

Reward Shifts in Forced-Choice and Free-Choice Autoshaping With Rats

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Successive negative contrast (SNC) involves a disruption of behavior when the paired reward is unexpectedly reduced from a large to a small amount, relative to a control always receiving the small amount. Five experiments with rats explored SNC in the Pavlovian autoshaping procedure in which a retractable lever is paired with the delivery of food pellets. In Experiment 1, a 12-to-2 pellet downshift either early in training (after 3 sessions) or late in training (after 20 sessions) yielded no significant evidence of SNC either in terms of lever pressing or goal entries. Experiment 2 showed that pre-session feeding (another form of reward devaluation) suppressed lever pressing in nonreinforced tests early in training. However, no statistical evidence of lever pressing suppression was found late in training. Pre-session feeding also suppressed lever pressing late in training if the test session included reinforcements. Experiment 3, using reward downshift, showed that adding a nontarget lever produced no statistical evidence of response suppression to the target lever during the downshift. Lever pressing to the target lever increased and goal entries tended to decrease after a 12-to-2 pellet downshift. Using a within-subject design and two target levers with distinct reward values (Experiment 4), reward downshift produced evidence of lever pressing enhancement in single-lever trials, but lever pressing suppression and a switch in preference to the unshifted lever in nonreinforced free-choice trials. Experiment 5 replicated these within-subject SNC effects, but found only modest evidence for a successive positive contrast effect in free-choice behavior. These results suggest that autoshaping in rats may induce response invigoration in forced-choice situations, but response suppression in free-choice situations.

Keywords: reward devaluation, successive negative contrast, free choice, forced choice, autoshaping

Tinklepaugh (1928) and Elliott (1929) provided some of the earliest evidence on the role of expectancy in associative learning. Tinklepaugh found that monkeys refused to eat a less-preferred piece of lettuce while expecting a more-preferred banana; similarly, Elliott showed that rats trained to solve a complex maze for highly rewarding bran mash cereal increased errors after finding low-value sunflower seeds instead. Both lettuce (for monkeys) and sunflower seeds (for rats) were sufficiently rewarding on their own, as shown by the performance of control conditions in each experiment, but were less rewarding when a more valuable reward was expected. Devaluation procedures such as these, in which the expectancy of a valued outcome is violated in some way, help us understand the components of associative learning and highlight

the relative value of rewards (i.e., incentive relativity; Flaherty, 1996).

Elliott's (1929) procedure eventually became known as successive negative contrast (SNC; Spear & Hill, 1965; Zeaman, 1949). In a typical SNC experiment, rats receive access to a large reward for a series of daily preshift sessions followed by postshift sessions in which the reward is substantially lower in quality or quantity. When compared with a control group that received only the small reward, downshifted animals exhibit response suppression during one or a few sessions, followed by a recovery of behavior to the level of unshifted controls. Because the original experiments involved instrumental behavior (i.e., traversing a maze or runway), the effect is known as instrumental SNC (iSNC). The consummatory version of this effect, cSNC, has received substantial attention in recent decades (Flaherty, 1996; Papini, Fuchs, & Torres, 2015). In the cSNC situation, independent groups are typically exposed to short sessions of free access to either 32% sucrose or 4% sucrose; subsequently, the former group is exposed to a 32-to-4% sucrose downshift, whereas the latter remains at 4% sucrose as an unshifted control. Reward downshift leads to transient response suppression (Flaherty, 1996) and it has consequences that implicate negative emotion (Amsel, 1992; Papini & Dudley, 1997; Papini et al., 2015). For example, response suppression is correlated with elevated corticosterone levels (Mitchell & Flaherty, 1998; Pecoraro, de Jong, & Dallman, 2009), fever (Pecoraro, Ginsberg, Akana, & Dallman, 2007), and reduction in sensitivity to physical pain (Jiménez-García et al., 2016; Mustaca & Papini, 2005); it is reduced by benzodiazepine anxiolytics (Flaherty, Coppotelli, & Potaki, 1996; Flaherty, Grigson, & Rowan, 1986), ethanol (Becker

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& Flaherty, 1982; Kamenetzky, Mustaca, & Papini, 2008), and cannabinoid agonists (Genn, Tucci, Parikh, & File, 2004); and it is modulated by opioids (Pellegrini, Wood, Daniel, & Papini, 2005; Wood, Daniel, & Papini, 2005; Wood, Norris, Daniel, & Papini, 2008). Response suppression after reward downshift is also attenuated by amygdala disruption (Kawasaki, Annicchiarico, Glueck, Morón, & Papini, 2017; Kawasaki, Glueck, Annicchiarico, & Papini, 2015). Downshifted animals learn a new response that allows them to escape from the downshift location (Daly, 1974; Norris, Pérez-Acosta, Ortega, & Papini, 2009). Furthermore, voluntary oral consumption of ethanol and chlordiazepoxide solutions (both reducing SNC when administered systemically, see above) selectively increase following reward devaluation relative to pre-shift sessions, to unshifted controls with access to these anxiolytic solutions, or to downshifted animals receiving access to water (Manzo, Donaire, Sabariego, Papini, & Torres, 2015; Manzo et al., 2014).

There are conditions under which the SNC effect fails to occur in rats. For example, rats trained in a runway to consume sucrose solutions in the goal box later show no SNC in the alley when sucrose concentration is downshifted (e.g., Rosen & Ison, 1965). Interestingly, animals that failed to show evidence of anticipatory response suppression in the alley later rejected the downshifted sucrose reward in the goal box (Flaherty & Caprio, 1976; Sastre, Lin, & Reilly, 2005). This puzzling result suggests a dissociation between different measures of behavior in a reward devaluation situation. In our lab we encounter similar problems in a different situation: autoshaping with rats (Papini, Ludvigson, Huneycutt, & Boughner, 2001; Pellegrini & Papini, 2007). Autoshaping is a Pavlovian procedure in which the presentation of a lever is paired with the delivery of food pellets in a response-independent manner. Although the procedure is Pavlovian, omission procedures in which pressing the lever leads to withholding the reward impair the response (e.g., Davey, Oakley, & Cleland, 1981). This result suggests that once lever pressing starts, the response-reward instrumental contingency acquires some control over behavior.

Implementing a reward downshift in the autoshaping situation has produced inconclusive results. In one experiment, a 12-to-1 pellet devaluation led to an SNC effect, but unlike in many runway experiments, the effect developed slowly over several sessions (Papini et al., 2001). Runway SNC has also been reported in some cases to develop gradually (Di Lollo & Beez, 1966) and to be extended over many trials (Adamson & Gunn, 1969). Nonetheless, autoshaping experiments revealed other learning phenomena involving reward devaluations, including increased lever pressing after surprising nonreward in early extinction trials and during partial reinforcement acquisition (Anselme, Robinson, & Berridge, 2013; Dudley & Papini, 1995; Glueck, Torres, & Papini, 2018; Thomas & Papini, 2001), increased resistance to extinction after training with a small, rather than a large reward (Papini et al., 2001), and increased resistance to extinction after training with partial rather than continuous reinforcement (Boughner & Papini, 2006). The autoshaping SNC experiment described above involved a relatively long preshift training phase, a result consistent with accounts that well-trained anticipatory responses can become automatic and fall under the control of stimulus value, rather than outcome value (e.g., Adams & Dickinson, 1981; Dickinson & Balleine, 1994). This is often characterized as a shift from action (expectancy dependent) to habit (stimulus-response control). Ha-

bitual behavior presupposes insensitivity to the emotional consequences of reward devaluation described above for the SNC task. Other reward devaluation procedures, such as posttraining pairing with a toxin or pre-session feeding, have shown response suppression effects when administered early in training, but not after extensive training (Adams, 1982; Leong, Berini, Ghee, & Reichel, 2016; Yin, Knowlton, & Balleine, 2004; for examples of persistent sensitivity to outcome devaluation, see Colwill & Rescorla, 1986). The action-habit distinction has received little attention in the SNC literature.

Experiment 1

Experiment 1 tested the hypothesis that the amount of training determines the emergence of the SNC effect in autoshaping. In previous experiments in which we recorded both lever presses (sign tracking) and goal entries (goal tracking), we noticed that whereas lever pressing tends to increase monotonically across acquisition sessions, goal entries increased during the initial training sessions and then decreased to a low level (e.g., Torres, Glueck, Conrad, Morón, & Papini, 2016). Figure 1 shows the performance of rats in a previous experiment according to the two dependent variables used in the present experiments (Glueck et al., 2018, Experiment 7). As shown in Figure 1, goal entries typically peak during the initial 2–6 sessions, with 10 trials per session; thereafter goal entries decreased and remained at very low levels, not even changing during autoshaping extinction (extinction is not shown in Figure 1). Unlike in other labs (e.g., Flagel, Watson, Robinson, & Akil, 2007; Robinson, Yager, Cogan, & Saunders, 2014; Sarter & Phillips, 2018), the rats we have used in our experiments have never shown a monotonic function in goal entries analogous to lever pressing. Based on this observation and on the notion that goal entries represent food anticipation (e.g., Morrison, Bamkole, & Nicola, 2015), we hypothesized that changes in goal entries reflect the action-to-habit transition and therefore scheduled the reward downshifts to occur either after three (early) or 20 (late) sessions of autoshaping training in inde-

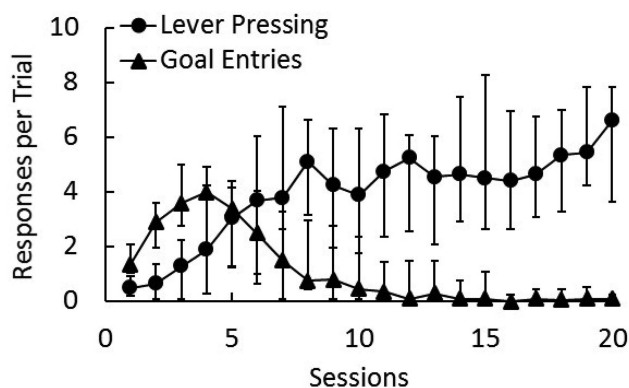


Figure 1. Autoshaping performance (medians \pm interquartile ranges) of naïve female Wistar rats ($n = 20$) trained under similar conditions as those used in the present experiments, except for the following. There were 10 trials per session (instead of 6 here) and each trial ended with the delivery of five food pellets (rather than 12 or 2 pellets here). Lever pressings and goal entries were recorded as in the present experiments. Data from Glueck et al. (2018, Experiment 7).

pendent groups. If our presumption was correct, we should see evidence of SNC in the early condition, but not in the late condition.

Method

Subjects. The subjects were 30 male, experimentally naïve, Wistar rats bred from breeders purchased from Harlan Labs (Indianapolis, IN), with ad libitum weights averaging 411.8 g ($SEM \pm 4.8$ g). Animals were 90 days old when food deprivation was introduced. Rats were housed in individual wire-bottom cages with an enrichment retreat and water always available. The colony room was maintained on a 12 h light/dark schedule (light on at 07:00 h) with constant temperature (22–23 °C) and humidity (50–65%). At 90 days of age, rats were gradually deprived of food to 81–84% of their ad libitum weight; this deprivation level was maintained throughout the experiment by supplementary food provided between 15 and 60 min after the daily training session. The sex of the animals allocated to each of the experiments reported in this article depended on availability. Animals were run simultaneously.

