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Transfer across reward devaluation tasks in inbred Roman rat strains

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ABSTRACT

Emotional counterconditioning resulting from pairings between a state of frustration and food reward explains transfer across situations involving reward omission. This experiment explored the hypothesis that a similar emotional counterconditioning mechanism is also involved in recovery from reward devaluation. Inbred Roman high- and low-avoidance rat strains (RHA-I and RLA-I) were trained in consummatory and instrumental successive negative contrast tasks (cSNC and iSNC) in counterbalanced order. RLA-I rats have consistently shown high levels of anxiety in a variety of situations, relative to RHA-I rats. Therefore, a stronger evidence of transfer was expected in RLA-I rats than in RHA-I rats. Whereas both strains showed the effects in the original training phase, only RLA-I rats benefitted from prior exposure to one reward devaluation task. The transfer was positive and symmetrical (i.e., exposure to one SNC task attenuated the second effect). RHA-I rats produced no evidence of transfer. The results suggest that emotional counterconditioning is involved in recovery from reward devaluation tasks. Despite extensive psychogenetic selection for low-avoidance/high-anxiety behavior, RLA-I rats showed the ability to develop resilience as a function of prior experience.

1. Introduction

In the successive negative contrast task, reward devaluation leads to a transient deterioration of behavior accompanied by signs of negative emotion (Flaherty, 1996; Papini, Fuchs, & Torres, 2015). For example, after learning a runway task for a large food reward, the instrumental approach behavior deteriorates following a downshift in the amount of food, relative to an unshifted control always receiving the small reward magnitude—instrumental successive negative contrast, iSNC (Crespi, 1942). Similarly, sucrose licking, a consummatory approach behavior, is sharply reduced following a downshift in the concentration of the solution relative to an unshifted control—consummatory successive negative contrast, cSNC (Vogel, Mikulka, & Spear, 1968). In both iSNC and cSNC, the disruption of goal approach is temporary; after a few sessions with the

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new incentive conditions, approach behavior recovers and reaches the level of unshifted controls. What mechanisms control the recovery of approach behavior following reward devaluation?

Learning theories that allow only for changes in cognitive factors typically do a poor job at predicting the SNC effect (e.g., Hull, 1943; Rescorla & Wagner, 1972). The associative model proposed by Rescorla and Wagner (1972) predicts a graduate decline in associative strength to a stimulus paired with a downshift in reward magnitude. However, behavioral change stops when strength reaches the level supported by the new reward (i.e., the level of the unshifted control), never predicting contrast. The rapid, excessive disruption of approach behavior that usually follows an episode of reward devaluation suggests an emotional component. Amsel's (1992) frustration theory, for example, explains SNC in terms of the development of an internal response of primary frustration initially elicited by the negative discrepancy between expected and obtained rewards, and later anticipated on the basis of associated stimuli. This anticipatory frustration is assumed to induce rejection/avoidance of the goal, thus leading to the deterioration of approach behavior. Amsel (1992) never quite explained what mechanism is responsible for the recovery of approach behavior in the SNC situation. Daly and Daly (1982) proposed a theory combining the Rescorla–Wagner model with Amsel's frustration theory, which suggests that recovery from reward devaluation requires the extinction of anticipatory frustration as the animal learns to expect the new reward. However, they provided no evidence for such a mechanism.

More recently, two separate processes have been suggested to account for the recovery of approach behavior in the SNC situation: memory update and emotional counterconditioning (Daniel, Ortega, & Papini, 2009; Ortega, Glueck, Uhelski, Fuchs, & Papini, 2013; Wood, Norris, Daniel, & Papini, 2008). Memory update replaces knowledge about the large, preshift reward with knowledge about the small, postshift reward (Papini, 2003). Consistent with this hypothesis, administration of the memory-interfering drug chlordiazepoxide immediately after the first or second downshift trial impaired recovery in the cSNC task (Ortega et al., 2014). Such impairment would reflect an interference with the encoding of new information about the devalued reward, thus extending the effects of the negative discrepancy between expected and obtained rewards. The apparent absence of spontaneous recovery of the cSNC effect (Norris, Daniel, & Papini, 2008) also suggests that this memory update process is extensive. To account for the absence of spontaneous recovery of cSNC, Mustaca et al. (2009) suggested that a process of memory reconsolidation results in a substantial replacement of the preshift reward memory by the postshift reward memory (i.e., the memory of the devalued incentive).

In addition to memory update, the frustration response induced by reward downshift during postshift trials is accompanied by access to a devalued, but still partially rewarding stimulus. Unlike extinction, where no reward is available, in the SNC task approaching the goal would result in a pairing of anticipatory frustration (an aversive internal state) with food (a reward). Pairings of an aversive event with a reward usually results in an attenuation of the rejection/avoidance behavior induced by the aversive event, a process called counterconditioning (Pavlov, 1927). Amsel (1992) suggested that emotional counterconditioning resulting from pairings between anticipatory frustration and food is responsible for increased resistance to extinction after partial reinforcement, compared to continuous reinforcement. Similarly, a role of emotional counterconditioning in recovery from SNC is suggested by results demonstrating that partial reinforcement training during preshift sessions attenuates both iSNC and cSNC effects by increasing approach behavior (Mikulka, Lehr, & Pavlik, 1967; Pellegrini, Muzio, Mustaca, & Papini, 2004; Wood, Daniel, & Papini, 2005).

