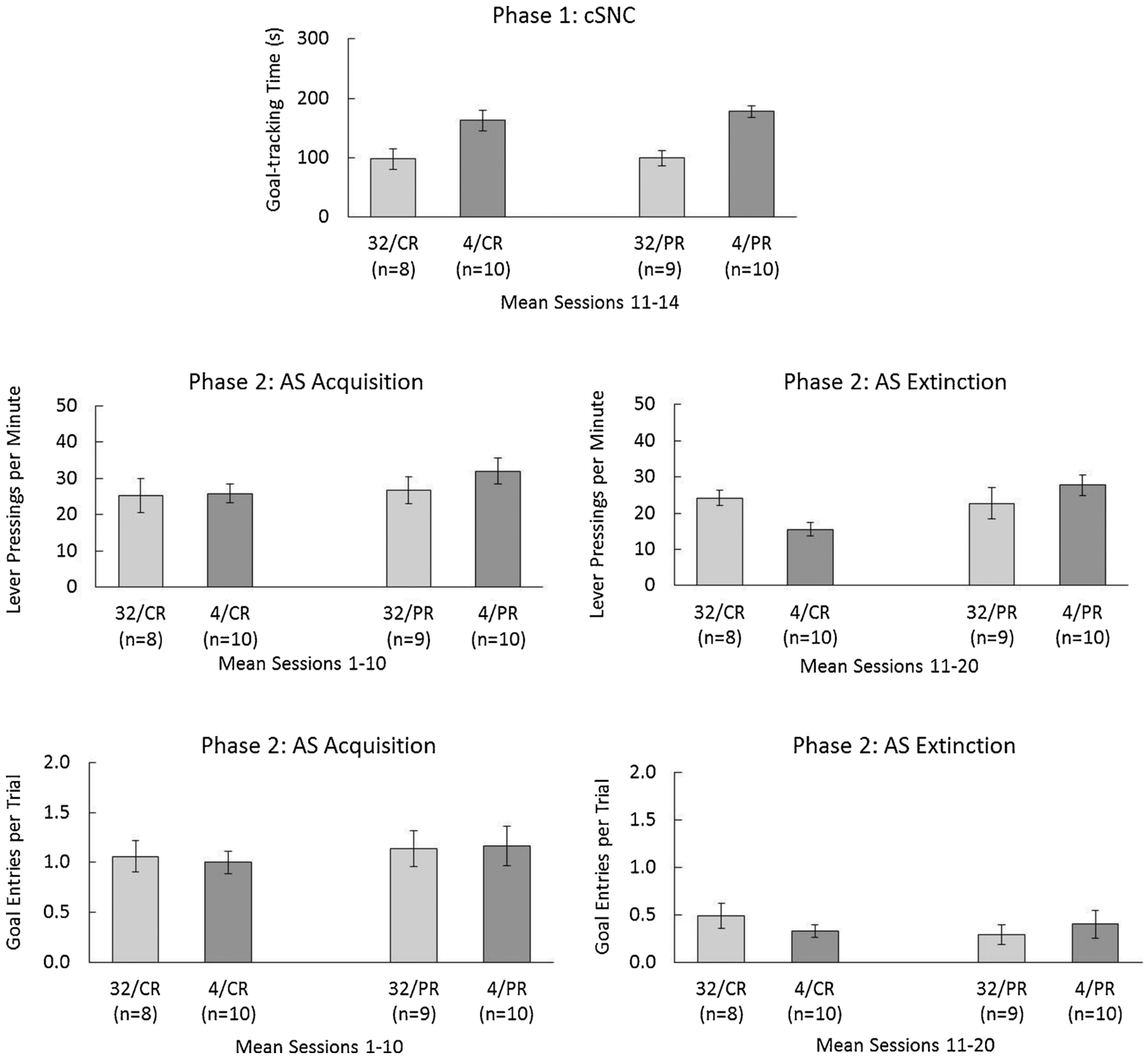

Fig. 5. The cSNC effect in Phase 1 (top) followed by AS acquisition under either PR or CR, and finally AS extinction. AS performance is plotted in terms of lever pressing (middle) and goal entries (bottom). A significant cSNC effect did not affect acquisition under CR, but in enhanced lever pressing and goal entries in extinction after CR. Results from Experiment 2b.

3.3. Discussion

Experiment 2a produced no evidence of transfer from AS under PR vs. CR to consummatory performance in the cSNC situation. However, Experiment 2b yielded evidence of several transfer effects from cSNC to AS, all consistent with a role of frustration counterconditioning in the recovery from reward downshift. First, prior experience in the cSNC situation, whether in downshifted or unshifted animals, eliminated the PRAE in terms of lever pressing. The PRAE was evident in Experiment 2a, when AS training was administered during Phase 1. Second, a similar comparison of lever pressing in extinction revealed a significant PREE only in animals that had received unshifted reward experience in the cSNC situation. Exposure to reward downshift in Phase 1 eliminated the PREE in Phase 2. Third, prior experience with reward downshift in the cSNC situation also induced higher responding in extinction than prior unshifted experience in animals receiving CR training in AS acquisition, but not in animals receiving PR training in AS acquisition. Finally, none of these transfer effects was evident in terms of goal entries. Therefore, whereas AS was sensitive to prior experience in the cSNC situation, the opposite was not true.

The results of Experiment 2b imply positive transfer between these two tasks. Thus, pairings of a frustration state with 4% sucrose during recovery from reward downshift would countercondition anticipatory frustration. When frustration is again induced during extinction, even though the CR schedule should not support counterconditioning, animals displayed increased resistance to extinction (Groups CR/32 vs. CR/4 in extinction, Fig. 5, middle panel). The implication is that counterconditioning acquired in one situation (cSNC) transferred positively to another situation (AS extinction). These results were also consistent with those obtained in the transition from cSNC to OWA (Experiment 1b) and also with those involving transitions from PR in one task to extinction after CR in a different task (Ross, 1964), and across cSNC and appetitive iSNC tasks in Roman low-avoidance rats (Cuenya et al., 2015). These transfer effects are predicted by the properties of frustration counterconditioning described in Amsel's (1992) theory.

However, it should be noted that prior PR training failed to influence consummatory performance in the cSNC situation (Experiment 2a), just as iSNC in the OWA task failed to influence cSNC (Experiment 1a). These results are at variance with Amsel's (1992) theory and suggest that either the theory is at least partially wrong or the cSNC task is especially difficult to be influenced by prior reward downshift experience in the AS situation. Anselme's (2015, 2016) incentive hope hypothesis may provide an explanation of the absence of transfer observed in Experiment 2a, from AS to cSNC. Anselme's view is that the PRAE involves reward uncertainty (i.e., "hoping" that reward will occur in an uncertain situation), rather than a process related to surprising nonreward (i.e., anticipating reward omission). Incentive hope is neutralized by learning to expect large rewards before uncertainty is introduced, as it would be the case during preshift sessions in the cSNC situation (Robinson, Anselme, Fischer, & Berridge, 2014). As a result, there would be no basis to predict that PR experience in Phase 1 would affect the cSNC effect in Phase 2. Notice, however, that cSNC performance can be influenced by prior experience in the iSNC situation (Cuenya et al., 2015). In the experiments that followed, we explored this failure of AS to influence cSNC performance by varying conditions in either task.

4. Experiment 3

Based to a large extent on the results of transfer experiments, Amsel (1992) suggested that the internal state of secondary frustration could override the influence of external stimuli on behavior. Such reliance on internal states allowed the theory to explain transfer across situations. However, the original experiments all involved using PR training to induce frustration counterconditioning. The unidirectional transfer effects observed in Experiments 1–2 suggest that perhaps under some conditions external stimuli may seize control over internal emotional states such that increasing stimulus similarity across tasks may encourage transfer. Experiment 3 explored the influence of increasing the stimulus similarities between these tasks on transfer from AS to cSNC. These tasks were made more similar by using sugar pellets in AS acquisition, rather than food pellets as in previous experiments, while keeping the sucrose solution in the cSNC task.

4.1. Method

4.1.1. Subjects and apparatus

Forty female Wistar rats served as subjects for Experiment 3. Animals were of similar age and maintained and deprived as outlined in Experiment 2. The mean (± SEM) ad lib weight was 277.4 g (± 3.2). The same conditioning and consummatory boxes described in Experiment 2 were used here.