Apparatus. Conditioning took place in four standard operant chambers (MED Associates, St. Albans, VT), each enclosed in a cabinet to attenuate sound. The cabinets were equipped with a house light (GE 1820), a fan to promote airflow, and a speaker to emit white noise. Noise of the fan and speaker combined registered 80.1 dB (sound pressure level, Scale C). The conditioning boxes measured 20.1 × 28 × 20.5 cm (W × L × H), with the floor made of 0.4-cm diameter stainless steel bars spaced 1.6 cm apart. A pan filled with corncob bedding rested underneath the bars to collect droppings, which were removed between subjects. The external pellet hopper dispensed 45-mg precision food pellets (Bio-Serv, Flemington, NJ) into a food cup located 2 cm from the floor and at the center of the front wall. The food cup was equipped with photocells that captured head entries to automatically record goal entries. Two stainless steel retractable levers were located 1 cm from either side of the food cup and 6 cm from the floor, but only the left lever was used in this experiment. Levers were set to be depressed with minimum force so that virtually any response directed at the lever would likely be detected (Davey et al., 1981). A computer controlled the sequence and timing of events and the administration of rewards throughout the experiment, and automatically recorded each lever press (sign-tracking behavior) and entry into the food cup (goal-tracking behavior).

Procedure. Autoshaping acquisition training began the first day all rats were within their food-deprived weight range. No pretraining was administered as rats in these experiments readily find and eat pellets, and interact with the lever during the initial session. No left-over pellets were recorded in any of the sessions in this series of experiments. Additionally, the aim was testing the impact of the downshift early in acquisition, thus providing no pretraining guaranteed that there was little opportunity to develop habitual behavior. Since autoshaping is a Pavlovian task, rats were not required to do anything to obtain reinforcement, but they still regularly approached and pressed the lever. Rats were matched for ad libitum weight and then randomly assigned to one of three groups: early, late, and small ($n = 10$). Previous experiments based on between-groups designs with autoshaping from our lab have typically included at least eight subjects per group (for a recent example, see Glueck et al., 2018). Therefore we aimed at including

at least this number of subjects and more whenever possible in all the experiments in this series. All groups received one session per day. Group Small served as an unshifted control for both early and late. Each session consisted of six trials wherein one lever was presented for 10 s followed by pellet delivery (either 12 or 2 pellets, depending on the group). A variable intertrial interval (ITI) averaging 90 s (range: 60–120 s) separated successive trials. Similar intervals were inserted before the first trial and after the last trial of each session. The experimental groups first received preshift training for either three (early) or 20 sessions (late), where each lever presentation was followed by the delivery of 12 pellets. Following preshift, both experimental groups transitioned into the downshift phase where the same lever predicted the delivery of two pellets for 10 additional sessions. The unshifted control group received pairings between the lever and two pellets (small) for 30 sessions. The design is described in Table 1.

Two dependent variables were selected for analysis: lever presses and goal entries. Due to violation of the normality assumption in some cases, data from all the experiments reported in this article were analyzed using the nonparametric tests for dependent or independent samples, as required by the designs of each experiment. For consistency, data are plotted in terms of medians and interquartile ranges (IQRs) in all the figures. In Experiment 1, data were subjected to independent-sample Mann–Whitney tests and dependent-samples signed-rank Wilcoxon’s tests. IBM SPSS Statistics 24 was utilized for analyses across all experiments with an alpha value set at the 0.05 level. All tests were two-tailed. Effect sizes for the Mann–Whitney and Wilcoxon’s tests were calculated according to the formula $r = z/\sqrt{N}$ (Fritz, Morris, & Richler, 2012) using the online calculator (<https://www.ai-therapy.com/psychology-statistics/effect-size-calculator>). The Friedman test for k dependent samples was occasionally used in some experiments in this series; in that case, effect size was estimated using Kendall’s W in SPSS. All effect size values are reported as positive numbers for clarity. In Experiment 1, separate analyses were conducted to determine group differences in responses to the 12-versus two-pellet levers, using the final two preshift and first two postshift sessions, for both lever presses and goal entries. A look at the performance of rats in the entire experiment suggested that no relevant information was lost by restricting the analyses in this manner.

Results and Discussion

The overall performance was consistent with previous experiments from our lab (e.g., Figure 1). First, lever pressing increased monotonically across sessions in all groups, whereas goal entries

Table 1
Experimental Design Used in Experiment 1

| Group | n | Preshift | Postshift |
|-------|-----|----------|-----------|
| Early | 10 | (3) L12 | (10) L2 |
| Late | 10 | (20) L12 | (10) L2 |
| Small | 10 | (20) L2 | (10) L2 |

Note. All animals were adult males. The number of preshift and postshift sessions is given in parentheses. Each lever presentation (L) was reinforced with either 12 or two pellets per trial, depending on the group and phase of training.

peaked early in training and then decreased to remain at a low level for the rest of the experiment. Second, the 12-to-2 pellet downshift had little impact on either lever pressing or goal entries, whether the shift occurred early or late in training. Third, there was a tendency for rats to lever press more for two pellets than for 12 pellets during preshift sessions, but the opposite was true for goal entries. Figure 2 shows the results in terms of the two sessions preceding and following the downshift manipulation. Two comparisons were analyzed. First, for both preshift and postshift data, we compared downshifted versus unshifted groups (between-subjects analyses), whether early or late in training (unshifted animals served as controls for both downshifted groups). Second, we also compared preshift versus postshift results for each group separately (within-subject analyses).

When the early downshifted versus unshifted groups were compared, rats lever pressed more for two pellets than for 12 pellets in preshift, $U = 2.2$, $p = .03$, $r = .48$, but there was no statistical evidence of this difference in postshift responding, $U = 40.0$, $p = .45$, $r = .17$ (Figure 2A). Additionally, there was no evidence of differences in goal entries either during preshift, $U = 37.5$, $p = .34$, $r = .21$, or postshift, $U = 37.5$, $p = .35$, $r = .21$ (Figure 2B).

For the late comparisons, there was no evidence of a difference in lever pressing during either preshift or postshift sessions, $U_s > 35.0$, $ps > .28$, $rs < .25$ (Figure 2C). Rats checked the goal more frequently during 12-pellet lever presentations in preshift and postshift sessions, but the difference failed to reach significance, $U_s > 26.0$, $ps > .06$, $rs < .42$ (Figure 2D). Thus, a downshift in reward magnitude was insufficient to significantly disrupt responding to the lever or goal either early or late in training.

Second, we compared preshift versus postshift performance for each group. Of all the comparisons tested, the only significant one was an increase in goal entries from preshift to postshift in Group 12-2 for the early condition (Figure 2B), $z = -2.81$, $p = .01$, $r =$

.63. (For all other comparisons: $z_s < -1.94$, $ps > .05$, $rs < .44$.) Because the early condition coincides with the rapid change in goal entries during early acquisition, this effect is interpreted as a result of acquisition, rather than reward devaluation.

Several possible explanations can account for these results. The simplest one suggests that response suppression was not observed because these reward magnitudes did not control behavior differentially. For example, in the late condition, differences in lever presses before the downshift were not significant and thus it is not surprising that the downshift did not affect this response. This explanation would not work for lever pressing in the early condition, which showed preshift differences, but no evidence of a postshift effect. It is also possible that detecting a change in pellet quantity involves a delay that degrades the effect. Downshifted rats have learned to eat 12 pellets and, presumably, it is not until they eat the two pellets available after the downshift that they actually experience the change. By contrast, a change in reward quality (lettuce instead of banana) or in reward consumption (32-to-4% sucrose downshift) is probably detected faster (Flaherty, 1996). While plausible, this account fails to explain the effects on lever pressing during free-choice trials, as described in Experiments 4-5. It is also possible that SNC would be detected by a response other than those that were recorded. Rats show a variety of responses directed at the lever in the autoshaping procedure (Davey & Cleland, 1982). Although the force required to detect a response was adjusted to the minimum in these experiments, it is possible that recording some of them would have provided a different picture. However, the fact that lever pressing was sensitive to reward devaluation in free-choice trials (Experiments 4-5) suggests that, with the training parameters used here, it was possible to detect the SNC effect. The action-habit hypothesis also fails to accommodate these results; no effects of the reward downshift manipulation were observed either early or late in training, in

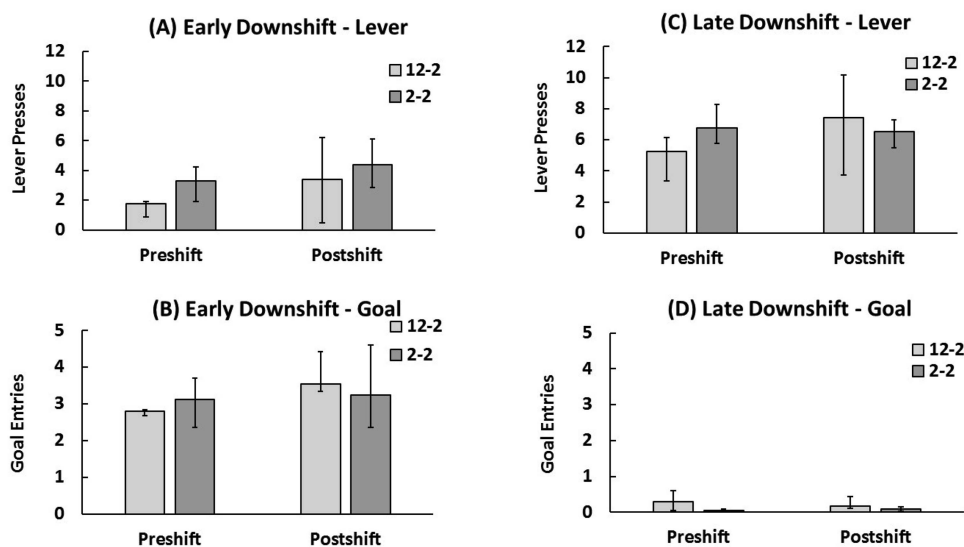


Figure 2. Medians (\pm interquartile range) lever presses (top) and goal entries (bottom) over the last two sessions prior to (preshift) and following (postshift) reward downshift. The left column shows the results for the early downshift, whereas the right column shows the results for the late downshift. Notice that the ordinates may vary across figures, although they were kept constant within each experiment; scale values were set to maximize the visualization of differences among conditions. See text for statistical results; Experiment 1.

either sign or goal tracking. Moreover, whether goal tracking was at its peak (early) or asymptotic (late), the downshift had no detectable effect on any of the response measures. One possibility is that the autoshaping procedure is fundamentally different from other situations that yield reliable iSNC and cSNC (Flaherty, 1996), and that it is relatively insensitive to detect an action-to-habit transition (Adams & Dickinson, 1981).