The experiment reported here looked for evidence that emotional counterconditioning plays a role in recovery from reward devaluation in terms of transfer across situations. Transfer effects refer to the influence of training in one situation on performance in a subsequent situation and have been studied extensively in the context of the effects of partial reinforcement on extinction (see Amsel, 1992). For example, Ross (1964) reported that partial reinforcement training transferred its effects across two situations even when extinction occurred in a different context, under a different motivational state, and involving a different response. Whether partial reinforcement training on one response led to increased (positive transfer) or decreased (negative transfer) persistence during extinction of the other response depended on the degree of compatibility between responses. In Ross' (1964) experiment, for example, jumping and running were compatible, but climbing and running were incompatible. Ross' (1964) theoretical interpretation suggests that counterconditioning of anticipatory frustration in one situation (during partial reinforcement training) strengthened the association between frustration and the target response in that situation. Later, in the second situation and under different conditions, the induction of frustration during extinction reactivated that previously trained response, thus resulting in increased or decreased behavioral persistence. Thus, transfer across situations offers a procedure for testing whether counterconditioning is a viable mechanism to account for recovery after reward devaluation. In addition, this study is the first to evaluate transfer effects across SNC tasks.

In this experiment, inbred Roman high- and low-avoidance rat strains (RHA-I and RLA-I, respectively) were exposed to two reward-devaluation tasks in a counterbalanced order: iSNC and cSNC. Extensive research demonstrates that RLA-I rats exhibit higher levels of anxiety than RHA-I rats in a wide range of situations (see Driscoll, Fernández-Teruel, Corda, Giorgi, & Steimer, 2009; Steimer & Driscoll, 2005; Torres & Sabariego, 2014), including iSNC and cSNC tasks (Gómez, de la Torre et al., 2009; Gómez, Escarabajal et al., 2009; Rosas et al., 2007; Torres et al., 2005). Moreover, exposure to partial reinforcement during preshift sessions reduces iSNC (Cuenya et al., 2012) and increases resistance to extinction (Gómez et al., 2008) in RLA-I rats, but not in RHA-I rats. Because emotional counterconditioning is assumed to increase with the strength of frustration, and given that RLA-I rats show greater vulnerability to reward devaluation than RHA-I rats, we predicted that RLA-I rats exposed to reward devaluation in one situation would show a greater degree of transfer to a different reward devaluation task than RHA-I rats (i.e., cSNC-to-iSNC or iSNC-to-cSNC). Because it is not possible a priori to determine whether licking

(cSNC) and running (iSNC) are compatible responses, transfer would be found if the first SNC effect reduced (positive transfer) or enhanced (negative transfer) the second SNC effect.

2. Method

2.1. Subjects

Forty-eight inbred male RLA-I and RHA-I rats from the Autonomous University of Barcelona were used. Their ad lib weight ranged from 318 to 442 g at the start of the experiment. Animals were paired housed in polycarbonate cages and deprived to 80–90% of their ad lib weight. This level of deprivation was maintained throughout the experiment by post training supplementary food administered approximately 30 min after the end of the experimental session. Animals had free access to water throughout the experiment. Room temperature was kept at about 20 °C. Animals were exposed to a 12:12 h light:dark cycle, with lights on at 08:00 h. Sessions were administered between 09:00 and 14:00 h. The experiment followed European Union directive guidelines for the use of animals in research (2010/63/EU) and Spanish Law (6/2013; R.D. 53/2013).

2.2. Apparatus

2.2.1. cSNC task

Consummatory training involved 6 Plexiglas boxes, each measuring 30 × 15 × 30 cm ($L \times W \times H$). The front wall had a hole through which the sipper tube of a graduated cylinder was inserted. The sucrose solutions (22%, 4%) were prepared w/w by mixing 22 g (or 4 g) of sucrose for every 78 g (or 96 g) of distilled water. A magnetic mixer (Nahita Magnetic Stirrer 680-9, Beriain, Spain) was used to dissolve the sucrose. Session length was measured with a manual stop watch (Extech, model 365510, Madrid, Spain).

2.2.2. iSNC task

The apparatus was a straight runway measuring 120 × 11 × 14 cm ($L \times W \times H$). The runway was divided into three sections separated by guillotine doors. The start, running, and goal sections measured 20 cm, 80 cm, and 20 cm, respectively. The walls and floor of the runway were painted green and covered by clear Plexiglas lids. Two guillotine doors separated the start and goal sections from the running section. 45-mg pellets (formula P; Research Diets, Lancaster, NH) were used as the reward (either 12 or 2 pellets, depending on the group). Pellets were placed on the floor at the distal end of the goal box. Response latencies (in seconds) were measured with a manual chronometer (Extech, Madrid, Spain). The chronometer was started when the start guillotine door was raised and was stopped when the rat had its four legs inside the goal box.