4.1.2. Procedure

Once animals had reached their deprivation weight, they were matched for weight and randomly assigned to either CR ($n = 20$) or PR ($n = 20$) training in acquisition sessions. The procedure was identical to that previously described in Experiment 2, with the exception that sugar pellets were used as reinforcement rather than food pellets during the AS training. Each sugar pellet contained protein (0%), fat (0%), carbohydrate (89.5%), fiber (0%), ash (0%), and moisture (< 10%), and provided 3.58 kcal/g. Animals in each AS condition were matched in pairs according to lever pressing performance and randomly assigned to either the 32-to-4% sucrose downshift condition or the 4% sucrose unshifted condition. This generated four groups: CR/32 ($n = 11$), CR/4 ($n = 9$), PR/32 ($n = 10$), and PR/4 ($n = 10$); the uneven distribution of animals among CR groups was the result of a mistake. cSNC training and additional procedures were the same as in Experiment 2.

4.2. Results and discussion

One animal in Group PR/4 was dropped from all analyses because it failed to acquire lever pressing and never entered the goal during CS presentations, thus leaving this group with $n = 9$. The top panels in Fig. 6 show the results of AS training. In terms of lever pressing, the PRAE emerged in a comparison between Groups CR/4 vs. PR/4, $U(9, 9) = 17$, $p < 0.04$. All other comparisons were nonsignificant. In terms of goal entries, however, both CR groups produced higher response levels than both PR groups, $Us < 15$, $ps < 0.02$. This inverse relationship between CR and PR groups in terms of lever pressing vs. goal tracking was observed before (Torres et al., 2016).

Despite the effects of PR training on behavior in the AS situation, there was no evidence that this affected consummatory behavior in the cSNC task. Thus, as shown in the bottom panel of Fig. 6, there were similar cSNC effects whether groups had previously received CR or PR training. In both cases, downshifted animals displayed consummatory suppression relative to unshifted controls, $Us < 11$, $ps < 0.004$.

The mean (± SEM) preshift goal-tracking times (s) in the cSNC task (not shown) over sessions 1–10 was: 111.1 (± 10.2), 116.3 (± 15.6), 141.3 (± 8.3), and 130.2 (± 11.6) lick frequency for Groups CR/32, CR/4, PR/32, and PR/4, respectively. Pairwise comparisons failed to detect any significant difference among groups, $Us > 32.0$, $ps > 0.50$. In conclusion, increasing reward similarity across phases produced no evidence of transfer from AS to cSNC.

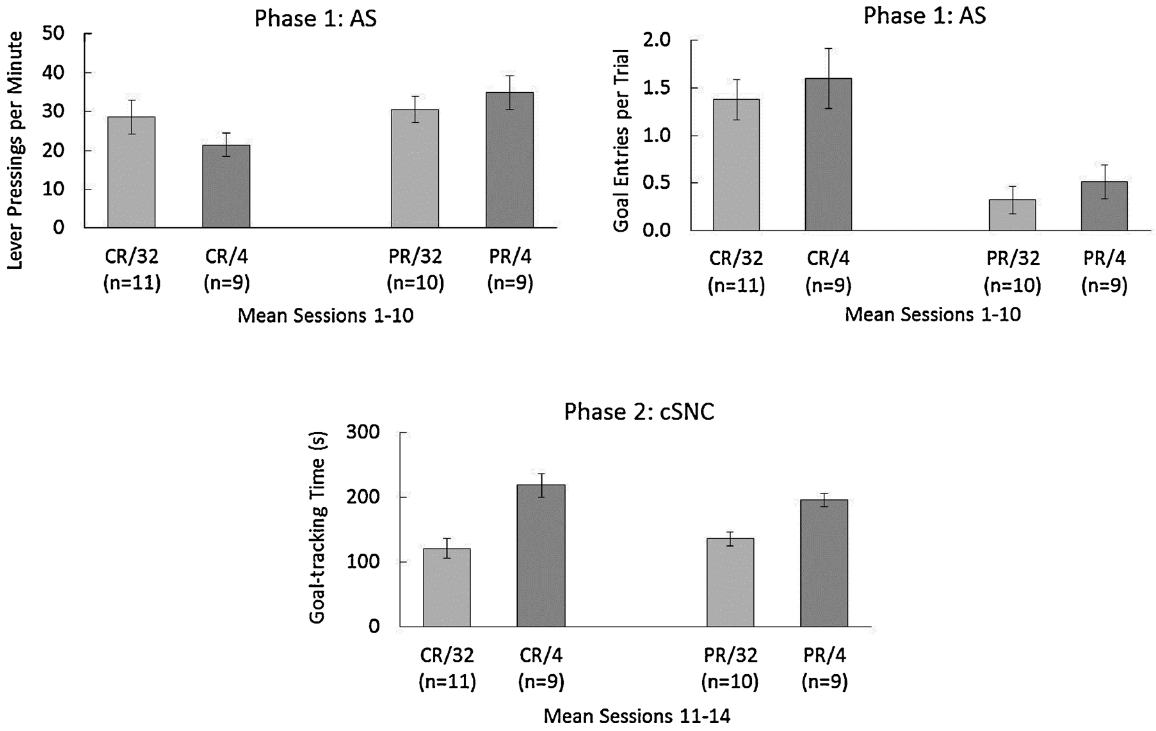

Fig. 6. AS acquisition under PR or CR in Phase 1 (top) followed by cSNC in Phase 2 (bottom). Sucrose pellets (instead of the usual food pellets) were presented in AS training. There were significant PRAE in Phase 1 and significant cSNC effects in Phase 2, suggesting that prior PR training failed to influence the cSNC effect. Results from Experiment 3.

5. Experiment 4

A potential explanation for the lack of transfer from AS to cSNC is that there was insufficient counterconditioning during Phase 1 in Experiments 2–3. To test this hypothesis, the number of trials per AS session was increased from 10 in Experiments 2 and 3 to 30 in the present experiment (the total number of acquisition trials was thus increased from 100 to 300 trials). Tripling the number of trials should enhance chances of counterconditioning during AS training and thus increase the possibility of observing transfer from AS to cSNC.

5.1. Method

5.1.1. Subjects and apparatus

Forty female Wistar rats served as subjects. Animals were of similar age, and maintained and deprived as in Experiment 2. The mean (± SEM) ad lib weight was 282.1 g (± 3.6). The same conditioning and consummatory boxes described in Experiment 2 were used here.

5.1.2. Procedure

Once animals had reached their deprivation weight (at approximately 96 days of age), they were matched for weight and randomly assigned to either 100% CR or 50% PR for autoshaping acquisition training. The procedure was identical to that previously described in Experiment 2a, except for the number of trials per session. There were 10 sessions of acquisition, at 1 session/day, with each session including 30 trials, for a total of 300 acquisition trials. All other aspects of autoshaping acquisition and cSNC training were as described in Experiment 2a.

5.2. Results and discussion

Because of a programing error, goal-entry data were lost in this experiment. Fig. 7, top panel, shows the overall acquisition performance of groups given PR and CR, and segregated according to the treatment scheduled for Phase 2, namely, access to 32% or 4% sucrose during preshift trials. There was a strong PRAE in lever pressing, $U(20,20) = 87.0$, $p < 0.003$, suggesting that the PR manipulation affected behavior and provided opportunities for counterconditioning to occur during autoshaping acquisition. Groups trained in either CR or PR in Phase 1 did not differ from each other, $Us(10, 10) > 45$, $ps > 0.76$. Thus, there was no evidence of biased assignment in AS performance relative to the conditions that were to be enforced in the cSNC task.