Experiment 2

Experiment 2 tested the claim that autoshaping may be insensitive to the action-habit transition using a different reward-devaluation procedure. Contemporary rodent models have employed a variety of techniques to study the role of reward devaluation in learning. One way to devalue an expected outcome is to pair the outcome with sickness following acquisition training, either by forced rotation to induce dizziness (Holland & Rescorla, 1975) or by administration of a toxin such as lithium chloride (LiCl) to induce gastrointestinal discomfort (Adams, 1982). LiCl was used to devalue sucrose reward in an autoshaping experiment with rats and its effects were measured in terms of sign versus goal-tracking responses (Morrison et al., 2015). Reward devaluation reduced the frequency of goal entries, but had no significant effect on lever pressing (see also Nasser, Chen, Fiscella, & Calu, 2015). Another option is to decrease motivation to work for a reward by allowing pre-session free access to the reward before behavioral testing (Balleine, 1992). Typically, the results of these devaluation manipulations are assessed in the absence of the appetitive reinforcer previously subjected to devaluation. These procedures are similar to SNC in that animals exposed to devaluation exhibit response suppression relative to nondevalued controls. In all cases, the reward undergoes a reduction in incentive value, whether because it is downshifted in quality or quantity (from banana to lettuce or from 12 to 2 pellets), because the reward's hedonic value is reversed (from appetitive to aversive after pairings with a toxin), or because motivation to respond for the reward is reduced (pre-session feeding). Experiment 2 examined the effects of pre-session feeding on autoshaping, which, to our knowledge, has not been tried before. The goal was to determine whether the autoshaping parameters we are using make this preparation sensitive to reward devaluation. The effects of pre-session feeding on autoshaping behavior were assessed with food either present or absent during the session in a within-subject fashion. Both testing conditions were implemented to maximize the potential for finding reward devaluation effects. In food-deprived rats, it was expected that providing pre-session feeding would not be sufficient to produce significant satiety. In addition, food-deprived rats that receive training show resistance to satiation, that is, they sometimes continue to respond even when given free access to food (Capaldi & Myers, 1978; Morgan, 1974). Therefore, testing with food present was introduced to maximize the devaluation effect.

Method

Subjects and apparatus. The subjects were 32 experimentally naïve Wistar rats (16 males, 16 females). We assigned a similar total number of subjects to each of these experiments; however, the use of within-subjects designs increases the power to

detect effects. Male ad libitum weights averaged 439.7 g ($SEM \pm 6.7$ g); female ad libitum weights averaged 279.5 g ($SEM \pm 4.4$ g). Animals were 90 days old when food deprivation was introduced. Rats were housed, maintained, and trained under the same conditions and in the same apparatus described in Experiment 1. Animals were run simultaneously.

Procedure. Acquisition training proceeded similarly to the previous experiment, with the computer controlling lever presentations and recording lever presses and goal entries. Rats were matched by ad libitum weight and randomly assigned to one of two groups ensuring eight males and eight females per group: early or late. Group names refer to the point in training when rats received a reward devaluation manipulation. Acquisition training lasted for either three (early) or 20 (late) sessions. Each 10-s lever presentation predicted the delivery of 12 pellets. There were six trials per session separated by a mean ITI of 90 s (range: 60–120).

Following acquisition, devaluation occurred in blocks of two sessions, for a total of six sessions. On the first devaluation session (Session 4 for early; Session 21 for late), rats were placed in the conditioning box for 5 min; half the animals found 42 pellets that they could eat freely (pre-session feeding), whereas the other half were just exposed to the box without pellets (post-session feeding). At the end of the 5 min, animals were relocated to their home cage for 2 min and then placed into the conditioning box for the autoshaping session. This session proceeded identically to acquisition, including pellet delivery (reinforced testing). Following the session, all animals were removed from boxes and placed in their home cages for 2 min, and then were put back into the conditioning boxes for 5 min. Animals that did not receive pre-session feeding were given access to 42 pellets (post-session feeding), whereas animals that had received pre-session feeding remain in the empty box for 5 min. After 5 min, animals were returned to the home cage. On the second devaluation session (Session 5 for early; Session 22 for late), the sequence was identical except that animals that had received post-session feeding now received pre-session feeding, whereas animals that had received pre-session feeding now received post-session feeding.

On the third and fourth devaluation sessions (Sessions 6–7 for early; Sessions 23–24 for late), the procedure was identical to that used in the previous two devaluation sessions, except that the autoshaping session was conducted without food delivery (non-reinforced testing). Finally, on the fifth and sixth devaluation sessions (Sessions 8–9 for early; Sessions 25–26 for late), the procedures were identical to those used on the first and second devaluation sessions. The design is described in Table 2, with each group of 16 animals divided to show pre-versus postshift feeding counterbalancing.

The same 45-mg food pellets delivered during autoshaping sessions were used in pre-session and post-session feeding. Pilot data indicated that rats could eat 42 pellets during a 5-min session, but this amount was not enough to satiate them (i.e., post-trial feeding was needed to maintain their weights). Moreover, 42 pellets was the total amount delivered per session in Experiments 4 and 5 (see below). Responses were collapsed within blocks of sessions to compare behavior following pre-session feeding (devaluation manipulation) and post-session feeding (control condition). Thus, the devaluation (pre-session feeding) and control conditions (post-session feeding) were run according to a within-subject de-

Table 2
Experimental Design Used in Experiment 2

| <i>n</i> | Acquisition | Tests 1 and 3 | | Test 2 | |
|----------|-------------|------------------|------------------|-----------------|-----------------|
| 8 | (3) Early | Pre → L12 → Box | Box → L12 → Post | Pre → L0 → Box | Box → L0 → Post |
| 8 | (3) Early | Box → L12 → Post | Pre → L12 → Box | Box → L0 → Post | Pre → L0 → Box |
| 8 | (20) Late | Pre → L12 → Box | Box → L12 → Post | Pre → L0 → Box | Box → L0 → Post |
| 8 | (20) Late | Box → L12 → Post | Pre → L12 → Box | Box → L0 → Post | Pre → L0 → Box |

Note. In each subgroup, four animals were adult males and four adult females. Subgroups were combined by averaging responses from pre-session feeding (pre) and from post-session feeding (post), whether in reinforced test sessions (L12) or nonreinforced test sessions (L0). Thus, $n = 16$ for each of the two groups (early and late). The number of sessions before testing is given in parentheses in the Acquisition column.

sign. All other procedural features were as described in Experiment 1.

Results and Discussion

Within-subject analyses of lever pressing behavior were conducted using a series of Wilcoxon signed-ranks test. Figure 3 shows the results collapsed according to whether testing occurred under regular autoshaping training (reinforced tests pooled) versus in the absence of food (nonreinforced test).

Lever presses (Figure 3A) yielded the following results. For reinforced tests, there were no statistical differences in responding between pre-fed and post-fed conditions early in training, $z = -1.14$, $p = .26$, $r = .20$, but pre-fed responding was significantly lower than post-fed responding late in training, $z = -2.25$, $p = .02$, $r = .40$. This result indicates that pre-session and within-session feeding summated late in training to reduce lever pressing, although no evidence for that effect was observed early in training. By contrast, nonreinforced tests indicated significantly less responding in pre-fed than post-fed animals early in training, $z = -2.07$, $p = .04$, $r = .37$, but no statistical differences were observed late in training, $z = -0.08$, $p = .94$, $r = .01$.

Goal entries (Figure 3B) produced uniformly negative results in all comparisons, $z_s < -1.67$, $p_s > .09$, $r_s < .26$.

A previous autoshaping study involving reward devaluation using LiCl reported significant behavioral effects on goal entries, but not on lever pressing (Morrison et al., 2015). In Experiment 2, the results using pre-session feeding as a devaluation technique were just the opposite: devaluation affected lever pressing, but there was no evidence that it affected goal entries (see Figure 3B). These results suggest that not all devaluation procedures lead to similar behavioral outcomes (Holland, 2008). It appears, then, that although reward downshift, reward-LiCl pairings, and pre-session feeding may all be referred to as reward devaluation procedures, their behavioral consequences can be dissociated. Still, there are important procedural differences across relevant experiments that prevent meaningful conclusions beyond a call for caution in generalizing.

These results also show that lever pressing (but not goal entries) in autoshaping is sensitive to at least one reward devaluation procedure. The implication is that the absence of SNC in Experiment 1 cannot be attributed to some peculiar aspect of the autoshaping procedure used in these experiments. As in previous experiments involving reward devaluation, we observed an effect early in training, but not late in training in nonreinforced testing. This outcome is consistent with the action-habit hypothesis (Ad-

ams & Dickinson, 1981). However, unlike in most other demonstrations of this effect, there was a reward devaluation effect late in training, but only with reinforced testing. This interaction between the time of the devaluation (early vs. late) and the type of test (reinforced vs. nonreinforced) precludes simple explanations in terms of relative satiety and amount of training. The late effect observed here may be consistent with the action-habit distinction. It could be argued that after extensive training, to observe such a reward-devaluation effect requires a reactivation of the reward representation that can be accomplished more effectively in reinforced tests than in nonreinforced tests. Typically (e.g., Adams, 1982; Morrison et al., 2015), testing the effects of reward devaluation is done in the absence of the reward. This procedure tends to produce sensitivity to the devaluation early in training, but not late in training, as it was the case in the present experiment under nonreinforced testing conditions.

Experiment 3

Lever presentation as a reward signal is peculiar in that it involves the manipulation of a moving object. Rats may find this behavior rewarding, as suggested, for example, by experiments in which extensive nonreinforced exposure to a retractable lever reliably induced low, but persistent, levels of lever pressing in rats (Boughner & Papini, 2006). Therefore, we considered the possibility that rats continued to respond after a reward downshift simply because responding provides an alternative source of reward that increases in value when food amount is downshifted. Experiment 3 explored this hypothesis with the addition of a second lever that could act as a target, but had no reward history of its own. The presence of a second lever in this experiment is analogous to the presence of an additional response target in experiments on adjunctive behavior. For example, Thomka and Rosellini (1975) exposed rats to a reward downshift in a conditioning box in which they also had continuous access to water. Each of 30 cycles of a fixed-time 30-s schedule ended in six pellets for one group and two pellets for the other for eight sessions. A six-to-two pellet downshift led to an increase in water consumption above the level of unshifted controls always given two food pellets per cycle. If lever manipulation per se played a role in the absence of a SNC effect in Experiment 1, then the addition of a nontarget lever (NTL) may allow for reward downshift to lead to a greater lever pressing suppression to the target lever (TL) than is the case in the regular condition where no alternative lever is available. This hypothesis requires a comparison between condi-