2.3. Procedure

Half of the animals (12 RHA-I and 12 RLA-I rats) were exposed to cSNC in Phase 1 and to iSNC in Phase 2, whereas the other half was exposed to these tasks in a reverse order, that is, to iSNC in Phase 1 and to cSNC in Phase 2. In each task there were downshifted and unshifted groups. Thus, a total of eight groups (2 strains × 2 tasks × 2 conditions per task) received training, each with an $n = 6$.

2.3.1. cSNC task

Rats were moved from the colony to an adjacent experimental room in their own home cage and in squads of six. Each rat was assigned to one of six boxes and always trained in that box. The order of training of the squads varied across days. Training consisted of a total of 20 daily sessions. There were 16 preshift sessions and 4 postshift sessions. Sessions were administered at a rate of one per day on every day of the week.

One habituation day preceded the preshift. On this first day, rats were placed into the training box and given a 5-min period without access to sucrose solution. Preshift sessions began on the second day. Each animal was placed in the experimental box with spouts attached to graduated bottles. A maximum time of 5-min was allowed for the rat to complete the session from its first contact with the spout. Once 5-min had elapsed, the animal was taken out from the experimental box and placed back in its home cage. The amount of sucrose solution consumed was registered.

Animals received 16 preshift sessions in which they had access to either 22% or 4% sucrose, depending on the group. These were followed by 6 postshift sessions in which all animals received access to 4% sucrose.

2.3.2. iSNC task

Rats were moved from the colony room to an adjacent experimental room in their home cage and in squads of 18 animals. The floor of the apparatus was vacuumed and wiped with a 5% ethanol solution after every squad of rats finished its session. Sessions were administered at a rate of one per day on every day of the week.

Three habituation sessions preceded training. On the first, rats were placed in the start box with both guillotine doors open and given five 2-min trials of access to the entire runway. On the second, rats were given two 2-min trials of access followed by three goal-box feedings (the animal was confined to the goal box and given the appropriate number of pellets,

either 12 or 2 depending on the group). The last habituation session consisted of three goal-box feeding trials. Subjects were given a maximum of 30 s to consume the food and were then removed from the goal box. The rats were given six Noyes pellets in the home cage 30 min after the third habituation session along with their daily ration of lab chow.

Preshift training began on the fourth day. Each animal was placed in the start box with the start door closed and the goal door opened. The start door was then opened and the rat was allowed to run down the runway to obtain the food reward (12 or 2 pellets, depending on the group). A maximum time of 20 s was allowed for the rat to complete the trial. If the rat did not reach the goal box before 20 s had elapsed, it was gently pushed into the goal box by the experimenter and 20 s was recorded as response latency for that trial. When the rat reached the goal box, the goal door was quietly closed and a stopwatch was started. The rat was given a maximum of 30 s to consume the food reward. As soon as the rat had finished eating or 30 s had elapsed, it was removed from the goal box and placed back in its home cage between trials. Each rat received 6 trials per session for 5 preshift sessions.

On the first postshift session, the rats that had received 12 pellets per trial were downshifted to 2 pellets per trial. The rats receiving 2 pellets per trial remained unchanged. There were 6 postshift sessions with 6 trials per session and an intertrial interval of approximately 20 min.

2.3.3. Statistical analysis

The dependent variables were sucrose intake (ml) for cSNC and running latency (s) for iSNC. The average latency for each animal, in each session, was transformed to its log10 to improve normality and allow for the use of parametric statistics. These variables were subjected to two sets of analysis of variance. First, Phase (1 vs. 2) × Contrast (downshifted vs. unshifted) × Session analyses were computed on each strain separately. These analyses aimed at determine transfer effects for each strain and task. Because our aim was to determine the length of these SNC effects for each strain and phase, LSD pairwise tests with error terms derived from the main analysis were computed on postshift data comparing downshifted vs. unshifted groups at each postshift session. Second, Strain (RHA-I vs. RLA-I) × Contrast (downshifted vs. unshifted) × Session analyses were computed on each task separately. These analyses provided evidence for strain differences in behavior. In all cases, LSD pairwise tests were calculated to determine the source of significant interactions. Greenhouse–Geisser corrections were used whenever sphericity was violated (notice variations in degrees of freedom for repeated-measure factors). All statistics were run with the IBM SPSS statistics package (v. 21), with the alpha value set at the 0.05 level. For simplicity, only statistics for significant effects are reported in the narrative, except when nonsignificance is close to the alpha value.

3. Results

In the cSNC task, data from 18 out of 768 preshift sessions (2.3%) were lost and replaced by the group average for statistical and plotting purposes. Moreover, by mistake two animals received 4 postshift sessions and five animals received 5 postshift sessions, rather than the scheduled 6 postshift sessions, in the cSNC task. Therefore, it was decided to analyze and plot only 4 postshift sessions for all animals. By the fourth postshift session, all animals had fully recovered from reward downshift in the cSNC task. No data were lost in the iSNC task.