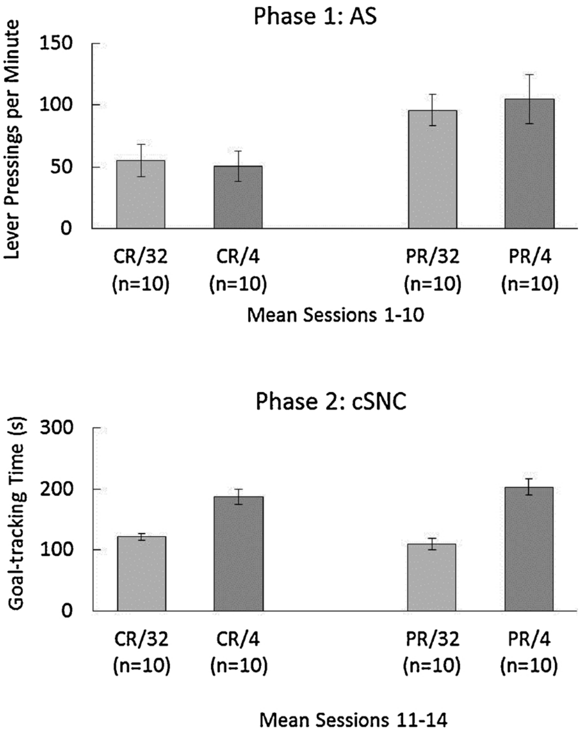

Fig. 7. AS acquisition under PR or CR in Phase 1 (top) followed by cSNC in Phase 2 (bottom). AS training involved 300 trials (rather than the usual 100 trials). There were significant PRAE and cSNC effects, implying that extended opportunities for counterconditioning during PR training in Phase 1 did not affect the effects of reward devaluation in Phase 2. Results from Experiment 4.

Fig. 7, bottom panel, shows similar cSNC effects in groups that had previously received PR or CR training in autoshaping. In both cases there was significant suppression of goal-tracking times in animals given a 32-to-4% sucrose downshift relative to unshifted controls, $Us(10, 10) < 5$, $ps < 0.002$. Moreover, neither downshifted or unshifted pairs of groups differed during Phase 2, $Us(10, 10) > 37.0$, $ps > 0.36$. Thus, despite extensive opportunities for counterconditioning during autoshaping acquisition in PR animals, reward devaluation proceeded undisturbed during cSNC training.

Goal-tracking times (s) in the cSNC task (not shown) averaged (± SEM) over sessions 1–10 was: 111.7 (± 9.4), 154.2 (± 10.4), 132.7 (± 5.7), and 144.6 (± 14.5) for Groups CR/32, CR/4, PR/32, and PR/4, respectively. Goal-tracking times were lower in Group CR/32 than CR/4, $U(10, 10) = 16.0$, $p < 0.02$, but Groups PR/32 and PR/4 did not differ, $U(10, 10) = 38.0$, $p > 0.36$.

These results suggest the lack of transfer from AS to cSNC seen in Experiment 2 was probably not due to insufficient counterconditioning during the AS acquisition. Alternatively, the lack of transfer from AS to cSNC could reflect a relatively weak cSNC effect. If previous PR training were to accelerate recovery from reward downshift and the recovery would occur fast relative to CR training, a ceiling effect on goal-tracking times could make it difficult to detect transfer. One procedure that enhanced the size of the cSNC effect in previous experiments was to increase the number of preshift sessions (Pellegrini, Muzio, Mustaca, & Papini, 2004). Experiment 5 focused on this manipulation as a means of inducing transfer.

6. Experiment 5

Frustration theory (Amsel, 1992) suggests that transfer from AS to cSNC should either reduce or enhance the cSNC effect depending on the interaction between the dominant responses in each phase (e.g., Ross, 1964). Because it is not possible a priori to determine the direction of the transfer, the final experiments in this series were designed to maximize chances by introducing manipulations that enhance the cSNC effect (Experiment 5), that match training in terms of the target response (Experiment 6), and that reduce the cSNC effect (Experiment 7). On the assumption that the difficulty to observe transfer in previous experiments relates to ceiling/floor effects, enhancing cSNC should increase chances of transfer if prior PR training reduces the size of the cSNC effect (positive transfer), whereas reducing cSNC should increase the likelihood of transfer if prior PR training increases the size of the cSNC effect (negative transfer). In Experiment 5, the effects of PR vs. CR training in the AS situation were tested after an extended preshift phase in the cSNC task. Pellegrini et al. (2004) observed that an increase from the typical 10 sessions to 20 sessions of preshift training increased the size of the cSNC effect.

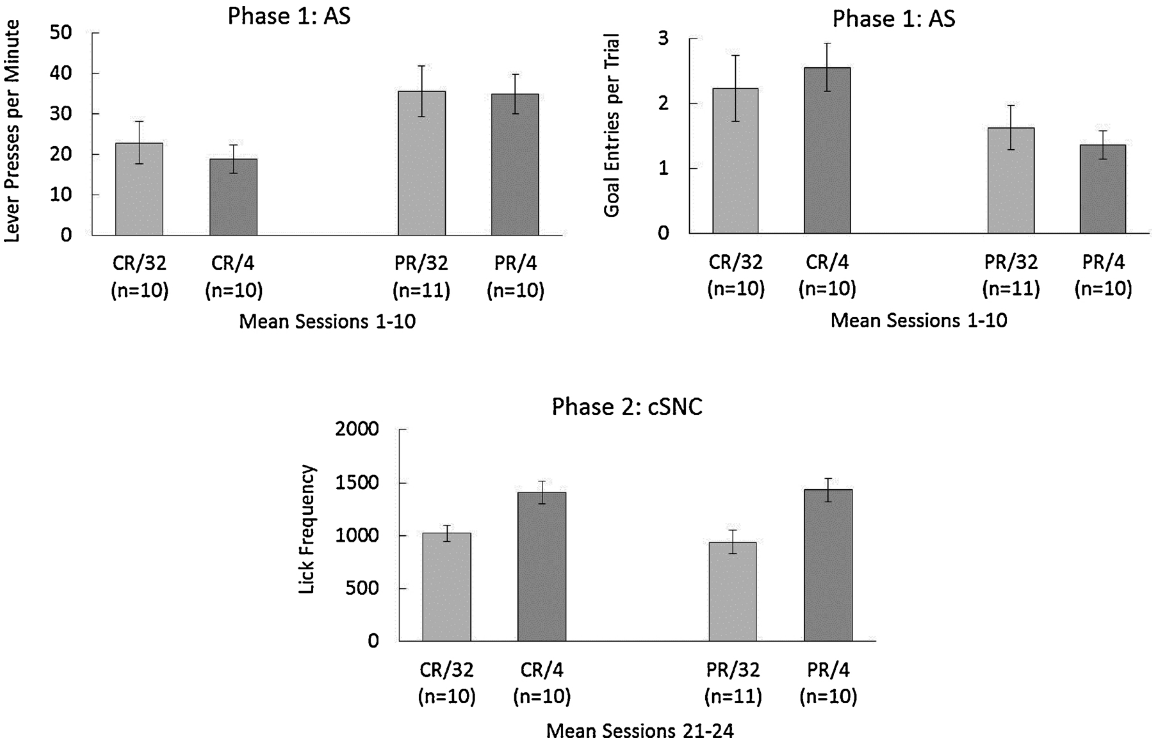

Fig. 8. AS acquisition under PR or CR in Phase 1 (top) followed by cSNC in Phase 2 (bottom). The preshift period during Phase 2 was extended to 20 sessions (in place of the typical 10 sessions). Significant PRAE and cSNC effects suggest the absence of transfer in this experiment. Results from Experiment 5.

6.1. Method

6.1.1. Subjects and apparatus

Forty-one female Wistar rats served as subjects for Experiment 5. Animals were of similar age and maintained and deprived as outlined in Experiment 2. The mean (± SEM) ad lib weight was 270.0 g (± 3.2). The same conditioning and consummatory boxes described in Experiment 2 were used in Experiment 5.

6.1.2. Procedure

Once animals had reached their deprivation weight they were matched for weight and randomly assigned to one of two training groups based on AS reinforcement schedules: CR (100% continuous reinforcement) or PR (50% partial reinforcement). The AS acquisition procedure was identical to that in Experiment 2.

Following the final AS acquisition session, animals were assigned to cSNC groups such that lever-pressing responses were similar across schedules: CR/32, CR/4, PR/32, and PR/4. The cSNC phase of this experiment was identical to Experiment 2 except that the preshift consisted of 20 sessions, one session per day. Additionally, as a means of detecting transfer, the dependent measure in this experiment was the total number of licks the animal made during each session.

