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Complex effects of reward upshift on consummatory behavior

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ABSTRACT

Exposing rats to an upshift from a small reward to a larger reward sometimes yields evidence of consummatory successive positive contrast (cSPC), an effect that could be a suitable animal model of positive emotion. However, cSPC is an unreliable effect. Ten experiments explored the effects of an upshift in sucrose or saccharin concentration on consummatory behavior under several conditions. There was occasional evidence of cSPC, but mostly a combination of increased consummatory behavior relative to preshift reward concentrations and a reduced behavioral level relative to unshifted controls. Such a pattern is consistent with processes causing opposite changes on behavior. Reward upshift may induce processes that suppress behavior, such as taste neophobia (induced by an intense sucrose taste) and generalization decrement (induced by novelty in reward conditions after the upshift). An experiment tested the role of such novelty-related effects by preexposing animals to either the upshift concentration (12% sucrose) or water during three days before the start of the experiment. Sucrose-preexposed animals drank significantly more than water-preexposed animals during the upshift, but just as much as unshifted controls (i.e., no evidence of cSPC). These results suggest that cSPC may be difficult to obtain reliably because reward upshift induces opposing processes. However, they also seriously question the ontological status of cSPC.

1. Introduction

Most contemporary research on the behavioral effects of shifts in reward value centers on the negative case in which a large reward is downshifted to a small reward. Reward downshift leads to a transient deterioration of behavior, whether anticipatory or consummatory (Papini et al., 2015). The positive case, that is, an enhancement of behavior after an upshift from a small to a large reward, has been reported, claimed to be an artifact, and then reported again, as will be shown below. However, there is no evidence in the published literature of a standardized preparation leading to a systematic body of knowledge. As a result, exploring the effects of reward upshifts on behavior takes the reader to relatively old sources. For example, Tinklepaugh (1928) observed that monkeys that saw a piece of banana (highly preferred) placed underneath a cup rejected a leaf of lettuce (less preferred, but acceptable) when the experimenter replaced the rewards outside the animal's view and also showed aggressive behavior directed at the experimenter. Tinklepaugh (1928) also presented monkeys with the opposite shift, namely, offering a piece of banana after having seen the experimenter hiding a leaf of lettuce under the cup. In these trials, however, the monkeys "made their choices and seized the food without noticeable signs of any particular emotion, and without hesitation" (Tinklepaugh, 1928, p. 230). He speculated that the reward shifts may have been surprising, but this was only noticeable in the negative contrast situation. Similar results were reported by Crespi (1942) with rats and shifts in reward magnitude (amount of food), rather than reward quality (type of food). In both cases, the results were interpreted as involving an asymmetric emotional response, with the reward downshift inducing a stronger reaction than the upshift (see also Zeaman, 1949). In current terminology (see Flaherty, 1996; Zeaman, 1949), these effects are referred to as successive negative and positive contrast in instrumental behavior (iSNC, iSPC), emphasizing the sequence of reward shifts (successive), the direction of the change (positive or negative), and the comparison between current and past reward values (contrast).

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This asymmetry in reports of iSPC and iSNC effects led Spence (1956) to suggest that only the negative case was a replicable effect. He reported three experiments that showed evidence of iSNC, but no evidence of iSPC (Spence, 1956, pp. 130–132). Using a simultaneous contrast procedure alternating trials with large and small rewards, Bower (1961) also reported reliable evidence of simultaneous negative contrast, but no simultaneous positive contrast effect. Bower (1961) and Campbell et al. (1970) suggested that a performance ceiling could make positive contrast difficult to detect, a problem that was addressed by introducing conditions that tended to lower performance, including a response-reward temporal delay and a small number of preshift trials. Mellgren (1971) upshifted rats in a runway after 24, 48, or 72 trials from one to 6 food pellets and compared their performance with a group always receiving 6 pellets (i.e., an unshifted control). In addition, all rats experienced a 20-s reward delay after entering the goal box. Under these conditions, iSPC was observed in all groups, although the effect was largest in the group upshifted after 24 trials because the performance of unshifted controls was still relatively low (see also Mellgren, 1972; Mellgren et al., 1973; Shanab et al., 1969). In addition to these runway/maze experiments, the asymmetry between contrast effects was also reported using the autoshaping (Pavlovian) procedure with rats in which the presentation of a lever ends after 10 s with the response-independent delivery of food pellets. While the procedure is Pavlovian, omission experiments suggest that lever pressing has a strong instrumental component (e.g., Davey et al., 1981). With this procedure, Papini et al. (2001) reported evidence of iSNC and the related magnitude of reinforcement extinction effect (faster extinction after acquisition with a large, rather than small, reward), but no evidence of iSPC.