3.1. RHA-I strain

3.1.1. cSNC task

The results for RHA-I rats in the cSNC and iSNC tasks are presented in Fig. 1. Independent Phase × Contrast × Session analyses were computed for each task. For RHA-I rats, the cSNC task led to similar consummatory behavior during both preshift and postshift sessions, whether the task was administered in Phase 1 (original) or 2 (after iSNC experience). For preshift sessions, this similarity was captured by significant main effects of phase, contrast, and session, $Fs > 20.19$, $ps < 0.001$, but nonsignificant interactions effects, including the triple interaction. For postshift sessions, however, there was a significant triple interaction, $F(3, 60) = 3.02$, $p < 0.04$. There was also a significant contrast by session interaction, $F(3, 60) = 14.00$, $p < 0.001$, and significant main effects of phase, contrast, and session, $Fs > 4.97$, $ps < 0.04$. LSD pairwise tests revealed that the source of the triple interaction was twofold: 4% sucrose groups were different only on Session 20, $F(1, 20) = 10.99$, $p < 0.004$, whereas 22% groups differed only on Session 17, with consummatory behavior being higher in Phase 2 than in Phase 1, $F(1, 20) = 4.49$, $p < 0.05$. For both phases, 22% sucrose performance was significantly lower than 4% sucrose performance on the first downshift session, Session 17, $Fs(1, 20) > 7.27$, $ps < 0.02$. Therefore, the only evidence consistent with transfer in the cSNC task was an increase in consummatory behavior in downshifted RHA-I animals on Phase 2 relative to Phase 1. However, the cSNC effect was present in both phases.

3.1.2. iSNC task

Fig. 1 shows that the effect was present in both phases and it was relatively small. A similar analysis for preshift sessions indicated significant main effects for phase, contrast, and session, $Fs > 5.21$, $ps < 0.04$. None of the interactions reached significance. Postshift behavior yielded the following significant effects. There were phase by session, $F(5, 100) = 2.33$, $p < 0.05$, and contrast by session effects, $F(5, 100) = 3.27$, $p < 0.01$. There was also a session effect, $F(5, 100) = 2.38$, $p < 0.05$. All other effects, including the triple interaction, were not significant. LSD pairwise tests revealed that the source of the contrast by session interaction were significant differences between downshifted and unshifted groups on Sessions 6–8, $Fs(1, 20) > 4.66$,

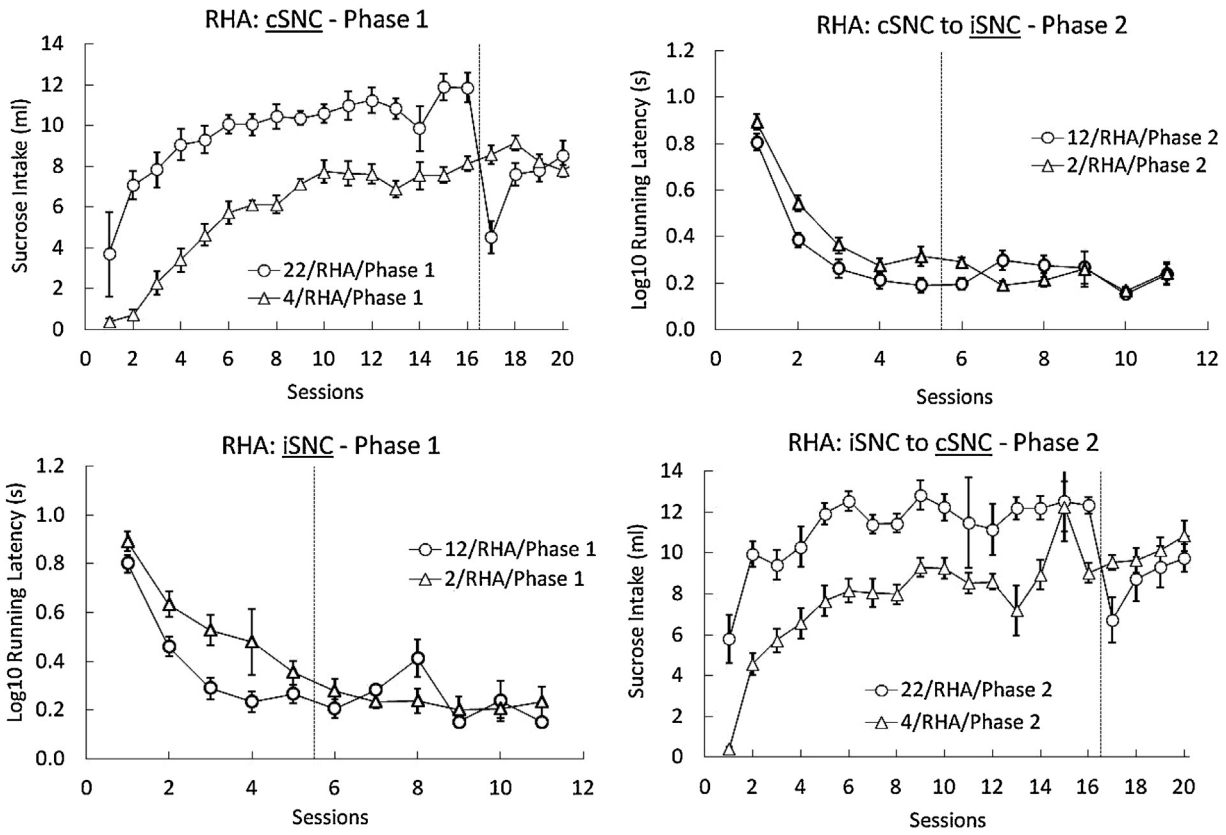

Fig. 1. Mean (±SEM) sucrose consumption or running latency (log10 transformation) in RHA-I rats during original training (Phase 1, left-hand panels) and transfer training (Phase 2, right-hand panels). Numbers if group labels represent the reward magnitude in the cSNC task (22% and 4% sucrose) and iSNC task (12 and 2 pellets per trial). The results from the iSNC task on Phase 1 are reproduced with permission from Cuenya et al., The effect of partial reinforcement on instrumental successive negative contrast in inbred Roman high- (RHA-I) and low- (RLA-I) avoidance rats (Cuenya et al., 2012).