6.2. Results

Fig. 8, top panels, shows the mean lever pressing and goal entries for acquisition sessions 1–10 during Phase 1. There was a strong PRAE in lever pressing, $U(20,21) = 106.5$, $p < 0.008$, and a reversed PRAE in goal entries, $U(20, 21) = 114$, $p < 0.02$, suggesting that PR training provided opportunities for counterconditioning during acquisition. Groups that received CR training did not differ either in terms of lever pressing or goal entries, $Us(10, 10) > 34$, $ps > 0.25$; the same applied to groups given PR training, $Us(10, 11) > 46.5$, $ps > 0.54$. These results support the assumption that there was no biased assignment in AS performance relative to the groups set up in Phase 2.

Fig. 8, bottom panel, shows that the cSNC effects in groups that had previously received PR or CR training in AS were very similar. There was a significant suppression of lick frequency after a 32-to-4% sucrose downshift in groups that received previous CR training, $U(10, 10) = 16$, $p < 0.02$, and also in groups that were trained in PR, $U(10, 11) = 18$, $p < 0.01$. Moreover, downshifted, $U(10, 10) = 51$, $p > 0.77$, and unshifted, $U(10, 11) = 48$, $p > 0.87$, pairs of groups failed to differ during Phase 2. Thus, despite extensive opportunities for counterconditioning during autoshaping acquisition in PR animals, reward devaluation proceeded undisturbed during cSNC training.

Average (± SEM) preshift performance in the cSNC task (not shown) over sessions 1–20 was: 1245.7 (± 69.7), 1311.7 (± 72.4), 1352.0 (± 68.8), and 1287.5 (± 117.9) lick frequency for Groups CR/32, CR/4, PR/32, and PR/4, respectively. Pairwise comparisons failed to detect any significant difference among groups, *U*s > 37, *p*s > 0.36. There was no evidence that prior AS training affected consummatory performance in the cSNC task.

The results of this experiment provided no evidence of positive transfer from AS to cSNC. If anything, there was a nonsignificant trend in the opposite direction to the extent that the significance of the cSNC effect was somewhat larger in PR than in CR groups. Such a trend would normally be ignored, but the fact that a similar nonsignificant tendency toward negative transfer was observed in Experiments 3 and 4 makes it intriguing. Ross (1964) demonstrated similar, but significant, results in his study in a group in which he suggested the behaviors trained during the first (climbing) and second phase (running) of acquisition training were competing responses. The possibility that transfer from AS to cSNC is of a negative type seems difficult to reconcile with the evidence of positive transfer from cSNC to AS extinction observed in Experiment 2b. How could two behaviors be compatible in one direction (licking→ lever pressing/goal entries), but competing in the other (lever pressing/goal entries→licking)? One obvious problem is that whereas Experiment 2b tested for transfer during extinction, subsequent experiments attempted to induce transfer via PR training. Thus, whereas the cSNC task was the same, the AS task was not strictly the same across experiments. We return to this topic in the General Discussion. The next experiment explored the possibility of transfer across tasks based on the same response: licking.

7. Experiments 6

Previous experiments in this series involved exploring whether transfer would occur between tasks differing in several parameters, notably the type of response. On the one hand, the AS task involves anticipatory responses of which two types were under observation, lever pressing and goal entries. On the other hand, the cSNC task involves consummatory behavior. The distinction between anticipatory (also called appetitive) and consummatory behavior (Craig, 1917) has led to some significant differences in terms of underlying mechanisms. In terms of reward devaluation, the consummatory and instrumental (anticipatory) versions of SNC (cSNC and iSNC) differ in terms of behavioral and neural mechanisms (Torres & Papini, 2017) and these differences could be relevant in the context of transfer effects. To determine whether the type of response is a relevant factor for transfer, Experiment 6 implemented PR vs. CR training in terms of the same motor response used in the cSNC task: licking. In Phase 1, animals received training in a Pavlovian taste conditioning situation with two stimuli: a lightly flavored strawberry milk (S_1) and heavily flavored chocolate milk (S_2). Phase 2 involved the same cSNC task used in previous experiments.

7.1. Method

7.1.1. Subjects and apparatus

Twenty-seven female Wistar rats, approximately 90 days old, deprived to 81–84% of their ad libitum weight, served as subjects. Animals were maintained under the same condition previously stated in Experiment 2. The mean (± SEM) ad lib weight was 300.1 g (± 5.2). Pavlovian taste conditioning and cSNC training took place in the previously described cSNC boxes used in Experiment 2. One difference was that two sipper tubes were used during training in the Pavlovian taste conditioning task (Phase 1). As usual, one sipper tube was used during cSNC training (Phase 2).

7.1.2. Procedure

Pavlovian taste conditioning began once animals reached their appropriate deprivation weight (at approximately 96 days of age). Rats were matched for weight and randomly assigned into one of 2 schedule groups: CR (100% reinforcement) or PR (50% reinforcement). Animals received the same incentives, lightly flavored strawberry milk (20 g of Strawberry Nesquick® dissolved in 2 L of fat-free milk) as the first stimulus (S_1), and more heavily flavored chocolate milk (160 g of Chocolate Nesquick® dissolved in 2 L of fat-free milk) as the second stimulus (S_2) throughout the CR or PR training. Rats received 10 daily acquisition sessions, consisting of 10 discrete trials, separated by variable intervals averaging 90 s (range: 60–120 s). Each trial began with the presentation of a bottle containing lightly flavored strawberry milk (S_1) for 15 s in the central sipper tube hole. If no response was detected after 10 s, the sipper tube was retracted and the animal received a score of zero for the number of licks performed during that stimulus presentation. A reinforced trial ended with the retraction of the strawberry milk sipper tube (S_1) and the immediate presentation of a bottle containing heavily flavored chocolate milk (S_2) for 5 s through the lateral sipper tube hole. If no response was detected after 10 s, the sipper tube was retracted and the animal received a score of zero for the number of licks performed during the stimulus presentation. A nonreinforced trial ended with the retraction of the strawberry sipper tube. During acquisition, each trial was reinforced for the CR group (100%), but only 50% of the trials were randomly reinforced for the PR group. A computer controlled the administration of events and recorded the number of licks to each sipper tube and for each trial.

Following the final daily session of Pavlovian taste conditioning, animals underwent cSNC training in the same boxes, although the exact box an animal was tested in was varied to minimize potential confounds associated with the testing box itself. During this phase, animals only had access to one sipper tube presented through the central elliptical hole in the apparatus. Animals were assigned and trained under identical procedures as previously described in Experiment 2, with the only exception being that the dependent variable was lick frequency.

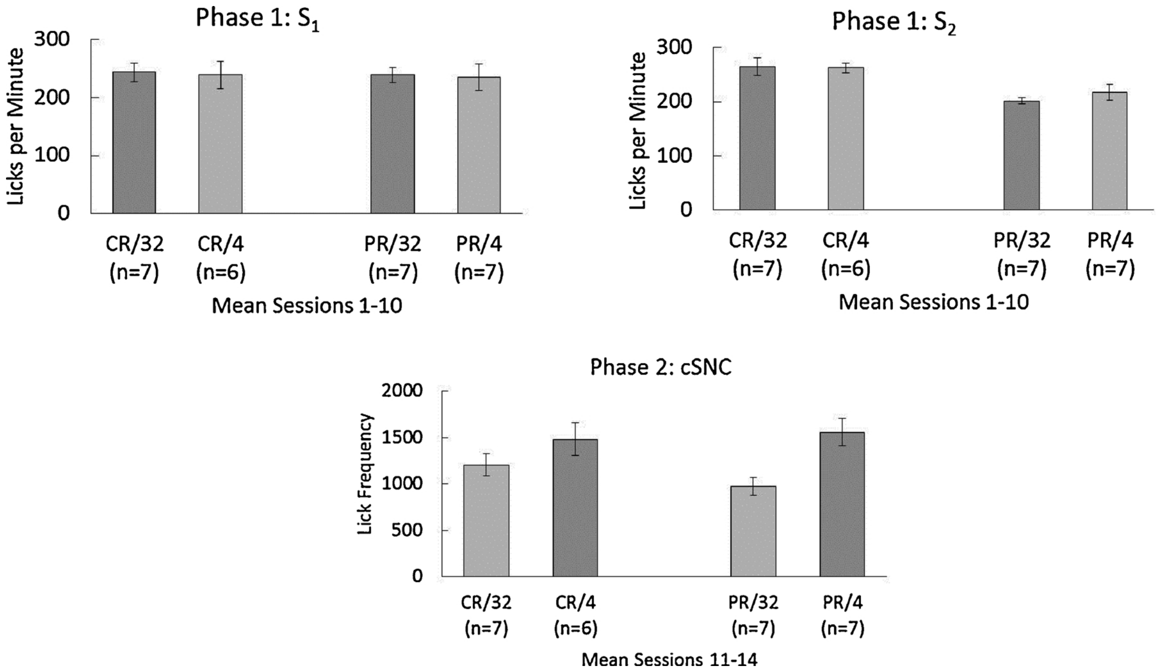

Fig. 9. Taste conditioning involving a weak strawberry flavor (S_1) followed by a strong chocolate milk solution (S_2). Whereas S_1 was always presented, S_2 was presented on a random half of the trials for PR animals (top), but in every trial for CR animals. This was followed by cSNC training (bottom). PR on S_2 enhanced the cSNC effect relative to CR on S_2, thus providing evidence for negative transfer from PR taste conditioning to cSNC. Results from Experiment 6.