In the runway procedure, the response-reward delay introduces a potentially frustrating experience that complicates the interpretation of the upshift manipulation (e.g., Rashotte and Surridge, 1969). Another manipulation that led to demonstrations of iSPC consisted of downshifting the reward a few trials before an upshift, again introducing a frustrating event (Benefield et al., 1974; Maxwell et al., 1976). In the consummatory version of the successive contrast paradigm (cSNC, cSPC), using alternation of access to large and small rewards (32% vs. 4% sucrose solutions) across days, Flaherty et al. (1983) reported that early in training rats show evidence of both cSPC and cSNC. However, whereas the negative effect remained significant, the positive effect dissipated as the unshifted, large-reward control group increased consumption of 32% sucrose. This could be interpreted as a ceiling effect. Again, alternating reward magnitudes introduces the potential for an interaction between positive and negative emotional states.

In addition to the iSPC and cSPC effects mentioned above, there are other contrast procedures that seem to produce evidence of positive contrast reliably. For example, in consummatory simultaneous positive contrast, animals receive rapid alternation of access to large (32% sucrose) and small (4% sucrose) rewards (Flaherty and Largen, 1975). Under these conditions, rats exhibit increased consumption of 32% sucrose when the alternating bottle offers 4% sucrose rather than when the second bottle offers 32% sucrose (simultaneous positive contrast), and reduced consumption of 4% sucrose when the alternating bottle offers 32% sucrose, rather than 4% sucrose (simultaneous negative contrast). Based on the extensive opportunities for sensory (i.e., peripheral) interactions, on different licking microstructure (Grigson et al., 1993), and on the fact that simultaneous negative contrast does not appear to be influenced by benzodiazepine anxiolytics (Flaherty et al., 1977), Flaherty (1996, p. 131) concluded, "SNC and simultaneous negative contrast are different phenomena." Extrapolating from this evidence comparing successive vs. simultaneous *negative* contrast effects, we assumed that it would be advisable to start our study of the effects of reward upshift on consummatory behavior with the cSPC procedure.

The present series of experiments was an attempt at identifying conditions that would induce cSPC routinely. Unlike the case for SNC, there seems to be no systematic treatment of SPC in the literature; this may imply that the phenomenon is not robust or that appropriate parameters have not yet been identified. Having a standard situation to study the effects of upshifts in reward value on behavior is important from several perspectives. Theoretically, cSPC would speak to the issue of the symmetry of contrast effects; in conjunction with cSNC, cSPC could be used to introduce an animal model of negativity bias (i.e., the tendency of negative events to weight more than positive events; Baumeister et al., 2001); and it would expand the neurobiological analysis of reward comparison mechanisms to the positive discrepancy case. From a translational perspective, a standard preparation to study cSPC could be developed into an animal model for positive emotion, potentially connecting lab research on animal learning and emotion with issues of health and well-being (Xu and Roberts, 2010). The translational value of cSNC as a model of anxiety, conflict, and psychological pain has been recently reviewed (Papini et al., 2015), so we have hypothesized that cSPC could do the same for the case of positive emotion. However, as the experiments reported below will show, we were left with a dilemma: Either we argue that we have yet to find a set of conditions that would reliably produce cSPC or we are forced to reconsider Spence's (1956) view that questions the very existence of SPC as a phenomenon.