ps < 0.05. Notice that downshifted RHA-I animals performed below unshifted controls on Session 6 (first downshift session), but then the groups reversed on Sessions 7–8. LSD pairwise tests were also computed to compare downshifted vs. unshifted groups at each postshift session. For Phase 1, groups differed only on Session 8, $F(1, 20) = 5.10$, $p < 0.04$, whereas for Phase 2, they differed only on Session 7, $F(1, 20) = 7.56$, $p < 0.02$. Thus, the iSNC was present in both phases. Overall, these results provided no evidence of a transfer effects in RHA-I rats since both the cSNC and iSNC effects were detected in one postshift session in each phase.

3.2. RLA-I strain

3.2.1. cSNC task

The results for RLA-I rats in the cSNC and iSNC tasks are presented in Fig. 2 and were interpreted in terms of independent Phase × Contrast × Session analyses for each task. In the cSNC task, the preshift consummatory behavior was more stable during Phase 1 than during Phase 2, but the trend for higher consumption of 22% sucrose than 4% sucrose was similar in both phases. The analysis detected these differences in terms of a phase by session interaction, $F(6, 124) = 3.58$, $p < 0.003$. There were also simple main effects of contrast and session, *Fs* > 13.74, *ps* < 0.002. All other effects were nonsignificant. Performance during postshift sessions was drastically different across phases. Whereas there was a clear cSNC effect during Phase 1, such an effect was absent during Phase 2, after prior experience in the iSNC situation. The analysis detected this transfer effect in terms of a triple interaction between phase, contrast, and session, $F(2, 45) = 3.98$, $p < 0.03$. There was also a significant phase by session interaction, $F(2, 45) = 3.67$, $p < 0.03$, but all other effects were nonsignificant. LSD pairwise tests confirmed that downshifted RLA-I rats performed below unshifted controls during Phase 1, Session 17, $F(1, 20) = 6.01$, $p < 0.03$. Group differences on the other sessions were not significant. Unlike in Phase 1, downshifted and unshifted groups differed in none of the postshift sessions during Phase 2. LSD tests also showed that downshifted animals in Phase 1 performed significantly below downshifted animals in Phase 2 during Session 17, $F(1, 20) = 7.36$, $p < 0.02$, but not in any other session. However, unshifted groups did not differ in any of the postshift sessions across phases.