7.2. Results and discussion

Mean performance to both stimuli in Phase 1 is plotted in Fig. 9, top panels. Lick frequency was calculated per minute of stimulus presentation to compensate for the trials in which S_2 was not presented due to the PR schedule. Both PR and CR animals readily consumed the lightly flavored strawberry milk (S_1) and the heavily flavored chocolate milk (S_2) across sessions. Although the expectation was that PR and CR schedules would yield differential performance during S_1 presentations, animals in all four groups responded similarly to the strawberry milk stimulus, whether trained under PR or CR, $Us > 19, ps > 0.80$. However, lick frequency for S_2 was higher in CR groups than in PR groups, $U(13, 14) = 22, p < 0.01$. Thus, licking for chocolate milk produced a reversed PRAE. Similar results were obtained when the comparison involved the means of the last three sessions of training (sessions 8–10), suggesting that the reversed PRAE persisted to the end of acquisition training in Phase 1. There was one exception: during the last three acquisition sessions, licking rate was lower in PR/32 than in PR/4 animals, $U(7, 7) = 7, p < 0.03$. For the purpose of the present experiment, the goal was to provide an opportunity for counterconditioning to occur; so the fact that there was no effect on S_1 and the group difference in S_2 was in the opposite direction implies that training perhaps was not sufficient to generate frustration counterconditioning. However, the effects of PR training are sometimes observed in extinction, rather than during acquisition training (e.g., Boughner & Papini, 2006), so these results do not necessarily invalidate the possibility of counterconditioning.

The main results are presented in Fig. 9, bottom. In Phase 2, animals previously exposed to CR training showed a trend toward a cSNC effect, but the difference was not significant, $U(7, 6) = 12, p > 0.19$. However, evidence of negative transfer emerged in the performance of groups previously given PR training. Indeed, Group PR/32 exhibited significant consummatory suppression after a 32-to-4% sucrose downshift relative to Group PR/4, $U(7, 7) = 5.0, p < 0.02$.

Not shown in Fig. 9 is the preshift performance in the cSNC task. The mean (± SEM) lick frequency over sessions 1–10 was: 1055.7 (± 105.0), 1145.4 (± 125.1), 946.9 (± 87.7), and 1224.3 (± 84.1) for Groups CR/32, CR/4, PR/32, and PR/4, respectively. None of the pairwise comparisons achieved significance, $Us > 10, ps > 0.08$. Thus, there was no evidence that prior Pavlovian training affected consummatory performance during preshift sessions in the cSNC task.

Using flavored stimuli in Pavlovian taste conditioning to induce transfer yielded the first evidence consistent with transfer from PR training to cSNC training. This evidence came in the form of negative transfer, that is, increased consummatory suppression after reward downshift in animals previously given PR training in the Pavlovian taste task. There are two possible accounts of this transfer effect: response similarity and a weak cSNC effect. Prior research suggested that receiving counterconditioning and transfer testing with the same behavior (e.g., running; Ross, 1964) should lead to positive transfer. In such a case, animals in the PR/32 condition should have demonstrated positive transfer (i.e., an attenuation of the cSNC effect) during Phase 2. Instead, prior PR training enhanced the cSNC effect. These results cannot be explained in terms of response incompatibility since the target response was licking in both phases of the experiment. A contrasting feature of these procedures is the location of the target response across phases, at least with respect to S_2. Whereas during taste conditioning, the partially reinforced S_2 stimulus was located on the right side of the front wall, the cSNC task was carried out by presenting a sipper tube in the center of the front wall. Interestingly, a similar incompatible location applies to the AS vs. cSNC tasks. Although conducted in different boxes, levers were located on one side of the autoshaping boxes whereas the sipper tube was located in the center of the front wall in contrast boxes. Could it be possible that counterconditioning after training in the taste conditioning task or in AS directed licking to one side of the box during reward downshift in the cSNC task, thus reducing licking to the centrally located sipper tube and yielding evidence of negative transfer? This remains to be evaluated.

The second account suggests that the transfer effects of prior PR training on the cSNC task require relatively weak training parameters in the latter because the transfer is negative. This possibility was explored in Experiment 7.

8. Experiment 7

If the transfer effect from lever pressing to licking is actually negative, then decreasing the size of the cSNC effect might minimize a floor effect and create room to observe transfer in terms of enhanced consummatory suppression in Phase 2. Previous research revealed that decreasing the discrepancy ratio between preshift and postshift incentives weakens the SNC effect (Papini & Pellegrini, 2006). For example, such manipulation has been shown to increase task sensitivity to detect strain differences between Roman high- and low-avoidance rats (Gómez et al., 2009; Rosas et al., 2007). To increase chances of observing negative transfer, AS training (Phase 1) was extended to 20 sessions and the reward discrepancy in the cSNC task was reduced from the traditional 8:1 ratio (32-to-4% sucrose downshift) to a 5.5:1 ratio (22-to-4% sucrose downshift), as used in Gómez et al.'s (2009) study.

Furthermore, several previous studies have found evidence of increased extinction responding after PR training even after an interpolated phase of CR training (Mellgren et al., 1979; Ross, 1964). Based on the success of these studies, 5 sessions of AS reacquisition under CR followed by 5 sessions of AS extinction (Phase 3) were included in all the groups. Based on the results of Experiment 2b, we predicted increased responding in extinction in Group PR/22 than in Group PR/4 during Phase 3. However, there are three potential problems to observe positive transfer with this design. First, a 22-to-4% sucrose downshift may not yield sufficient counterconditioning to achieve observable effects in Phase 3, extinction. Second, even if significant effects were observed during Phase 3, it would be difficult to ascertain whether increased responding in extinction in Group PR/22 was due to PR or the 22-to-4% sucrose downshift. Finally, extensive PR training in Phase 1 may produce near-asymptotic levels of counterconditioning for recovery from reward downshift in Phase 2 to have any measurable effect. For any or all of these reasons, we expected a weak effect, if anything.

8.1. Method

8.1.1. Subjects and apparatus

Forty female Wistar rats, approximately 90 days old, deprived to 81–84% of their ad libitum weight, served as subjects. Animals were maintained and housed as described in Experiment 2. The mean (± SEM) ad lib weight was 277.0 g (± 3.4). The same conditioning and consummatory boxes described in Experiment 2 were used in Experiment 7.

8.1.2. Procedure

Once animals reached their deprivation weight (at approximately 96 days of age), they were matched for weight and randomly assigned into either the CR or PR condition. Phase 1 AS training was identical to that previously described in Experiment 2, except animals received 20 sessions of acquisition training (rather than 10 as previously).

Following the final day of AS training, animals received cSNC training as previously described in Experiment 2 (Phase 2), except that downshifted animals received 10 daily sessions of access to a 22% sucrose solution (w/w, 22 g sucrose for every 78 g of distilled water) during preshift training, rather than the 32% sucrose used previously.

Following the final session of cSNC, all animals were run through 5 sessions of CR and 5 sessions of extinction in the AS task (Phase 3). The reacquisition sessions were identical to those experienced by CR animals during the first acquisition phase, whereas extinction sessions were as described in Experiment 2b. All other aspects of the training procedures were as described in Experiment 2.