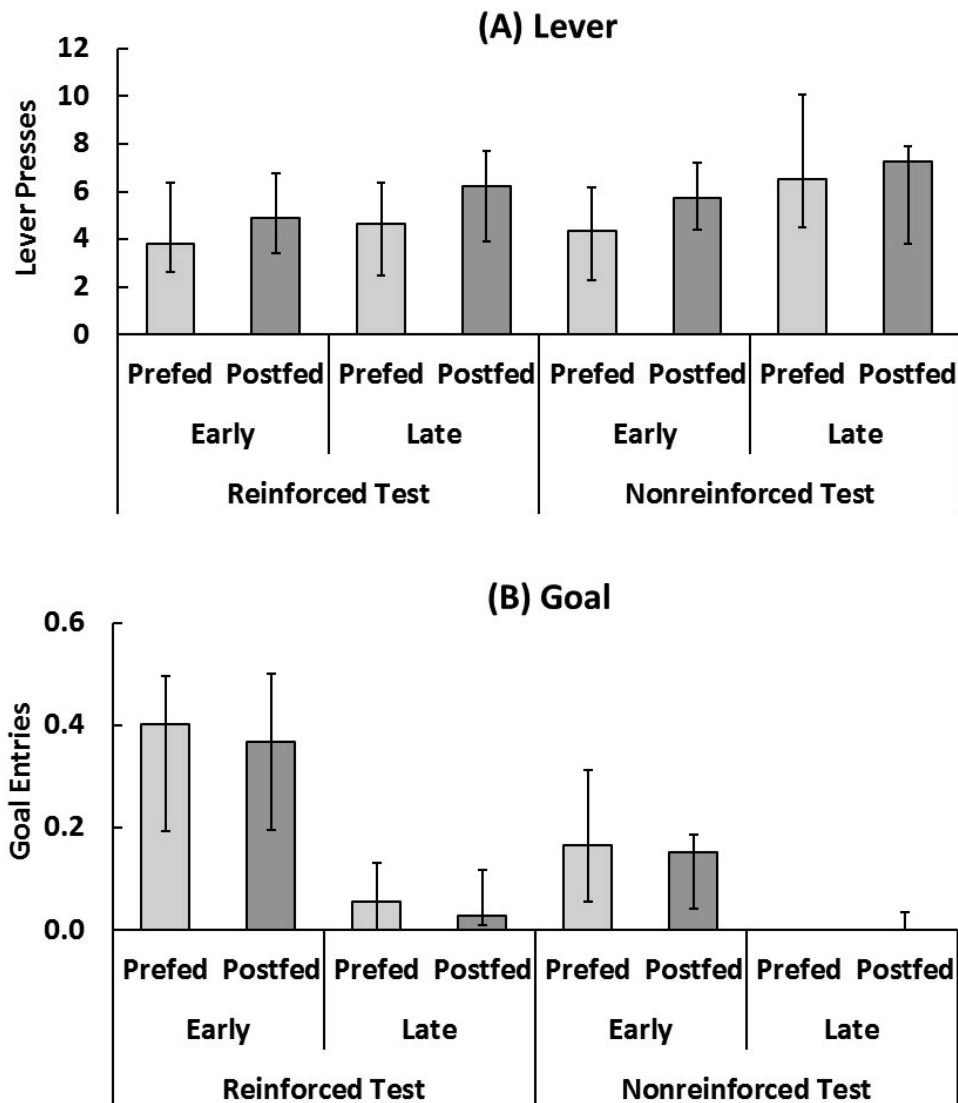


Figure 3. Median (\pm interquartile range) lever presses (top) and goal entries (bottom) over the two devaluation sessions in nonreinforced tests and the four devaluation sessions in reinforced tests. “Early” and “late” (between subjects) refer to the point during autoshaping training when animals were exposed to the devaluation procedure (pre-session access to food pellets). “Prefed” and “postfed” (within subjects) refer to the pre-session (reward devaluation) and postsession (control) feeding procedures. Notice that the ordinates may vary across figures, although they were kept constant within each experiment; scale values were set to maximize the visualization of differences among conditions. See text for statistical results; Experiment 2.

tions with and without NTLs; thus, no unshifted controls were included.

Method

Subjects and apparatus. The subjects were 23 experimentally naïve, male Wistar rats, with an average ad libitum weight of 394.2 g ($SEM \pm 5.3$ g). Animals were 90 days old when food deprivation was introduced. While three rats were bred in the Texas Christian University (TCU) vivarium, 20 were purchased directly from Harlan Laboratories (Indianapolis, IN). Housing,

maintenance, and training apparatus were as described in Experiment 1. Animals were run simultaneously.

Procedure. Subjects were randomly assigned to one of two groups matched for ad libitum weight. Both groups had a TL signaling reward delivery; Group Regular ($n = 11$) only had the TL present, whereas Group Extra ($n = 12$) had a second NTL added to the regular autoshaping procedure. Autoshaping training for all animals proceeded similarly to Experiment 1. The TL was associated with the delivery of 12 pellets, six trials per session, across 20 sessions in both groups; each trial was 10-s long and a 90-s variable ITI was used (range: 60–120 s). For Group Extra, a

second NTL was presented at the beginning of each session and remained available for the entire duration of the session. Interactions with the NTL were never reinforced, although if the NTL was pressed during a trial with the TL, the NTL response would have been paired with food delivery. TL versus NTL assignment was counterbalanced for right versus left lever position across animals. During Sessions 21–25, animals in both groups were downshifted and trained with the TL preceding the delivery of only two pellets. Responses to one or both levers, depending on the group, were recorded simultaneously during each trial. It was hypothesized that the NTL would provide an alternative activity for rats to engage in, especially during reward downshift sessions, thus allowing an SNC effect to emerge in terms of responding to the TL. The design is described in Table 3. Other procedural features were as in Experiment 1.

Results and Discussion

Wilcoxon signed-ranks test for dependent samples and Mann-Whitney tests for independent samples were used in the present experiment. Rats produced almost no responses to the NTL during trials, interacting with the TL significantly more during both preshift and postshift sessions, $z_s \geq -4.11$, $p_s \leq .01$, $r_s > .62$. However, comparisons between Groups Extra versus Regular in terms of their TL performance provided no statistical evidence of differences in any of the dependent variables, $U_s > 50$, $p_s < .21$, $r_s < .26$ (Figure 4A).

Interestingly, rats in both groups pressed the TL significantly more during the first two sessions after the 12-to-2 pellet reward downshift than they did during the final two preshift sessions, $z_s \geq -2.49$, $p_s \leq .01$, $r_s > .42$ (Figure 4A). A similar bias, but in the opposite direction (i.e., less responding in postshift than in preshift sessions) was observed in terms of goal entries (Figure 4B). Thus, goal entries decreased significantly from pre- to postshift in Group Extra, $z = -2.08$, $p = .04$, $r = .47$, and trended in that direction without reaching statistical significance for Group Regular, $z = -1.79$, $p = .07$, $r = .36$.

These results leave us with two conclusions. First, the presence of an additional lever made no difference during reward downshift. Second, not only did rats not suppress lever pressing, but they actually displayed significantly higher lever pressing and a lower level of goal entries after the downshift, relative to preshift sessions. In this experiment, both groups (extra and regular) were exposed to reward devaluation. Response invigoration after reward

Table 3
Experimental Design Used in Experiment 3

| Group | <i>n</i> | Preshift | Postshift |
|---------|----------|---------------------------|------------------------|
| Regular | 11 | (20) L12 [or R12] | (5) L2 [or R2] |
| Extra | 12 | (20) L12, R0 [or R12, L0] | (5) L2, R0 [or R2, L0] |

Note. All animals were adult males. In Group Regular, each presentation of the target lever was followed by the delivery of 12 pellets during preshift sessions and by 2 pellets during postshift sessions. In Group Extra there was a nonreinforced nontarget lever during preshift and postshift sessions. Lever assignment to the left or right target (L12 or R12, reinforced) or nontarget (L0 or R0, nonreinforced) condition was counterbalanced and is shown in brackets. For each phase, the number of sessions is shown in parentheses.

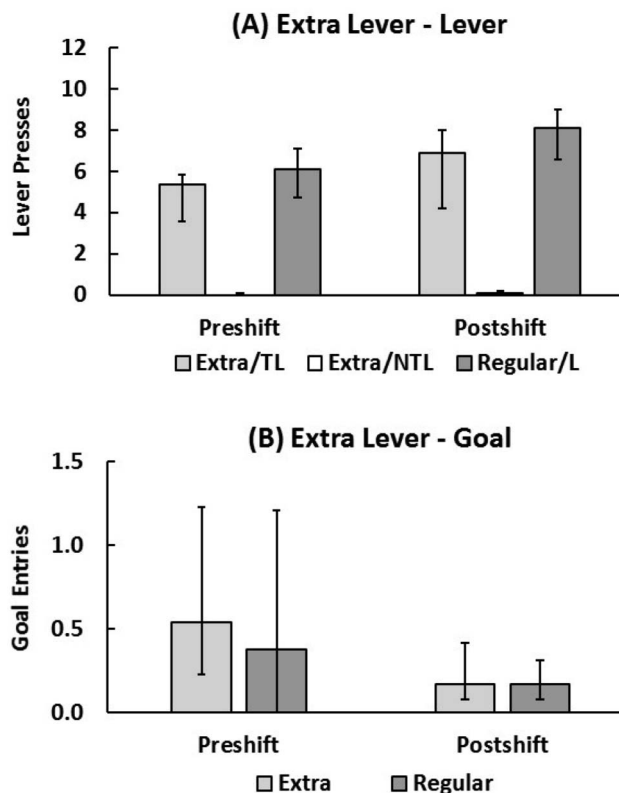


Figure 4. Median (\pm interquartile range) lever presses (top) and goal entries (bottom) over the two sessions before (preshift) and after (postshift) reward downshift. Groups differed in terms of having (extra) versus not having (regular) an extra, nontarget lever (NTL) available during the entire session. Pressing this NTL had no scheduled consequence. Notice that the ordinates may vary across figures, although they were kept constant within each experiment; scale values were set to maximize the visualization of differences among conditions. See text for statistical results; Experiment 3.

omission or devaluation has long been claimed to be a nonassociative property of frustration (Amsel & Roussel, 1952). Similar effects have also been observed in autoshaping with rats exposed to occasional nonreinforced trials (Dudley & Papini, 1995, 1997), in the transition from continuous reinforcement to extinction (Papini et al., 2001; Thomas & Papini, 2001; Torres et al., 2016), during partial reinforcement training (Anselme et al., 2013; Glueck et al., 2018; Torres et al., 2016), and after a reward downshift (Papini et al., 2001). As in the case of runway behavior, lever pressing in the autoshaping situation could also be sensitive to the invigorating effects of frustration. The following experiment explores another alternative-response option, except this time the alternative lever has its own reward history.

Experiment 4

One difference between Experiment 1 (where no evidence of reward devaluation was found) and Experiment 2 (where evidence of reward devaluation was observed) is the type of design: between-subjects versus within-subject design, respectively. Experiment 4 explored this dimension by implementing a reward downshift manipulation in a within-subject context. Animals were

trained with two levers, one paired with 12 pellets and the other with two pellets. Eventually, the 12-pellet lever was downshifted to two pellets while the two-pellet lever remained as the unshifted control. In addition to single-lever trials, animals were also exposed to occasional free-choice trials in which the two levers were simultaneously presented. No reward was delivered in free-choice trials.

SNC effects have been explored in free-choice situations with mixed results. In some maze studies, animals showed reduced running speeds after the downshift in forced choice situations (i.e., when there was a single alternative and the option was to respond or not), but exhibited no tendency to prefer the unshifted option when given a free choice (e.g., Spear & Spitzner, 1969). This result was considered puzzling, given that rats are known to learn to escape from situations associated with surprising reward reductions (e.g., Daly, 1974). If the downshifted option acquired aversive incentive value, then one would expect that faced with a choice between an option associated with downshifted reward and one associated with an unshifted reward of equal magnitude, animals would prefer the latter. Eisenberger, Frank, and Park (1975) trained one group to approach a stimulus for a large reward while a control group was training to approach the same stimulus for a small reward. Then, the large-reward group was downshifted whereas the small-reward group was left unchanged. SNC was apparent in this phase. Finally, the animals were given a choice between the arm in which they had received training (downshifted for one group and unshifted for the other) and a second, new arm. Both choices were reinforced with the small reward magnitude. In these trials, unshifted rats preferred the familiar arm over the new arm, whereas downshifted rats were indifferent in their choice. A similar design involving an upshift also yielded evidence of successive positive contrast (SPC) in terms of more frequent choice of the upshifted arm relative to the unshifted arm in two independent groups.