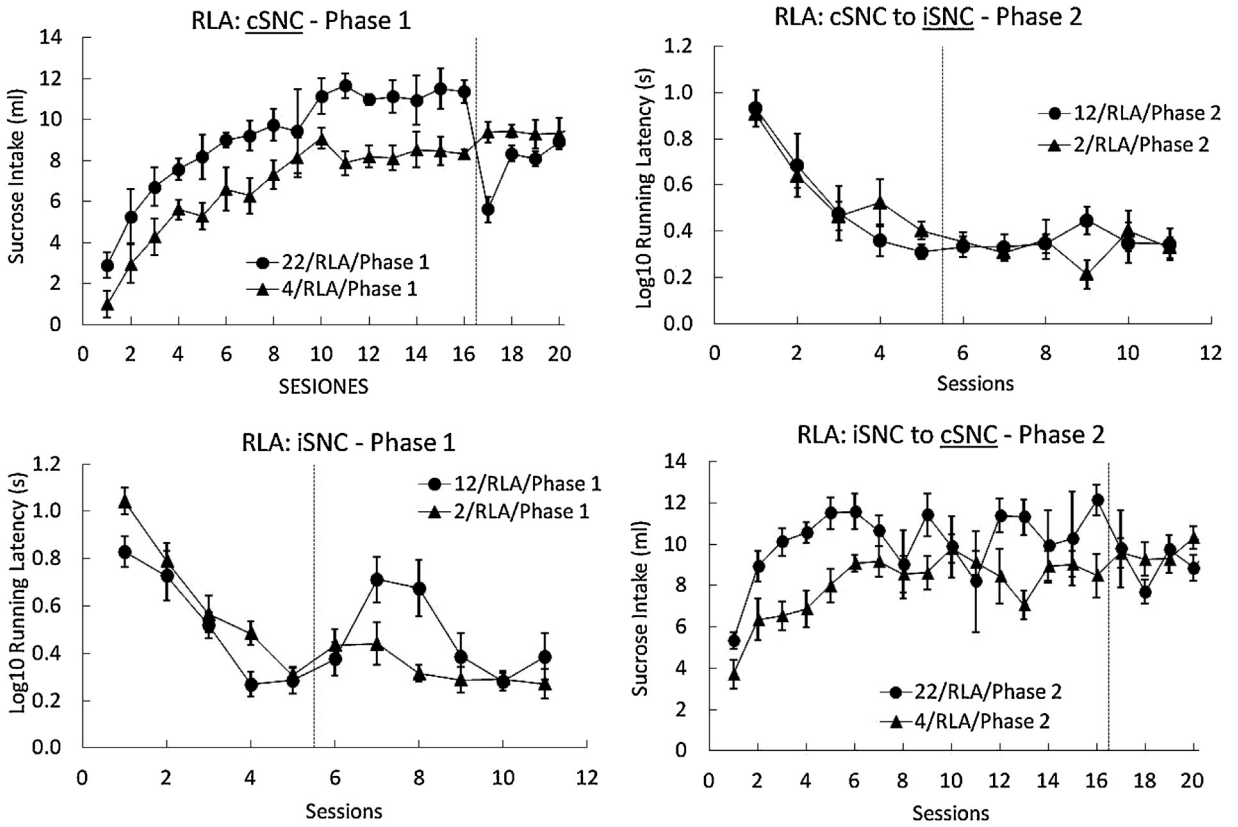

Fig. 2. Mean (±SEM) sucrose consumption or running latency (log10 transformation) in RLA-I rats during original training (Phase 1, left-hand panels) and transfer training (Phase 2, right-hand panels). Numbers if group labels represent the reward magnitude in the cSNC task (22% and 4% sucrose) and iSNC task (12 and 2 pellets per trial). The results from the iSNC task on Phase 1 are reproduced with permission from Cuenya et al., The effect of partial reinforcement on instrumental successive negative contrast in inbred Roman high- (RHA-I) and low- (RLA-I) avoidance rats (Cuenya et al., 2012).

3.2.2. iSNC task

Fig. 2 also shows the performance of RLA-I rats in the iSNC task. Preshift performance was similar across conditions, with a small tendency for animals to show lower latencies when running for 12 pellets than for 2 pellets. However, only the change across sessions was significant, $F(4, 80) = 93.68$, $p < 0.001$. As shown in Fig. 2, there was a clear iSNC effect on Phase 1, but an almost complete absence (except for the fourth postshift session) of the effect on Phase 2. This translated into a significant triple interaction, $F(3, 67) = 2.66$, $p < 0.05$. There were also significant session by phase and session by contrast interactions, $Fs > 2.84$, $ps < 0.04$, and a significant session effect, $F(3, 67) = 3.19$, $p < 0.03$. Additional simple main effects failed to reach significance. The sources of the triple interaction, determined by LSD pairwise tests, were the following. In Phase 1, downshifted vs. unshifted comparisons yielded significant differences for Sessions 7 and 8, $Fs(1, 20) > 6.91$, $ps < 0.02$; groups did not differ in the other sessions. In Phase 2, groups differed only on Session 9, $F(1, 20) = 5.45$, $p < 0.03$. Moreover, in comparisons of Phase 1 vs. Phase 2, downshifted groups differed only on Sessions 2 and 3 across, $Fs(1, 20) > 8.93$, $ps < 0.008$. Finally, unshifted groups did not differ across phases. Therefore, whereas RLA-I rats showed a clear transfer effect in the cSNC task, with prior expression of the iSNC effect effectively eliminated the cSNC effect, the reversed transfer effect was obscure by a significant iSNC effect in a late postshift session during Phase 2.

3.3. Strain comparisons

3.3.1. Phase 1

Strain × Contrast × Session analyses were computed on Phase 1 data separately for preshift and postshift sessions in each of the two tasks. For the cSNC task, preshift performance was higher for animals reinforced with access to 22% sucrose than with 4% sucrose, $F(1, 20) = 53.11$, $p < 0.001$. Consummatory behavior also increased across sessions, $F(6, 124) = 45.60$, $p < 0.001$. All other effects were nonsignificant, including the main effect of strain. As for postshift session data, there was a significant contrast by session effect, $F(3, 60) = 18.79$, $p < 0.001$. There were also contrast and session effects, $Fs > 13.19$, $ps < 0.003$. All other effects were nonsignificant, but the strain effect was the one that came closest to significance, $F(1, 20) = 3.81$, $p = 0.065$. LSD pairwise comparisons on the contrast by session interaction indicated that downshifted groups were significantly lower than unshifted controls on Sessions 17 and 18, $Fs(1, 20) > 10.03$, $ps < 0.006$. No differences were observed on other sessions.

The conclusion from these results is that both preshift performance and the cSNC effect were similar across RHA-I and RLA-I rat strains during original training in Phase 1.