8.2. Results and discussion

Fig. 10, top panels, shows the results of Phase 1 for lever pressing and goal entries. A comparison of PR and CR groups yielded nonsignificant effects for both dependent measures, $Us(20, 20) > 134$, $ps > 0.07$. The PRAE was marginal in this experiment. PR and CR groups assigned to the downshifted and unshifted conditions in the following phase did not differ from each other, $Us > 31$, $ps > 0.15$.

As expected, Phase 2 showed no cSNC effect for groups previously trained with CR, $U(10, 10) = 37$, $p > 0.32$, but a significant cSNC effect in groups previously receiving PR training, $U(10, 10) = 17$, $p < 0.02$. No other pairwise comparison was significant. Therefore, prior experience with PR enhanced the cSNC effect in consummatory behavior.

Preshift performance in Phase 2 is not shown in Fig. 10. The mean (± SEM) lick frequency over sessions 1–10 was: 1170.6 (± 98.8), 954.6 (± 84.2), 1036.1 (± 60.8), and 1168.9 (± 78.4) for Groups CR/22, CR/4, PR/22, and PR/4, respectively. None of the pairwise comparisons achieved significance, $Us > 29$, $ps > 0.13$. Thus, there was no evidence that prior AS training affected

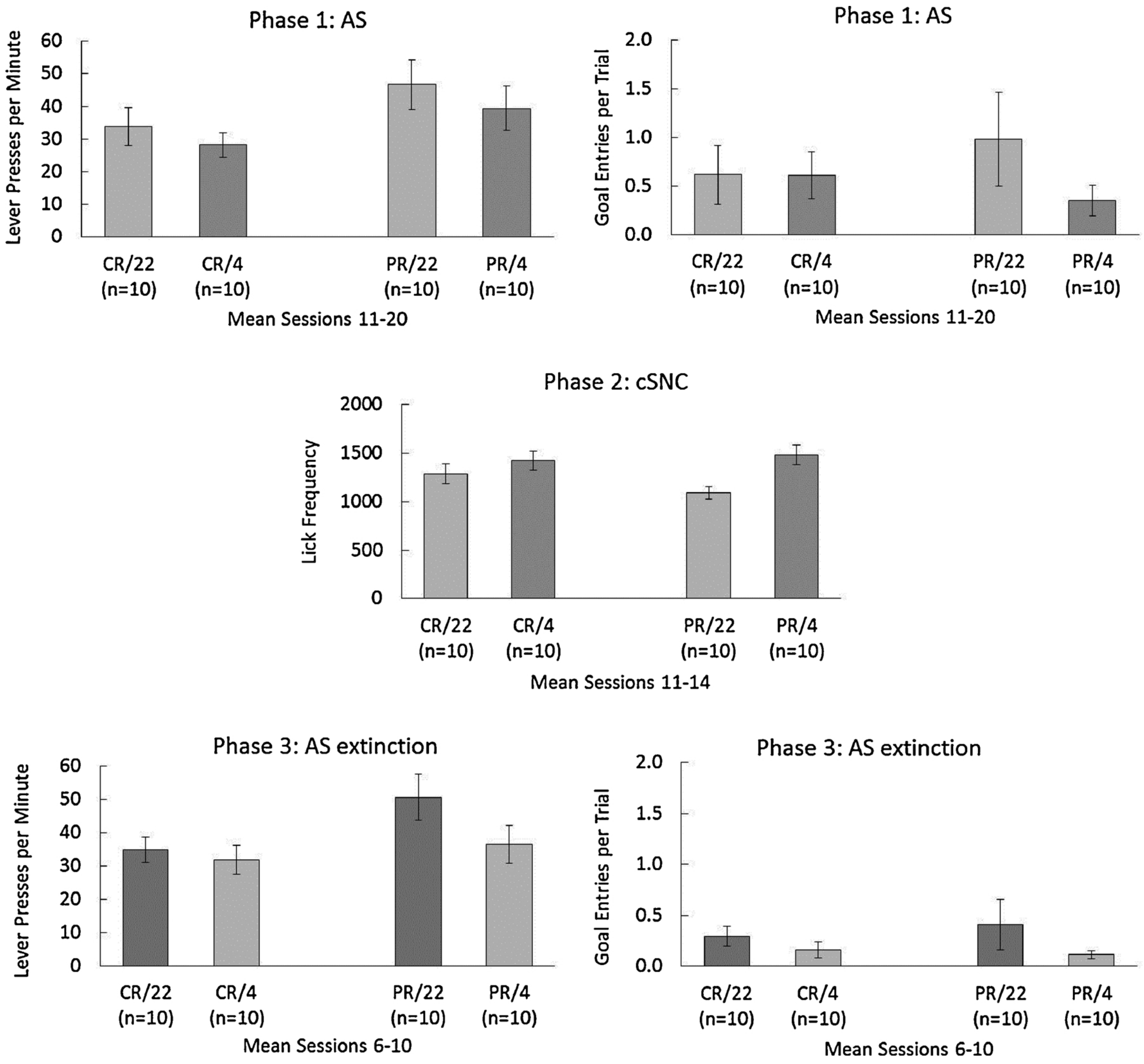

Fig. 10. AS acquisition under PR or CR in Phase 1 (top), followed by cSNC in Phase 2 (middle), and ending in AS acquisition under CR (not shown) and AS extinction (bottom). PR training in Phase 1 induced a cSNC effect under conditions that weaken this effect (22-to-4% sucrose downshift), thus providing evidence for negative transfer. Then, AS performance was highest in Group PR/22, which had received both PR and reward devaluation in prior phases; however, this effect failed to reach significance. Results from Experiment 7.

preshift consummatory performance in the cSNC task.

AS extinction performance during Phase 3 is presented in Fig. 10, bottom, for lever pressing and goal entries. Although there was a trend toward positive transfer in that mean lever-press responding was higher in Group PR/22 than in either PR/4 or CR/22, these differences failed to reach significance, Us(10, 10) > 26, ps > 0.07. None of the comparisons involving goal tracking in extinction reached significance, Us(10, 10) > 38, ps > 0.39. AS reacquisition (not shown) yielded nondifferential performance in all pairwise comparisons and for both lever pressing and goal entries, Us(10, 10) > 24, ps > 0.05.

These results provided evidence of negative transfer from PR to cSNC using a reduced reward discrepancy in the cSNC task and also a hint of positive transfer, albeit nonsignificant, in terms of increased performance in extinction after both PR and cSNC experience. As expected, the evidence for positive transfer was weak. This suggests that it may be intrinsically difficult to obtain evidence of positive and negative transfer within the same training parameters in the AS and cSNC training situations. The reason is that transfer appears to be asymmetrical, positive in one direction, but negative in the other. As a result, the training parameters that facilitate one type of transfer would tend to counteract the other type of transfer.

9. General discussion

The goal of these experiments was to determine whether the counterconditioning of frustration was a viable mechanism to understand the process of recovery from reward devaluation in the cSNC task (see Fig. 1; Papini, 2003). The strategy we followed was

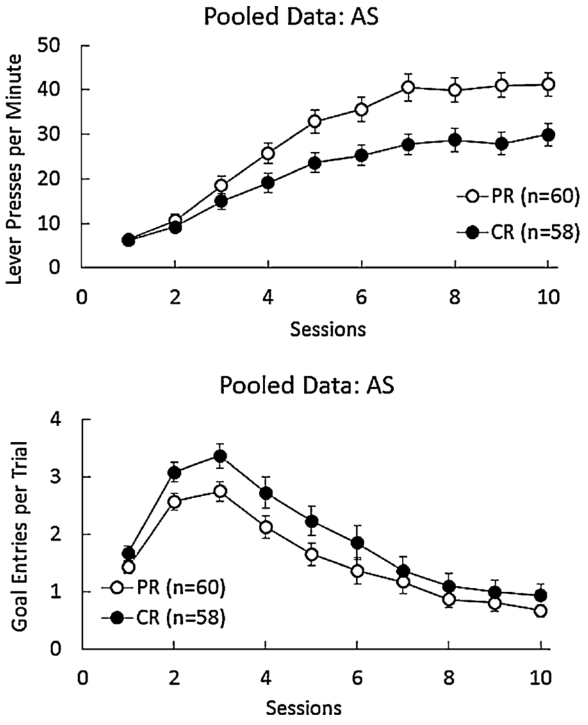

Fig. 11. AS data pooled from Experiments 2b, 6, and 7, showing the PRAE in lever pressing and the reversed effect in goal entries. Two aspects are worth noticing. First, the group difference in goal entries develops before the group difference in lever pressing. Second, goal entries increase early in training, but then decrease as AS progresses.