One problem with the design used by Eisenberger et al. (1975) is that choices were reinforced and thus it is difficult to ascertain whether group differences reflected the relative value of the two options or a combination of relative value and current reinforcement. Consistent with this possibility, two of the three experiments showed choices to be random during the first four-trial block of the choice phase. A second problem with this design is that, in the case of SNC, animals exposed to the downshift chose this option and the new option about equally often across trials; this can hardly be taken as evidence that the downshifted option had acquired aversive incentive value. Less ambiguous choice effects could be obtained in a within-subject design in which both options have a known reinforcement history, as done in the present Experiment 4.

In Experiment 4, a single group of rats received training with two levers (right [R], left [L]), each associated with different amounts of pellets (R12, L2 or R2, L12; counterbalanced across animals). Training involved single-lever trials in all sessions, except for 10 of them beginning at the end of the acquisition phase. In these 10 sessions, in addition to the single-lever trials, the last trial in the session was a nonreinforced free-choice trial in which the two levers were presented simultaneously and the animal was free to respond to either one or none of them. Thus, rather than looking at a measure of percentage of correct responses, we assessed the number of responses directed at each lever during these free-choice trials. Five of these sessions occurred before the

reward devaluation (preshift) and five after the devaluation (postshift). A session with only single-lever trials was interpolated between successive sessions with a free-choice trial. Therefore, this design can be described as a within-subject SNC procedure analogous to that used by Daniel, Wood, Pellegrini, Norris, and Papini (2008) in a consummatory situation.

The present design circumvented the two problems of the Eisenberger et al. (1975) experiment pointed out above. However, this procedure also introduced the potential for a direct comparison of the two reward magnitudes as typically done in simultaneous contrast experiments (Flaherty, 1996). During preshift training, such simultaneous contrast would have inflated the incentive value of the 12 pellets while reducing the value of the 2 pellets. As a result, a 12-to-2 pellet downshift could have a greater impact in a within-subject situation than in the between-subjects situation used in previous experiments. However, based on the response invigoration observed in previous experiments, we expected that the ability to compare outcomes within a single session would (a) increase lever pressing to the downshifted lever in forced-choice, postshift trials, and (b) switch preference to the unshifted lever in free-choice, postshift trials.

Method

Subjects and apparatus. The subjects were 32 experimentally naive, female Wistar rats all bred at the TCU vivarium, with an average ad libitum weight of 300.7 g ($SEM \pm 5.76$ g). Animals were 90 days old when food deprivation was introduced. Housing, maintenance, and training apparatus were as described in Experiment 1. Animals were run simultaneously.

Procedure. Autoshaping acquisition training was as in the previous experiments, except for the addition of a second lever with an associated reward magnitude for all animals. One lever predicted the delivery of 12 pellets, whereas a second lever was always followed by the delivery of two pellets. The assignment of a lever to one of the reward magnitudes was counterbalanced, such that 16 rats had the large, 12-pellet reward associated with the right lever and the two-pellet reward associated with the left lever, and 16 rats had the opposite arrangement. Rats were trained for a total of 27 sessions, receiving six trials per session, 3 right-lever and 3 left-lever trials, followed by their respective rewards, 12 or two pellets. Single-lever trials are referred to as forced-choice trials, that is, trials in which the animal can respond or not to the lever or goal. Each lever presentation lasted 10 s and trials were separated by a variable ITI averaging 90 s (range: 60–120 s). Beginning with Session 9, in addition to the six single-lever trials, every other session ended with a simultaneous free-choice trial, in which both levers were presented for 10 s and responses to each were recorded. Free-choice trials allowed rats to respond to one lever, to the other lever, or not to respond at all (notice that both levers were associated with the same goal, thus only one measure of goal entries was possible in free-choice trials). On Session 18, the lever previously associated with 12 pellets was downshifted to two pellets, whereas the original two-pellet lever remained unshifted. In downshifted sessions, animals were exposed to three forced-choice trials with each lever. In addition, a free-choice trial continued to be presented at the end of every other session, beginning on Session 19, to ascertain changes in lever preference following reward downshift, and continuing until Session 27, the final ses-

sion. Therefore, five free-choice trials were administered before the downshift (assessing the effect of reward magnitude on free choice) and five free-choice trials after the downshift (assessing the effects of reward downshift on free choice). The design is described in Table 4. Other procedural features were as described in Experiment 1.

Results

Within-subject analyses were conducted using the Wilcoxon signed-ranks test. Friedman tests for related samples were used for goal entries during free-choice trials. Forced-choice data were collected from preshift Sessions 9, 11, 13, 15, and 17 and from postshift Sessions 19, 21, 23, 25, and 27. Free-choice data also come from the same sessions, in each of which the last trial involved the nonreinforced presentation of both levers simultaneously. This selection of data allowed for an assessment of both forced-choice responding in single-lever trials and preference in free-choice trials in the same sessions.

Forced-choice trials. For lever presses (Figure 5A), there was no statistical difference between forced-choice responses to the 12- and two-pellet levers in preshift sessions, $z = -0.32$, $p = .75$, $r = .04$. During postshift sessions, however, there was a higher level of lever pressing in the downshifted, 12–2 pellet lever than in the unshifted, 2–2 pellet lever, $z = -2.29$, $p = .02$, $r = .28$. This result was due to an increase in lever pressing from pre- to postshift sessions in the downshifted lever, $z = -3.09$, $p = .01$, $r = .38$; no significant change in lever responding was observed in the unshifted lever, $z = -1.08$, $p = .28$, $r = .14$. These outcomes extend to within-subject conditions what has previously been observed in between-subjects designs (e.g., present Experiment 3; Dudley & Papini, 1995, 1997). In all these cases, reward downshift led to an increase in lever pressing relative to unshifted conditions in the autoshaping situation.

In terms of goal entries (Figure 5B), rats were checking the magazine significantly more during preshift trials with the two-pellet lever than with the 12-pellet lever, $z = -3.17$, $p = .01$, $r = .39$. Nonsignificant differences were observed in previous experiments with a single reward magnitude (see Figures 2B and 4B). This difference was nonsignificant during postshift trials, $z = -1.68$, $p = .09$, $r = .21$. Reward downshift was accompanied

by a reduction in goal entries for both levers, $z_s > -3.79$, $p_s < .01$, $r_s > .48$.

Free-choice trials. In free-choice trials the goal is to determine which of two alternatives, if any, attracts the most responding. Thus, the key measure was the distribution of lever pressing responses when both levers were simultaneously available, rather than, for example, response invigoration relative to some other trial. In preshift free-choice trials, rats pressed the 12-pellet lever significantly more than the two-pellet lever, $z = 2.78$, $p < .006$, $r = .35$ (Figure 5C). However, an analysis of lever presses on a trial-by-trial basis indicated dynamic changes across the five preshift trials. Differences between levers were not significant during the initial three free-choice trials, $z_s < -1.7$, $p_s > .10$, $r_s < .21$, but a clear difference in favor of pressing the 12-pellet lever was observed in choice Trials 4–5, $z_s > -2.62$, $p_s < .01$, $r_s > .33$.

Preference was reversed in postshift trials, when lever presses were significantly higher for the unshifted lever relative to the downshifted lever, $z = 2.06$, $p < .05$, $r = .26$ (Figure 5C). A trial-by-trial analysis shows, again, dynamic changes as lever preference was immediately reversed after the downshift event. During the initial two free-choice trials, animals now responded more to the unshifted lever than to the downshifted lever, $z_s > -2.03$, $p_s < .05$, $r_s > .26$. However, this effect was transient as performance was no longer statistically different between the two levers during the last three free-choice trials, $z_s < 1.52$, $p_s > .13$, $r_s < .20$.

Although the two levers were presented simultaneously in free-choice trials, there was a single magazine to which the animals could respond. As a result, the figure depicting goal entries has a single function (Figure 5D). As expected based on prior experiments (e.g., Torres et al., 2016), goal entries decreased across free-choice trials without being affected by reward downshift, $z = 3.12$, $p < .002$, $r = .41$. A trial-by-trial analysis using the Friedman test for dependent samples (with Kendall's W to estimate effect size) indicated that the response decrement across the 10 test trials was significant, $\chi^2 = 36.16$, $p < .01$, $W = 0.13$.

Discussion

These results demonstrate for the first time a striking reversal in responding during a session involving reward devaluation. Whereas lever pressing responding was enhanced by the downshift relative to preshift performance during forced-choice trials, the same lever that had elicited invigorated performance was rejected when the animal had an opportunity to choose between both levers in free-choice trials. We discuss these two results in the following paragraphs.

Within the same session involving reward devaluation, the sign-tracking bias was enhanced, whereas goal tracking was reduced in two measures: between the downshifted versus unshifted lever in postshift sessions and also from preshift to postshift performance within the same lever. Moreover, reward magnitude did not induce significantly different levels of lever pressing during preshift sessions, but there was a higher level of goal entries to the two-pellet lever than to the 12-pellet lever. This was different from what was observed in Experiment 1 (12 > 2 for lever, but 12~2 for goal) and in Experiment 3 (12~2 for both lever and goal). Thus, reward downshift accentuated an already existing bias toward sign tracking when only one lever was present in forced-choice trials. The

Table 4
Experimental Design Used in Experiment 4

| <i>n</i> | Preshift | Magnitude free choice | Postshift | Downshift free choice |
|----------|--------------|-----------------------|-------------|-----------------------|
| 16 | (17) R12, L2 | (5) R0 vs. L0 | (10) R2, L2 | (5) R0 vs. L0 |
| 16 | (17) L12, R2 | (5) L0 vs. R0 | (10) L2, R2 | (5) L0 vs. R0 |

Note. All animals were adult females. Numbers in parentheses denote the number of sessions. Sessions that included free-choice test trials were embedded into the final sessions of preshift or postshift training and administered every other day. Levers (right [R] or left [L]) were assigned to the reward magnitudes (12 or 2 pellets per trial) in a counterbalanced manner. In the final analysis, data from levers associated with the same reward magnitude (e.g., L12 and R12) from each counterbalanced subgroup were pooled. Similarly, downshifted and unshifted levers from each counterbalanced subgroup were also pooled. Thus, lever comparisons were based on $N = 32$.