The results for the iSNC task were the following. For preshift sessions, there was an interaction between session and strain, $F(2, 49) = 3.18$, $p < 0.05$. There were also main effects for contrast and session, $Fs > 10.34$, $ps < 0.005$. All other effects were nonsignificant, but the strain difference was closest to a significant value, $F(1, 20) = 4.12$, $p = 0.056$. LSD Pairwise tests on the strain by session interaction indicated that downshifted rats from both strains were significantly above unshifted controls on the second and third postshift sessions, $Fs(1, 20) > 4.87$, $ps < 0.04$. For postshift sessions, there was a contrast by session interaction, $F(4, 72) = 5.24$, $p < 0.002$. RHA-I rats responded significantly faster than RLA-I rats, $F(1, 20) = 15.05$, $p < 0.002$. There was also a significant reduction in latencies across sessions, $F(4, 72) = 8.49$, $p < 0.001$. All other effects were nonsignificant, with the session by strain interaction being closest to significance, $F(4, 72) = 2.47$, $p = 0.058$. LSD pairwise tests on the contrast by session interaction revealed that downshifted rats from both strains exhibited significantly higher latencies than unshifted controls on Sessions 7–8, $Fs(1, 20) > 5.55$, $ps < 0.03$. RHA-I rats ran generally faster than RLA-I rats in the runway. However, the apparently larger iSNC effect in RLA-I rats compared to RHA-I rats (compare the iSNC effect during Phase 1 in Figs. 1 and 2) did not receive statistical support.

3.3.2. Phase 2

Strain x Contrast x Session analyses were also computed for preshift and postshift sessions in each of the two tasks for Phase 2. In terms of the preshift performance in the cSNC task, the analysis indicated a significant contrast effect, $F(1, 20) = 24.16$, $p < 0.001$, and a significant increase across sessions, $F(5, 91) = 21.31$, $p < 0.001$. Other effects, including the main strain effect, were not significant. The postshift analysis revealed a significant strain by session interaction, $F(2, 42) = 3.71$, $p < 0.04$, and a session main effect, $F(2, 42) = 3.84$, $p < 0.03$. All other effects, including the main effect of strain, failed to reach significance. Despite a significant strain by session interaction, LSD pairwise tests failed to detect any difference across strains in any of the postshift sessions.

An analysis of the iSNC data from Phase 2 yielded the following results. In terms of preshift performance, again there was an indication that RHA-I rats ran generally faster than RLA-I rats, $F(1, 20) = 9.09$, $p < 0.008$. The session effect was also significant, $F(4, 80) = 122.76$, $p < 0.001$, but other effects were nonsignificant. The same strain effect was found in postshift sessions, with a significant main effect for strain, $F(1, 20) = 13.72$, $p < 0.002$. Other factors were nonsignificant. The overall results from Phase 2 show that strain effects were mostly observed in the instrumental task and were general, rather than specifically related to either the downshift or transfer manipulation.

4. Discussion

This study evaluated for the first time transfer effects across situations involving reward devaluation. The present results are in general agreement with our predictions. Based on prior research with Roman strains, we predicted stronger transfer effects in RLA-I rats than in RHA-I rats. However, the rather weak evidence of strain differences in SNC tasks during Phase 1 poses some interesting problems. This section centers on the discussion of three issues: (1) The transfer effects observed in RLA-I rats; (2) The apparent absence of evidence for transfer effects in RHA-I rats in which, nonetheless, SNC effects were actually observed; and (3) Additional behavioral differences between strains.

4.1. Transfer effects in RLA-I rats

RLA-I rats showed modest, but consistent transfer effects across phases. Transfer was positive in that exposure to one reward devaluation task attenuated the effects of a second reward devaluation task. Ross (1964), for example, manipulated the relationship between the target responses in each phase and observed either positive or negative transfer depending on their compatibility. When a running response was used in both phases, transfer was positive. However, when climbing was partially reinforced on Phase 1, but running was continuously reinforced on Phase 2, animals tended to exhibit components of climbing during extinction of the running response. The competition for expression between climbing and running resulted in negative transfer (i.e., enhanced extinction of running). Similar "regression" to patterns of behavior associated with situations involving reward uncertainty has been described in experiments involving changes in training context or target response (e.g., Boughner & Papini, 2008; Nation, Cooney, & Gartrell, 1979; Rashotte & Amsel, 1968). One implication of these results for the present experiment is that consummatory and runway running responses share a significant degree of compatibility, for otherwise the transfer effects observed in RLA-I rats would have been negative, rather than positive (i.e., enhanced, rather than reduced, contrast in one task after prior exposure to the other task).

Transfer was also symmetrical: Both tasks were influenced by prior exposure to the alternative task. Such symmetry occurred despite what a priori would appear to be striking differences between the two tasks. cSNC and iSNC differ in terms of at least the following factors: response (consummatory vs. anticipatory), reward (liquid vs. solid), context (conditioning box vs. runway), response topography (licking vs. running), number of trials per session (one vs. six), distribution of trials within a session (continuous vs. discrete), reward magnitude manipulation (solution concentration vs. pellet number), and spatial demands (localized vs. linear locomotion). cSNC and iSNC tasks also require the operation of different types of memory (Papini & Pellegrini, 2006; Pellegrini & Papini, 2007). The effects of the reward devaluation involve a failure of recognition memory (current sucrose concentration as different from the remembered one) in the consummatory task, whereas the