to look for evidence of frustration counterconditioning via transfer effects. According to Amsel's (1962, 1992) theory, frustration counterconditioning training in one paradigm should affect behavior in a subsequent paradigm when frustration is induced, regardless of the task, context, motivational state, or incentive. Prior frustration counterconditioning should either reduce the effects of frustration (positive transfer) or enhanced the effects of frustration (negative transfer) in the second task, depending on the extent to which the original and new responses interact. This response interaction stems from the theory's assumption that the underlying associative structure involves a direct connection between the internal state of frustration and the response—an S-R association. This hypothesis was supported by the findings of several other researchers (Cuenya et al., 2015; Mellgren et al., 1979; Nation et al., 1980; Rick et al., 2018; Ross, 1964). Two of the findings reported in this series confirm that recovery from reward devaluation in the cSNC situation involves frustration counterconditioning, namely, that cSNC experience reduced iSNC in the OWA task (Experiment 1b, Fig. 3) and it increased resistance to extinction in the AS task (Experiment 2b, Fig. 5). However, the current research has demonstrated that transfer might not be as straightforward as originally theorized.

The lack of transfer effects observed in experiments in which AS training preceded cSNC training could not be attributed to a failure of PR training to affect behavior because a clear PRAE was observed in these experiments. We pooled AS data from Experiments 2b, 6, and 7, in which training involved identical conditions, and plotted the results in Fig. 11. Clearly, PR training increased lever pressing and reduced goal entries relative to CR training; yet no transfer effects were observed in Experiments 2b and 6, but negative transfer emerged in Experiment 7. These results suggest that reward devaluation in the cSNC task is not as easily influenced by prior counterconditioning experience, although it is able to influence behavior in subsequent situations, as shown here in Experiments 1b (OWA) and 2b (AS extinction), and in Cuenya et al.'s (2015) study with RLA rats (SNC tasks). The hypothesis that frustration counterconditioning plays a role in recovery from reward devaluation requires that such recovery influences subsequent tasks involving frustration, but also is influenced by prior tasks involving counterconditioning. Thus, unidirectional transfer is at variance with this hypothesis and thus an effort was made to understand its source.

There was a nonsignificant trend in Experiments 3–5 toward slower recovery from reward devaluation in animals that had received AS under either similar conditions (sucrose pellets in Experiment 3) or increased chances for counterconditioning (extended PR training in Experiment 4). Moreover, even after extended preshift training in the cSNC task, a manipulation introduced to enhance the size of the cSNC effect, the trend was toward negative transfer. Although nonsignificant, these trends suggested that increasing the similarity between tasks could lead to detecting negative transfer from AS to cSNC training. This idea was resisted in view of the results of previous experiments in which the transfer had always been positive (Cuenya et al., 2015; Mellgren et al., 1979; Nation et al., 1980; Rick et al., 2018; Ross, 1964; present Experiments 1b and 2b).

Two strategies were followed to uncover significant evidence of negative transfer. The first strategy was to increase the similarity in response topography across phases. Ross (1964) had shown that the degree to which the responses associated to frustration are compatible determined the type of transfer, positive or negative, that would be observed in Phase 2. Thus, in Ross' experiment, PR on jumping led to positive transfer on running extinction (the two responses were hypothesized to be compatible), whereas PR on climbing led to negative transfer on running (they were thought to be incompatible). Presumably, by virtue of this S-R associative structure, the induction of frustration during extinction in Phase 3 would tend to elicit either jumping or climbing, thus either encouraging or interfering, respectively, with the required response of running. Such "regression" to response patterns previously acquired is consistent with the results of experiments involving changes in training contexts and target responses (e.g., Boughner & Papini, 2006; Nation, Conney, & Gartrell, 1979; Rashotte & Amsel, 1968). For example, Rashotte and Amsel (1968) trained rats to run slowly in a runway to obtain food and found that individual animals were not very effective (thus exposing themselves to PR training). To earn rewards, some rats developed idiosyncratic rituals in different segments of the runway so they would delay approach to the goal. Such rituals could be measured in terms of speed recorded in different sections of the runway. In a later phase, after CR training for running, a shift to extinction reactivated such idiosyncratic rituals (see also Amsel & Rashotte, 1969; Rashotte & Amsel, 1967).

To test whether positive transfer depended on such response compatibility, PR training was applied to the same nominal response in Phase 1, licking, also used in the cSNC task in Phase 2. In addition, liquid rewards were used and training in both phases took place in the same conditioning boxes, thus increasing the overall similarity between tasks. Under these conditions there was evidence that the cSNC effect was significant after PR training, but nonsignificant after CR training (see Fig. 9, middle). Thus, contrary to our prediction, the results showed evidence of negative transfer. Because in this case the response was the same, these results seem difficult to reconcile with Amsel's (1992) frustration theory, which predicted positive transfer instead. One potential explanation for negative transfer in this experiment emphasizes spatial cues. To distinguish between the two tasks, bottle locations for which counterconditioning would occur were different. During Phase 1 (taste conditioning), the counterconditioned manipulandum was the lateral bottle, whereas the medial bottle was used during Phase 2 (cSNC). If animals received counterconditioning of licking to the lateral bottle in Phase 1, then perhaps inducing frustration during reward devaluation in Phase 2 could have directed behavior toward the lateral portion of the box, which would have resulted in reduced licking to the centrally located bottle and an enhanced cSNC effect in PR animals. A similar argument could be articulated with respect to AS training. In this task, the lever was always located in a lateral portion of the front wall. Although the boxes used in AS and cSNC tasks are different, they are generally similar, a fact that could have supported substantial stimulus generalization across phases. This may account for the nonsignificant bias in the direction of negative transfer observed in some of the experiments. This argument is consistent with the regression of response rituals mentioned above (Amsel & Rashotte, 1969; Rashotte & Amsel, 1967, 1968), in so far as changes in speed were specific to various sections of the runway (i.e., spatially distinctive). Tests of this account would involve either manipulating the location of the manipulanda across phases or direct video observations to determine changes in the spatial allocation of behavior across groups during the critical reward downshift sessions of the cSNC task.

The second strategy to detect evidence of transfer was to weaken the cSNC effect. In Experiment 7, the cSNC effect was weakened by reducing the discrepancy between the pre- and postshifted sucrose solutions. This method was effective in detecting strain difference between inbred RHA and RLA rats (Gómez et al., 2009). Additionally, animals underwent AS reacquisition under CR schedule and then were run through AS extinction training. This method uncovered a negative transfer effect from PR to cSNC (Phase 2), and came close to a positive transfer effect from cSNC to AS extinction (Phase 3). Animals that had previously undergone PR training during AS acquisition and that had also been exposed to reward devaluation (Group PR/22) exhibited the highest lever pressing and goal entry levels of all groups (Fig. 10, bottom). As discussed above, the fact that this latter effect failed to reach significance highlights the asymmetric nature of the transfer effects observed here: positive transfer from cSNC to AS extinction, but negative transfer from PR training to cSNC. As a result, factors that would facilitate detection of one transfer effect would tend to interfere with detection of the other transfer effect.

One implication of these results is that transfer effects are likely based on a habitual, S-R associative basis, rather than on emotional changes such as the development of tolerance to frustration during PR training. A frustrating event reactivates responses previously linked to recovery from or coping attempts to deal with reward loss (Amsel & Rashotte, 1969; Rashotte & Amsel, 1967, 1968). As a result, whether one observes positive or negative transfer across situations may say less about the ability to overcome frustration than about the resurgence of previously effective strategies. Amsel's (1992) view of frustration counterconditioning says nothing about the possible development of tolerance to frustration. Rather, it accounts for changes in behavior as arising from a redirection of the behavioral control exerted by internal states of frustration away from rejection and avoidance responses, toward approach responses. An animal may "feel" just as frustrated, but its behavior may reflect what appears to be either less emotion (positive transfer) or stronger emotion (negative transfer) as a result of the behavioral biases induced by prior counterconditioning experience.