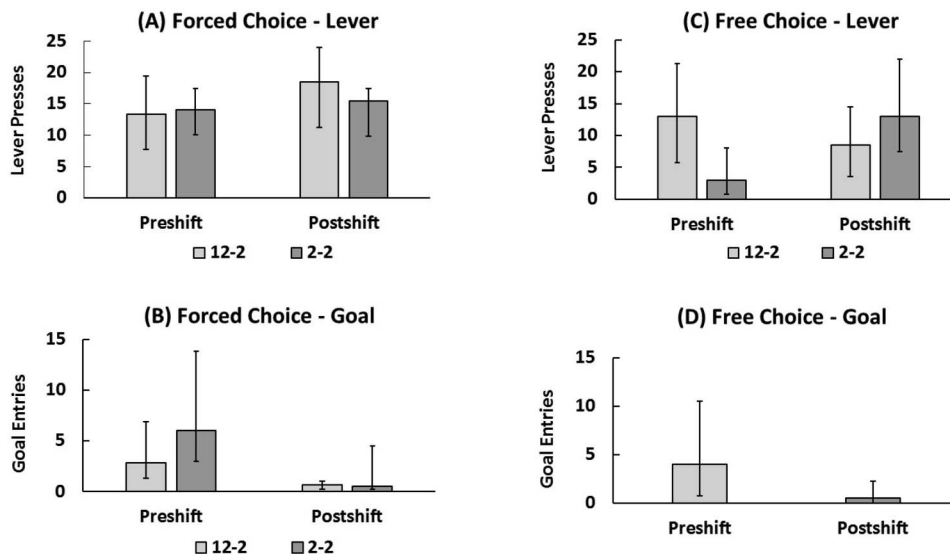


Figure 5. Median (\pm interquartile range) lever presses (top) and goal entries (bottom) over the five sessions before (preshift) and after (postshift) reward downshift. “Forced choice” (left column) refers to single-lever trials; the choice is between responding to the lever or the goal, and not responding. “Free choice” (right column) refers to two-lever, nonreinforced trials; the choice is between responding to one lever or goal, to the other lever or goal, and not responding. Notice that the ordinates may vary across figures, although they were kept constant within each experiment; scale values were set to maximize the visualization of differences among conditions. See text for statistical results; Experiment 4.

increase in lever pressing to the downshifted 12–2 lever in forced-choice trials suggests that rats do respond to the downshift manipulation when exposed to the two reward magnitudes during training. Thus, the failure to observe the SNC effect in Experiment 1 cannot be attributed to a lack of measure sensitivity, undetectable or insufficient reward disparity, or some factor peculiar to the autoshaping procedure. What is different from other situations involving SNC is that lever pressing responding after the downshift actually increased, rather than decreased in strength. A similar invigorating effect on autoshaped lever pressing was reported in animals trained to receive five pellets per trial after occasional trials in which the outcome was reduced to one pellet (Dudley & Papini, 1995, Experiment 4). As noted previously, preshift training involved conditions analogous to those of a simultaneous contrast design (Flaherty, 1996). If anything, such conditions should enhance reward disparity, thus inflating the value of the large reward (12 pellets) and deflating the value of the small reward (2 pellets).

A more complex set of results was observed in free-choice trials. In both preshift and postshift performance, the changes in lever pressing were transient. In preshift, a preference for the 12-pellet lever developed over the five choice trials, whereas in postshift trials preference for the unshifted lever was observed during the initial two choice trials, but it dissipated after that. Importantly, preference for these levers was reversed immediately after reward devaluation. Therefore, these data show a within-session dissociation between (a) sign tracking to the downshifted lever during single-lever, forced-choice trials (increasing after the downshift) versus (b) sign tracking to the downshifted lever during two-lever, free-choice trials (decreasing after the downshift), in both cases relative to performance directed at the unshifted lever.

The rapid switch in preference to the unshifted lever is similar to what was described in choice experiments involving reward downshift in a maze (Eisenberger et al., 1975) and, as pointed out above, it is consistent with data on escape from a location associated with a downshift in reward magnitude (Daly, 1974). However, the design used in the present experiment dissociated between single-lever and two-lever trials following reward downshift that, to our knowledge, has not been described before. Somewhat similar results, albeit with different training protocols, were reported in experiments with rats and children (Klossek, Yu, & Dickinson, 2011; Kosaki & Dickinson, 2010). In these experiments, a reward devaluation manipulation proved more effective after training in a choice situation than after training with a single response option, with outcome exposure equated across groups. Reward was devalued by pairings with LiCl in rats and by repeated video presentations in children. We will further compare our data with these experiments in the General Discussion section.

Experiment 5

The combination of forced- and free-choice trials proved sensitive to reward downshifts in two ways. In forced-choice trials, the downshifted lever commanded a higher level of lever pressing than the unshifted lever. However, in free-choice trials, and within the same session, there was a preference for the unshifted lever over the downshifted lever. Experiment 5 sought to replicate the SNC effect and extend the design to the case of SPC. While SNC is a robust effect that has been extensively replicated, the literature on SPC is far less clear. Isolated instances of SPC have been reported, but failures to observe the effect have also been published (see the

review in Annicchiarico et al., 2016). In one recent attempt to find conditions necessary to systematically and reliably produce the SPC effect following reward upshift, none of 10 experiments was successful, although they did produce evidence consistent with other processes, such as taste neophobia and generalization decrement (Annicchiarico et al., 2016). Given the apparent sensitivity of the procedure used in Experiment 4, the present experiment aimed to determine whether the combination of forced- and free-choice trials would allow for a demonstration of SPC following reward upshift in the autoshaping situation.

Method

Subjects and apparatus. The subjects were 27 male Wistar rats, experimentally naïve and bred in the TCU vivarium. Due to availability, subjects were trained in two replications, 16 rats in the first replication and 11 in the second replication; the procedures were identical. Ad libitum weights averaged 442.8 g ($SEM \pm 5.1$ g). Animals were 90 days old when food deprivation was introduced. Rats were kept under the same housing and maintenance conditions, and conditioning took place in the same four chambers described in Experiment 1.

Procedure. Autoshaping acquisition proceeded similarly to the previous experiment, with the addition of an upshift of 2–12 pellets on occasional sessions. The experiment involved a within-subject comparison of behavior (lever pressing and goal entries) during the presentation of two levers paired with rewards of different magnitudes across two phases of training. The first phase of the experiment consisted of seven sessions of acquisition training, one session per day, followed by the first preshift phase (Preshift 1). Preshift 1 mimicked acquisition and lasted an additional six sessions. Each session consisted of six trials wherein one of two levers was presented for 10 s, with a variable ITI that averaged 90 s (range: 60–120 s). Levers were counterbalanced and randomized such that each session consisted of a total of three right and three left lever presentations, with one lever always being associated with the large reward (12 pellets) and the other with small reward (2 pellets). Lever-reward assignment was counterbalanced so half of the rats had a high magnitude right lever and half had a high magnitude left lever. Each trial ended with the

automatic delivery of 12 or two reinforcement pellets, depending on the lever, for a total of 42 pellets per session (45 mg precision pellets). On the day following the final session of Preshift 1, all rats had the first postshift session (Postshift 1).

Postshift 1 proceeded identically to acquisition and preshift phases, except now rats experienced either an upshift (SPC condition) or a downshift (SNC condition) in one of the levers, while the other lever remained unshifted. In the SPC condition both levers were followed by 12 pellets and in the SNC condition all trials ended with the delivery of two pellets, for a total of 72 and 12 pellets per session, respectively. Thus, in the SPC condition, one lever was upshifted from two to 12 pellets per trial, whereas the other lever continued to be paired with 12 pellets as the unshifted control. Conversely, in the SNC condition, one lever was downshifted from 12 to two pellets per trial, whereas the other remained unshifted with two pellets. The Postshift 1 session ended with a nonreinforced free-choice trial, during which both levers were presented simultaneously for 10 s and sign tracking responses to each lever were independently recorded. The Preshift 1/Postshift 1 phases were repeated four times, to collect data from four preference tests for each rat. Having one probe trial per week was intended to maximize recovery from reward shifts. Moreover, similar free-choice trials during preshift to test for reward magnitude effects were not included to minimize potential transfer between phases.

Following the fourth Postshift 1 session all rats began the second phase of the experiment, Preshift 2. The conditions of Preshift 2 were the same as Preshift 1, with the same levers associated with high versus low magnitude of reinforcement for each rat for the same six sessions, one session per day. Postshift 2 began after the last day of Preshift 2. The design of Postshift 2 was the same as Postshift 1, but the animals previously in the SPC condition experienced SNC instead, and those that were first in the SNC condition now encountered SPC. The Preshift 2/Postshift 2 phases were repeated four times, just as Preshift 1/Postshift 1 phases. Thus, all animals were exposed to multiple downshifts and upshifts, counterbalanced to control for order effects. The design is described in Table 5. All other procedural features were as described in Experiment 1.

Table 5
Experimental Design Used in Experiment 5

| Acquisition | <i>n</i> | Repeated 4 times | | Repeated 4 times | |
|-------------|----------|------------------|--------------------------------|------------------|--------------------------------|
| | | Preshift 1 | Postshift 1 | Preshift 2 | Postshift 2 |
| | | | Downshift | | Upshift |
| (7) R12, L2 | 7 | (6) R12, L2 | (1) R2 , L2 | (6) R12, L2 | (1) R12, L12 |
| (7) L12, R2 | 7 | (6) L12, R2 | (1) L2 , R2 | (6) L12, R2 | (1) L12, R12 |
| | | | Downshift free choice: R vs. L | | Upshift free choice: R vs. L |
| | | | Upshift | | Downshift |
| (7) R12, L2 | 7 | (6) R12, L2 | (1) R12, L12 | (6) R12, L2 | (1) R2 , L2 |
| (7) L12, R2 | 6 | (6) L12, R2 | (1) L12, R12 | (6) L12, R2 | (1) L2 , R2 |
| | | | Upshift free choice: R vs. L | | Downshift free choice: R vs. L |

Note. Reward size counterbalanced across R and L lever. The sequence of reward shifts was also counterbalanced (i.e., downshift first vs. upshift first). The shifted lever (whether downshifted or upshifted) appears in bold. The numbers in parentheses refer to the number of sessions in each phase. There was one free-choice trial embedded in each postshift session. All animals were adult males. R = right lever; L = left lever; 12 and 2 = number of pellets per trial.

Results

The results were analyzed using the Wilcoxon signed-ranks test for pairwise contrasts between levers and for preshift-postshift comparisons. Friedman tests for related samples were used for goal entries during free-choice trials. By mistake, all 11 animals in the second replication were given one extra Preshift 1/Postshift 1 training phase, so they received an additional upshift or downshift prior to switching to the alternate phase. The results from the second replication were very similar to those of the first replication, so data from these extra sessions were omitted from all analyses. Preshift data refer to responding to the 12- and two-pellet levers during the eight sessions preceding each of the sessions involving reward shift. Postshift data refer to responding to the 12-2 and 2-2 levers across downshift sessions or to the 2-12 and 12-12 levers across upshift sessions. Choice data refer to responding to the shifted and unshifted levers for each of the free-choice, nonreinforced trial.

Reward downshift, forced-choice trials. Since the original goal of this experiment was to search for consistent effects of downshift and upshift on lever preference across trials, regardless of the order in which animals received downshift or upshift first in training, data were first pooled across all eight shifts and separated broadly by shift direction.

SNC data for lever pressing (Figure 6A) indicated a nonsignificant tendency for higher response level on the 12-pellet lever than on the two-pellet lever during preshift sessions, $z = -1.85$, $p = .06$, $r = .25$. This difference became significant for postshift sessions, $z = -2.32$, $p = .02$, $r = .32$. Preshift-postshift analyses yielded nonsignificant changes for both levers, $z_s < -0.91$, $p_s > .36$, $r_s < .13$.

For goal entries (Figure 6B), a comparison between levers yielded nonsignificant differences for preshift and postshift data, $z_s < -.82$, $p_s > .53$, $r_s < .10$. There was no statistical evidence of a change in goal entries from preshift to postshift sessions, $z_s < -1.93$, $p_s > .05$, $r_s < .27$.

Reward downshift, free-choice trials. Figure 7A shows that lever presses were lower for the downshifted lever than for the unshifted lever, $z = 2.94$, $p < .004$, $r = .40$. A trial-by-trial analysis indicated that the reward downshift event led to increased responding to the unshifted, two-pellet lever relative to the downshifted, 12-2 lever during the initial two trials, $z_s > -2.41$, $p_s < .02$, $r_s > .33$, but the effect was not significant during the last two choice trials, $z_s < -1.57$, $p_s > .11$, $r_s < .22$. There was no significant evidence of change across choice trials for goal entries, $\chi^2 = 0.90$, $p = .83$, $W = 0.01$.