instrumental effect depends on cued recall, that is, the ability to reactivate a memory of prior devaluation events as the animal approaches the goal. These tasks are also known to involve different neural circuitry. For example, lesions of the hippocampus (Flaherty, Coppotelli, Hsu, & Otto, 1998) and nucleus accumbens (Leszczuk & Flaherty, 2000) affect behavior in the iSNC situation, but leave the cSNC effect relatively intact, whereas the opposite was reported after lesions of the gustatory thalamus (Sastre & Reilly, 2006). Strikingly, the same animals that show cSNC with sucrose solutions in the goal box of a runway fail to demonstrate iSNC in their running response of approaching the goal (Sastre, Lin, & Reilly, 2005). Despite these differences, common features seem to be sufficient to establish a connection between cSNC and iSNC effects. These common features include the use of different reward magnitudes and the fact that the large reward is devalued to a small magnitude at one point. We argue that emotional counterconditioning is also a process common to both cSNC and iSNC taks. Such emotional counterconditioning occurring during recovery from one devaluation event would build up resilience against the otherwise disrupting effects of frustration when a second devaluation event occurs, thus resulting in positive transfer. Consistent with this hypothesis, RLA-I rats also exhibit resilience in an emotional self-medication task: Preference for ethanol offered after extinction sessions was reduced by prior exposure to partial, as opposed to continuous, reinforcement training (Manzo et al., 2015). Thus, reward devaluation and partial reinforcement training seem to endow at least RLA-I rats with a degree of resilience that allows them to cope with similar reward devaluation situations (present experiment) or reduce their postsession preference for ethanol (Manzo et al., 2015).

4.2. Transfer effects in RHA-I rats

The situation is different for RHA-I rats, which showed both cSNC and iSNC effects on each phase, that is, whether the task was trained with (Phase 2) or without (Phase 1) prior experience in reward devaluation. The observation of both SNC effects in the present experiment contradicts previous reports according to which RHA-I rats failed to exhibit iSNC (Rosas et al., 2007) or showed faster recovery from cSNC (Gómez, Escarabajal et al., 2009), relative to RLA-I rats. Although speculative, these differences across studies could relate to sex. Whereas the current experiment used males, prior research was done with females. In a direct comparison, females showed greater strain differences than males in a one-way avoidance iSNC task (Donaire, Sabariego, Gómez, Fernández-Teruel, & Torres, 2013).

As mentioned in the introduction, there is extensive evidence that situations assessing anxiety responses tend to differentiate RHA-I from RLA-I rats. For example, RHA rats do not exhibit emotional self-medication with ethanol after appetitive extinction sessions (Manzo, Gómez, Callejas-Aguilera, Fernández-Teruel et al., 2014), and show impaired fear conditioning (López-Aumatell, Blázquez et al., 2009), fear-potentiated startle (López-Aumatelli, Vicens-Costa et al., 2009), and conditioned taste aversion (Durcan, Garcha, & Stolerman, 1988; Martin & Baettig, 1980). These results suggest that RHA-I rats are in tune with environmental events, whereas RLA-I rats are prone to react emotionally to changes in the environment. This is also shown in situations involving exploratory behavior, in which RHA-I rats are prone to explore and RLA-I rats tend to freeze (López-Aumatell, Vicens-Costa et al., 2009; Manzo, Gómez, Callejas-Aguilera, Donaire et al., 2014). We suggest here that these strain differences extend to the ability to profit from previous emotional learning, an ability that is suggested to be more salient for RLA-I rats than for RHA-I rats. When applied to the current results, this hypothesis suggests that whereas RHA-I rats can respond emotionally to reward devaluation (thus exhibiting both cSNC and iSNC effects), emotional counterconditioning is insufficient to control behavior (thus failing to exhibit transfer across tasks).

4.3. Additional behavioral differences between strains

The only consistent strain effects were found in the iSNC situation and they were unrelated to the reward downshift manipulation. Rather, RHA-I rats performed the runway task at higher speeds than RLA-I rats during both pre- and postshift sessions. Similar strain differences in runway performance were reported in previous experiments with several dependent measures (Cuenya et al., 2012; Gómez et al., 2008; Gómez, de la Torre et al., 2009; Manzo, Gómez, Callejas-Aguilera, Fernández-Teruel et al., 2014; Rosas et al., 2007). These results may reflect strain differences in motor performance or in the incentive value of rewards. The possibility of motor performance differences seems unlikely in view of similar activity scores among the two strains in a home-cage test (Estanislau et al., 2013). However, there is evidence consistent with strain differences in incentive value. For example, RHA-I rats generally show better performance than RLA-I rats when instrumental behavior is rewarded by drugs of abuse (e.g., morphine, cocaine, and amphetamine), a result suggesting strain divergence in mesolimbic dopaminergic transmission (Giorgi, Piras, & Corda, 2007).

5. Conclusions

RLA-I rats showed both iSNC and cSNC effects when first exposed to these tasks (i.e., without previous reward-devaluation experience), whereas these phenomena were reduced or absent in transfer animals previously exposed to the alternative task. Unshifted groups were not affected by previous experience. RHA-I rats, however, exhibited both SNC effects, but no evidence of transfer across tasks was observed. Despite extensive psychogenetic selection for low-avoidance learning (since the 1960s), which resulted in a high-anxiety phenotype, experience with reward devaluation in one situation appears to

immunize these animals against frustration induced by reward devaluation in a different situation. These results open an opportunity to study the neurobiology of resilience in animals prone to emotional vulnerability.

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