That frustration may persist even after hundreds of trials under PR is suggested by an experiment reported by Ludvigson, McNesse, and Collerain (1979) involving so-called frustration odors. Rats (called "donors") trained in a PR schedule emit a distinct odor in trials when they received unexpected nonreward; other rats (called "observers") can perceive such odors and respond accordingly. Ludvigson et al.'s experiment showed that after hundreds of PR trials, donors still emitted frustration odors in every nonrewarded trial, as shown by the behavior of naïve observers introduced at various stages of training to minimize odor habituation. Therefore, animals had not become tolerant to the negative effects of frustration even after extensive opportunities for counterconditioning.

In summary, these results leave three conclusions. First, frustration counterconditioning is implicated in recovery from reward devaluation as well as in the adjustment to appetitive extinction. Second, transfer across situations involving reward loss engages an interplay between coping responses acquired during earlier frustrating experience and those currently being developed when confronted with new frustrating situations. Finally, conclusions about emotion must take into account the potential for behavioral interactions before results can be clearly ascribed to internal factors.

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References

Amsel, A. (1962). Frustrative nonreward in partial reinforcement and discrimination learning. Some recent history and a theoretical extension. *Psychological Review, 69*, 306–328.
Amsel, A. (1992). *Frustration theory: An analysis of dispositional learning and memory.* Cambridge, MA: Cambridge University Press.
Amsel, A., & Rashotte, M. E. (1969). Transfer of experimenter-imposed slow-responding patterns to extinction of a continuously rewarded response. *Journal of Comparative and Physiological Psychology, 69*, 185–189.
Anselme, P. (2015). Incentive salience attribution under reward uncertainty: A Pavlovian model. *Behavioural Processes, 111*, 6–18.
Anselme, P. (2016). Motivational control of sign-tracking behaviour: A theoretical framework. *Neuroscience and Biobehavioral Reviews, 65*, 1–20.
Boughner, R. L., & Papini, M. R. (2006). Survival of the partial reinforcement extinction effect after contextual shifts. *Learning and Motivation, 37*, 304–323.
Candido, A., Maldonado, A., Megias, J. L., & Catena, A. (1992). Successive negative contrast in one-way avoidance learning in rats. *Quarterly Journal of Experimental Psychology, 45B*, 15–32.
Craig, W. (1917). Appetites and aversions as constituents of instincts. *Proceedings of the National Academy of Sciences USA, 3*, 685–688.
Cuenya, L., Annicchiarico, I., Serafini, M., Glueck, A. C., Mustaca, A. E., & Papini, M. R. (2015). Effects of shifts in food deprivation on consummatory successive negative contrast. *Learning and Motivation, 52*, 11–21.
Cuenya, L., Sabariego, M., Donaire, R., Fernández-Teruel, A., Torres, C., & Papini, M. R. (2015). Transfer across reward devaluation tasks in inbred Roman rat strains. *Learning and Motivation, 52*, 22–31.
Flaherty, C. F. (1996). *Incentive relativity.* New York: Cambridge University Press.
Flaherty, C. F., Grigson, P. S., & Rowan, G. A. (1986). Chlordiazepoxide and the determinants of contrast. *Animal Learning and Behavior, 14*, 315–321.
Gómez, M. J., Esarabajal, M. D., de la Torre, L., Tobeña, A., Fernandez-Teruel, A., & Torres, C. (2009). Consummatory successive negative and anticipatory contrast effect in inbred Roman rats. *Physiology & Behavior, 97*, 374–380.
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.
Ludvigson, H. W., McNesse, R. R., & Collerain, I. (1979). Long-term reaction of the rat to conspecific (frustration) odor. *Animal Learning and Behavior, 7*, 251–258.
Mellgren, R. L., Hoffman, D., Nation, J., Williams, J. D., & Wrather, D. M. (1979). Transfer of persistence of responding across motivational and reward conditions. *American Journal of Psychology, 92*, 95–103.
Morales, A., Torres, C., Megías, J. L., Cándido, A., & Maldonado, A. (1992). Effect of diazepam on successive negative contrast in one-way avoidance learning. *Pharmacology Biochemistry & Behavior, 43*, 153–157.
Nation, J. R., Conney, J. B., & Gartrell, K. E. (1979). Durability and generalizability of persistence training. *Journal of Abnormal Psychology, 88*, 121–136.
Nation, J. R., Wrather, D. M., Mellgren, R. L., & Spivey, M. (1980). Transfer of the partial reinforcement extinction effect between escape (shock) and appetitive (food) conditioning. *Learning and Motivation, 11*, 97–116.
Ortega, L. A., Glueck, A. C., Daniel, A. M., White, M., & Papini, M. R. (2014). Memory interfering effects of chlordiazepoxide on consummatory successive negative contrast. *Pharmacology, Biochemistry and Behavior, 116*, 96–106.
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*, 160–186.
Papini, M. R. (2003). Comparative psychology of surprising nonreward. *Brain, Behavior and Evolution, 62*, 83–95.
Papini, M. R., & Dudley, R. T. (1997). Consequences of surprising reward omissions. *Review of General Psychology, 1*, 175–197.
Papini, M. R., Fuchs, P. N., & Torres, C. (2015). Behavioral neuroscience of psychological pain. *Neuroscience Behavioral Review, 48*, 53–69.
Papini, M. R., & Pellegrini, S. (2006). Scaling relative incentive value in consummatory behavior. *Learning and Motivation, 37*, 357–378.
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.
Rashotte, M. E., & Amsel, A. (1967). Acquisition and extinction, within subjects, of a continuously rewarded response and a response learned under discontinuous negatively correlated reward. *Psychonomic Science, 7*, 257–258.
Rashotte, M. E., & Amsel, A. (1968). Transfer of slow-response rituals to extinction of a continuously rewarded response. *Journal of Comparative and Physiological Psychology, 66*, 432–443.
Rick, P., Donaire, R., Papini, M. R., Torres, C., & Pellón, R. (2018). Can surprising nonreward and adjunctive behavior influence each other? *Animal Behavior and Cognition, 5*, 139–153.
Robinson, M. J. F., Anselme, P., Fischer, A. M., & Berridge, K. C. (2014). Initial uncertainty in Pavlovian reward prediction persistently elevates incentive salience and extends sign-tracking to normally unattractive cues. *Behavioural Brain Research, 266*, 119–130.
Rosas, J. M., Callejas-Aguilera, J. E., Escarabajal, M. D., Gómez, M. J., de la Torre, L., Agüero, A., et al. (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.
Ross, R. R. (1964). Positive and negative partial reinforcement extinction effect carried through continuous reinforcement, changed motivation, and changed response. *Journal of Experimental Psychology, 68*, 492–502.
Rowan, G. A., & Flaherty, C. F. (1987). The effects of morphine in the consummatory contrast paradigm. *Psychopharmacology, 93*, 51–58.
Silva, R. H., & Frussa-Filho, R. (2000). The plus-maze discriminative avoidance task: A new model to study memory-anxiety interactions. Effects of chlordiazepoxide and caffeine. *Journal of Neuroscience Methods, 102*, 117–125.
Torres, C., Cándido, A., Escarabajal, M. D., de la Torre, L., Maldonado, A., Tobeña, A., et al. (2005). Successive negative contrast effect in one-way avoidance learning in female Roman rats. *Physiology & Behavior, 85*, 77–82.
Torres, C., Glueck, A. C., Conrad, S. E., Morón, I., & Papini, M. R. (2016). Dorsomedial striatum lesions affect adjustment to reward uncertainty, but not to reward devaluation or omission. *Neuroscience, 332*, 13–25.
Torres, C., Morales, A., Cándido, A., & Maldonado, A. (1996). Succesive negative contrast in one-way avoidance: Effect of thiopental sodium and chlorpromazine. *European Journal of Pharmacology, 314*, 269–275.
Torres, C., & Papini, M. R. (2017). Incentive relativity. In J. Vonk, & T. K. Shackelford (Eds.). *Encyclopedia of comparative cognition and behavior* (pp. 1–13). New York: Springer.
Torres, C., & Sabariego, M. (2014). Incentive relativity: Gene-environment interactions. *International Journal of Comparative Psychology, 27*, 446–458.
Wood, M., 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., 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 Research, 193*, 28–36.