Reward upshift, forced-choice trials. Concerning lever comparisons (upshifted vs. unshifted lever), none of the comparisons achieved significance for lever presses (Figure 6C) or goal entries (Figure 6D), $z_s < -1.98$, $p_s > .11$, $r_s < .22$. The differences were also nonsignificant between preshift and postshift performance for both lever presses and goal entries, $z_s < -.98$, $p_s > .32$, $r_s < .14$.

Reward upshift, free-choice trials. Figure 7B presents the results of the free-choice trials in the reward upshift manipulation. Although there was a tendency for increased lever pressing for the upshifted, 2-12 lever relative to the unshifted 12-12 lever, the difference was not significant, $z = 1.91$, $p > .05$, $r = .26$. A trial-by-trial analysis also yielded nonsignificant differences across levers, $z_s < 1.67$, $p_s > .09$, $r_s < .24$. There were also no detectable changes in goal entries across choice trials, $\chi^2 = 0.52$, $p = .91$, $W = 0.01$.

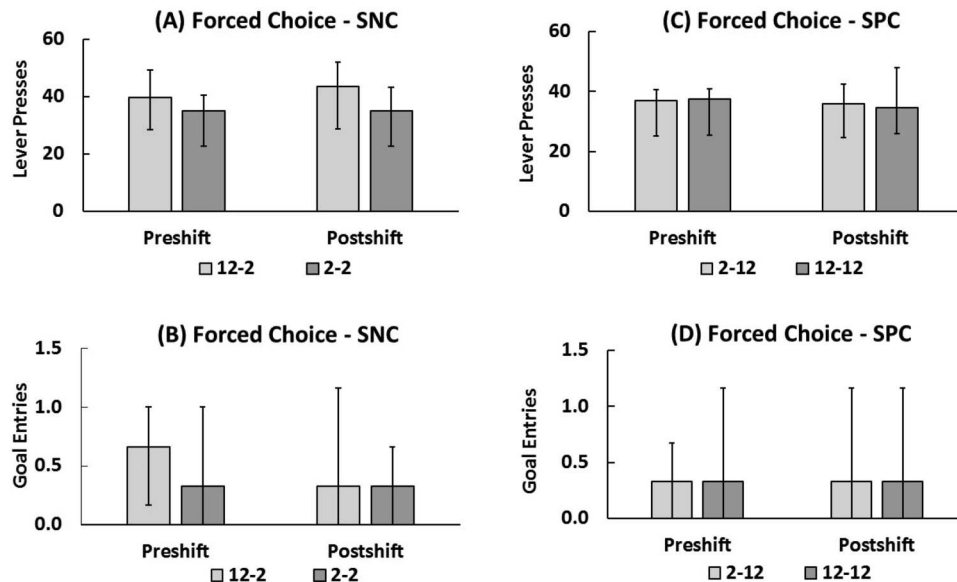


Figure 6. Median (\pm interquartile range) lever presses (top) and goal entries (bottom) over the two sessions before (preshift) and after (postshift) reward downshift. “SNC” and “SPC” refer to successive negative and positive contrast, respectively. “Forced choice” refers to single-lever trials; the choice is between responding to the lever or the goal, and not responding. Notice that the ordinates may vary across figures, although they were kept constant within each experiment; scale values were set to maximize the visualization of differences among conditions. See text for statistical results; Experiment 5.

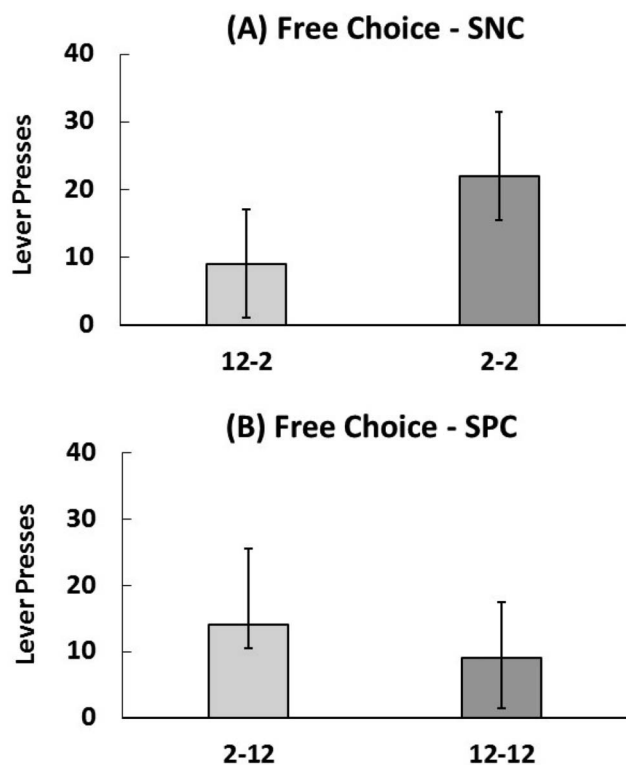


Figure 7. Median (\pm interquartile range) lever presses during the four postshift free-choice trials after reward shifts. “SNC” (top) refers to successive negative contrast. “SPC” (bottom) refers to successive positive contrast. “Free choice” refers to two-lever, nonreinforced trials; the choice is between responding to one lever or goal, to the other lever or goal, and not responding. Notice that the ordinates may vary across figures, although they were kept constant within each experiment; scale values were set to maximize the visualization of differences among conditions. See text for statistical results; Experiment 5.

Sequential effects. Pooling together the four shifted trials regardless of which animals received downshift first versus upshift first may obscure order effects resulting from the within-subjects approach. Therefore, we conducted additional analyses taking into account the order in which the treatments were administered (i.e., downshift first/upshift second vs. upshift first/downshift second).

No statistical differences were observed in forced-choice data for reward downshift or upshift when comparisons were tested as a function of the sequence (downshift first or upshift first) between shifted and unshifted levers, $z_s < 1.79$, $p_s > .07$, $r_s < .36$.

As for free-choice trials, a few interesting differences emerged when segregating the data according to the sequence of reward shift experience. For example, the SNC effect in lever pressing observed with all the data pooled was entirely due to animals that received reward downshift experience first. As shown in Figure 8A, SNC-first rats responded significantly more to the unshifted 2–2 lever than to the downshifted 12–2 lever, $z = 3.30$, $p < .002$, $r = .62$, whereas there was no evidence of differential responding to the levers in SNC-second rats, $z = 0.28$, $p > .77$, $r = .06$. A trial-by-trial analysis yielded a significantly higher lever pressing on the unshifted lever than on the downshifted lever on choice Trials 1, 2, and 4, $z_s > -2.17$, $p_s < .05$, $r_s > .41$. However,

downshift second revealed nonsignificant differences between levers in each of the four choice trials, $z_s < -1.48$, $p_s > .14$, $r_s < .30$. There were no statistical changes in goal entries across choice trials for downshift first or second, $\chi^2 < 6.1$, $p_s > .11$, $W_s < 0.15$.

Interestingly, the only hint of SPC was observed in lever pressing for the SPC-second group, the same group that had exhibited strong evidence of SNC (Figure 8B). The overall effect was significant for the SPC-second animals, $z = 2.04$, $p < .05$, $r = .39$, but not for the SPC-first animals, $z = 0.84$, $p > .40$, $r = .17$. On a trial-by-trial basis, the SPC effect emerged only in the fourth free-choice trial for lever presses, $z = -2.73$, $p < .007$, $r = .52$. None of the other comparisons were significant, $z_s < -1.41$, $p_s > .16$, $r_s < .33$. Changes across choice trials in goal entries were also nonsignificant, $\chi^2_s < 2.54$, $p_s > .46$, $W_s < 0.07$.

Discussion

Two surprising results were observed in Experiment 5. First, successive free-choice trials during reward downshift sessions revealed a transient SNC effect. This occurred despite six inter-

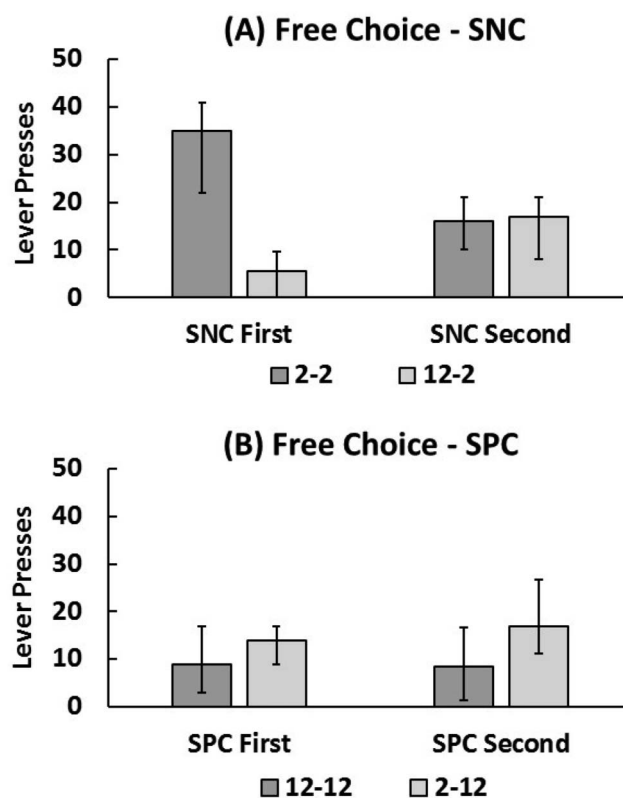


Figure 8. Median (\pm interquartile range) lever presses during the four postshift free-choice trials after reward downshift. The results are segregated according to the sequence of treatment (“first” or “second”). “SNC” refers to successive negative contrast (top) and “SPC” refers to successive positive contrast (bottom). “Free choice” refers to two-lever, nonreinforced trials; the choice is between responding to one lever or goal, to the other lever or goal, or not responding. Notice that the ordinates may vary across figures, although they were kept constant within each experiment; scale values were set to maximize the visualization of differences among conditions. See text for statistical results; Experiment 5.

vening sessions of training with 12 versus two pellets assigned to each of two levers between successive free-choice trials. Second, whether SNC and SPC effects were observed depended on their position in the training sequence. A transition from downshift to upshift produced strong evidence of SNC in free-choice trials when reward downshift was administered during the first phase (3 of 4 choice trials), and the only evidence of SPC when reward upshift was administered during the second phase (1 of 4 choice trials). These effects were observed in terms of lever pressing. However, a transition from upshift to downshift produced evidence of neither SPC nor SNC. Although there is little reason to expect sex differences in incentive contrast experiments (Flaherty, 1996), it is reassuring that the SNC effects in free-choice behavior were observed in males in the present experiment and in females in Experiment 4.

General Discussion

The main contributions from these results provide a demonstration of SNC in the free-choice performance of rats and a dissociation between free-choice and force-choice performance with response suppression in the former and response invigoration in the latter. The implications of these results for an understanding of behavior in situations involving reward devaluations are organized in six questions for discussion.

