



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.

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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 gradual 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. Amstel'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. Amstel (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 Amstel'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). Amstel (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 Amstel, 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

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