First, can devaluation-induced response invigoration help understand the slow emergence of the SNC effect in autoshaping? A previous autoshaping experiment from our lab involving SNC with rats showed a slow emergence of the effect after a 12-to-1 pellet downshift (Papini et al., 2001, Experiment 5). A potential explanation for this result relates to the fact that lever pressing tends to be enhanced after a reward devaluation in the autoshaping situation, whereas the SNC effect requires response suppression. This was explicitly analyzed in these experiments in terms of a preshift-postshift difference in behavior (see Figures 4A and 5A). Such enhancement is also obvious in Papini et al. (2001, Figure 6, bottom panel); the figure shows a spike of lever pressing during the first downshift session and a tendency for lever pressing to maintain a relatively high level for the following 10 sessions before a response decrement was observed. The response suppression typically observed in SNC effects would then have to counteract such response facilitation to be observed. A similar initial enhancement of behavior following reward devaluation has been reported in other situations. For example, Mast, Fagen, Rovee-Collier, and Sullivan (1980) trained 82–112-day-old infants to move a mobile attached to their legs by kicking. These infants exhibited increased kicking and negative vocalizations (e.g., crying, fussing) when the number of pieces in the mobile was reduced from 10 to two. Stout, Boughner, and Papini (2003) also reported an increase in instrumental lever pressing following surprising reward omissions and, as mentioned above, similar response facilitation has also been observed in autoshaping with rats (Anselme et al., 2013; Dudley & Papini, 1995, 1997; Glueck et al., 2018; Thomas & Papini, 2001). Of course, in some cases lever pressing invigoration has not been observed (e.g., the present Figures 2A, 2C, and 6A); however, to the authors' knowledge, lever pressing suppression immediately after reward devaluation or omission has not been reported in autoshaping with rats. Thus, suppression of autoshaped lever pressing in rats following reward

devaluation may, in some cases, be opposed by response invigoration. This would lead to the slow emergence, if at all, of the SNC in this situation (Papini et al., 2001). There is some evidence suggesting that such an enhancement of lever pressing has an emotional component. Autoshaping per se (i.e., lever-food pairings) is known to increase plasma levels of corticosterone and prefrontal levels of norepinephrine and serotonin, relative to control animals trained with the same number of lever and food deliveries, but presented independently (Tomie, Tirado, Yu, & Pohorecky, 2004). Additionally, ablation of the adrenal glands, which reduces or removes circulating corticosterone, did not affect autoshaping acquisition, but it eliminated the spike in lever pressing observed during the first extinction session, a result consistent with emotional activation after reward omission (Thomas & Papini, 2001). Whereas the factors that bias lever pressing toward invigoration or suppression are unclear, we conclude that in the autoshaping situation, rats tend to increase lever pressing when confronted with reward reductions or omissions.

Second, is SNC in autoshaping difficult to obtain because autoshaped lever pressing is prone to becoming an outcome-independent habit? We entertained the idea that reward devaluation failed to cause an SNC effect or caused it to develop very gradually (as in Papini et al., 2001) because extensive training would lead to habitual behavior, that is, elicited by antecedent stimuli rather than dependent upon anticipating the current value of the reward. Habitual behavior is the antithesis of the SNC effect; in fact, Tinklepaugh (1928) considered this factor when introducing quantitative downshifts in reward. In one experiment, when monkeys found one piece of food after observing the experimenter placing two pieces, they seemed to look for the missing piece. Tinklepaugh (1928) argued that

this might lead to the impression that the monkeys were responding in an habitual manner; that is, that having formed the habit of reaching twice to secure the two pieces of food, they would, if only one piece was found, reach the second time through habit. (p. 231)

This interpretation was discarded because searching would not occur when the monkey saw a single piece being placed under the container in some test trials. We tested this action-versus-habit hypothesis in Experiment 1 by varying the moment in training when the reward was downshifted, either early or late (e.g., Adams, 1982), but failed to observe any evidence of the SNC effect in either case. Experiment 2 led to results consistent with the action-versus-habit distinction using pre-session feeding as a reward-devaluation procedure. In nonreinforced tests, lever pressing was lower after pre-session feeding than after the post-session-feeding control early in training, but not late in training. This evidence suggests that not all procedures involving reward devaluation are equally sensitive to amount of training. Thus, pre-session feeding and reward downshift produced contrasting results in the autoshaping procedure. Clearly, therefore, the action-habit framework based on amount of training does not apply to the effects of reward downshift in autoshaping with rats.

Third, what are the implications of these results for the connection between habitual behavior and extended training? Interestingly, pre-session feeding produced evidence of reward expectancies controlling lever pressing late in training in reinforced tests, that is, on tests in which the presentation of the lever was followed

by food, as during training. As pointed out above, testing in reward devaluation procedures is typically administered in the absence of the reward (e.g., Adams, 1982; Morrison et al., 2015). Additional evidence that extensive training may not completely eliminate the control of behavior by reward expectancies comes from a variety of sources. For example, Papini et al. (2001, Experiment 5) introduced extinction after 40 sessions of training for the two unshifted controls from the contrast manipulation. After extensive training, lever pressing increased during the initial sessions of extinction, but response suppression developed faster after training with 12 pellets per trial than after training with one pellet per trial. This result suggests that autoshaped lever pressing was still guided by reward expectancies even after extensive training. Using instrumental contingencies with four responses and two rewards in a within-subject design in which one reward was devalued with LiCl, Colwill and Rescorla (1985) found evidence of selective response suppression also after extended training. Such evidence was obtained in free-choice trials in which animals were exposed to two response manipulanda, only one of which was previously paired with a devalued reward. Therefore, extended training is not sufficient to induce habitual behavior.

Fourth, what aspect of the free-choice procedure allowed rats to exhibit SNC in autoshaping, even after extensive training? Extensive training does not necessarily lead to habitual behavior, especially when testing involves extinction training or free-choice trials. SNC experiments preclude extinction training since by definition the reward is downshifted to a nonzero value, but they do not necessarily prevent the use of free-choice testing (Eisenberger et al., 1975). One aspect of free-choice training with different rewards is that it encourages comparisons among the rewards or among their signals (e.g., Trapold & Overmier, 1972). Experiments in which acquisition with one response option is compared with acquisition with two response options show that reward devaluation is more effective after extensive training in the free-choice situation than in the forced-choice situation (Dickinson, 2016). For example, Kosaki and Dickinson (2010) trained one group of rats to choose between two levers that produced different rewards (food pellets or sucrose solution), whereas a second group received training with one lever reinforced with one of the rewards while the other reward was delivered between trials (i.e., free-choice vs. forced-choice training). Thus, exposure to the rewards was matched across groups. Then one of the rewards was paired with LiCl for devaluation. When tested with both levers, animals that had received free-choice training suppressed pressing the lever associated to the devalued reward, whereas animals that had received forced-choice training show no appreciable disruption of lever pressing (for similar results with children, see Klossek et al., 2011). Comparable results were observed in Experiments 4 and 5, in which the use of a within-subject design highlights the dissociation between these two types of response patterns. Within the same session, reward downshift caused an increase in lever pressing in the downshifted lever relative to the unshifted lever in single-lever trials (forced choice), but an immediate decrease in lever pressing and a switch to preference for the unshifted lever over the downshifted lever in two-lever trials (free choice). In this case, both effects of reward downshift (increased in lever pressing in single-lever trials and preference for the unshifted lever in two-lever trials) show that the reward representation is either still active or can be reactivated even after extensive training.

Fifth, is the apparent SNC effect observed in Experiments 4 and 5 similar to the more typical SNC effects in either instrumental or consummatory behavior? An important aspect of SNC is the accompanying negative emotion that makes it a viable animal model for frustration or psychological pain (Papini et al., 2015). Two features of the free-choice SNC effect described here are consistent with negative emotion. First, when free-choice trials were administered every other day, the SNC effect was transient (Experiment 4). With interpolated training between successive free-choice trials, the SNC effect may be more permanent, especially without prior upshift experience (Experiment 5). The transient nature of this effect suggests that it is the result of a reward comparison process in which the value of the current reward (2 pellets) is pitted against the value of the remembered reward (12 pellets). If there is opportunity for the memory update of the new reward conditions, then the SNC should be reduced as the negative discrepancy between obtained and expected rewards is reduced (Papini, 2003). Second, the fact that preference for the unshifted lever after reward downshift was observed in the first free-choice trial suggests that animals may be escaping/avoiding the downshifted lever. In Experiment 4, there was a switch from preference of the 12-pellet lever in pre-shift sessions to preference of the two-pellet lever in post-shift sessions that occurred across adjacent sessions. Thus, after the downshift, an unshifted lever suddenly becomes more appealing than a downshifted lever. Results like these are consistent with the escape-from-frustration effect (Daly, 1974). For example, rats exposed to a surprising downshift from 32% sucrose to water learn a new response (jumping over a barrier) that moves them away from the downshift location faster than a control group that has always received water in that location, an effect that is eliminated by opioid-receptor blockage with naloxone (Norris et al., 2009). Since the levers used in the present experiments are located at opposite ends of the frontal wall, it is conceivable that a free-choice trial results in the escape/avoidance of the location associated with the downshifted lever. This immediate rejection of the downshifted lever is consistent with negative emotion. Of course, that alone would not explain why rats increase their responding for the unshifted lever; to account for this effect, an increase in value of the unshifted lever would seem to be needed. In a choice situation, therefore, incentive contrast may involve both a reduction in value of the devalued option and an increase in value of the unchanging alternative.

This dual contrast effect (i.e., devaluing the downshifted alternative and revaluing the unshifted alternative) may help explain a change to a search mode in downshift sessions. For example, rats exposed to reward downshift in one arm of a radial-arm maze display extensive search in other arms of the maze (Flaherty, 1996, pp. 87–88) and when trained in a regular conditioning box they increase activity levels and rearing responses (Pellegrini & Mustaca, 2000). Such changes in search behavior were noticed already in the initial studies on incentive contrast (Elliott, 1929; Tinklepaugh, 1928), although we know now that restraining rats in a tube that does not allow for search still leads to a cSNC effect (Lopez Seal, Cuenya, Suarez, & Mustaca, 2013). Thus, one corollary of the free-choice SNC found in the present experiments is that a change in search behavior observed in incentive contrast experiments may involve a reevaluation of potential incentive sites when the current one is devalued.

Finally, what implications do these results have for other instances in which SNC has failed to occur? There are three areas in which the SNC effect has consistently failed to occur: in runway experiments using sucrose solutions as the reward (Rosen & Ison, 1965; Sastre et al., 2005); in infant rats (Amsel, 1992; Suárez, Mustaca, Pautassi, & Kamenetzky, 2014); and in comparative research with bony fish, amphibians, and reptiles (Papini, 2002, 2014). In these cases, animals were trained to move (swim, walk, or run) from a start position to a goal where they could consume a reward (sucrose solutions, solid food, or water). These procedures resemble the forced-choice trials used in the present autoshaping experiments in that the option is to respond (approach the goal) or not. We have applied this logic to the case of SPC with limited results. As mentioned above, SPC has been more difficult to demonstrate in rats than SNC (Annicchiarico et al., 2016). This was also the case in Experiment 5, in which there was no evidence of SPC when animals were trained from the outset with reward upshifts and only modest evidence when receiving upshifts after being exposed to reward downshifts. Still, whether free-choice testing would prove more sensitive to detect SNC in the cases mentioned above is an empirical question that remains to be examined.

In conclusion, the present results provide the first evidence of a dissociation of forced- and free-choice performance in rats exposed to reward downshifts in the autoshaping situation. Autoshaped lever pressing tends to be either enhanced or undisturbed (but not suppressed) by reward downshifts when animals are confronted with a single lever. However, animals switch toward the unshifted lever when the test involves a free choice between a downshifted lever and an unshifted lever. This free-choice SNC effect offers a novel procedure to test the emotional, motivational, and cognitive aspects associated with incentive relativity.

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