2. Experiment 1

We started this series using Flaherty et al.'s (1983, Experiment 3) single-alternation procedure in an attempt to find evidence of both cSPC and cSNC within the same experiment. Three groups of rats were randomly assigned to a condition alternating 32% and 4% sucrose, one always receiving 32% sucrose (control for positive contrast), and one always receiving 4% sucrose (control for negative contrast). The training procedure was kept similar to that used by Flaherty et al. (1983) except that the dependent variable was the cumulative time in contact with the sipper tube (called goal-tracking time), instead of lick frequency (lick frequency was used in subsequent experiments of the present series).

2.1. Method

2.1.1. Subjects

The subjects were 24 male Wistar rats, all experimentally naive. These animals were bred at the TCU colony with breeders purchase from Harlan Labs (Indianapolis, IN). Breeders were kept in polycarbonate cages. They were weaned at around 21 days of age and kept in same-sex group polycarbonate cages until around 40 days of age, at which time they were transferred to individual wire-bottom cages. Water was freely available during their entire lives. At around 90 days of age (ad libitum weights: 431–518 g), rats were gradually deprived of food until they reached an 81–84% of their ad libitum weight. They received some food every day, but were kept at this level of deprivation during the course of the experiment by providing supplemental food after training sessions (see below). The colony room was subject to a 12:12 light:dark regimen, with lights on at 07:00 h, and under relatively constant temperature (~23 °C) and humidity (~50%). Behavioral training was scheduled during the light portion of the daily cycle. Housing and testing were carried out in an USDA-inspected research facility. All experimental procedures reported in this article were approved by the Institutional Committee on Animal Care and Use. Animal health was evaluated daily by researchers and periodically by a consulting veterinarian.

2.1.2. Apparatus

The 8 conditioning boxes (MED Associates, St. Albans, VT) described here were used in all the experiments reported in this article. Boxes were made of aluminum and Plexiglas (29.4 cm long, 28.9 cm high, and 24.7 cm wide), with floors made of steel rods. A tray with corncob bedding was placed below the floor to collect feces and urine. The sipper tube containing the sucrose solution was inserted through a hole in the feeder wall (1 cm wide, 2 cm high, and 4 cm from the floor, 1 cm in diameter). Diffuse light was provided by a house light located in the upper part of a wall opposite to the sipper tube. A computer located in an adjacent room controlled the presentation and retraction of the sipper tube, and recorded the rat's contact with it via a circuit involving the steel rods in the floor and the sipper. The dependent measure was the cumulative time in contact with the sipper tube (goal-tracking time, in 0.01-s units). Goal-tracking time correlates positively and significantly with fluid intake for both 32% and 4% sucrose concentrations (Mustaca et al., 2002), and it leads to similar results as lick frequency (Riley and Dunlap, 1979) and amount of fluid intake (Manzo et al., 2015). (Some of subsequent experiments in this series used lick frequency as a dependent variable and obtained similar results.) Each conditioning box was placed in a sound-attenuating chamber that contained a speaker to deliver white noise and a fan for ventilation. Together, the speaker and fan produced noise with an intensity of 80.1 dB.

2.1.3. Procedure

Animals were matched by ad libitum weight and randomly assigned to one of three groups ($n = 8$): Group 32–4 (single alternation of 32% and 4% sucrose across days), Group 32 (32% sucrose in every session), or Group 4 (4% sucrose in every session). Animals were weighed prior to the start of testing each day and then transported in their home cages mounted in transportation racks to the testing room, where they were transferred to the conditioning boxes. Once all conditioning boxes were ready, the computer program was started. House lights were turned on and an interval averaging 30 s (±15 s) was started. Each trial lasted 5 min from the first recorded contact with the sipper tube. During these 5 min, the sipper tube was continuously available to the animal. On the first two sessions, animals that did not reach 10 s of goal tracking were run twice and the second goal-tracking time was entered for analysis. The sipper tube was inserted 2 cm into the apparatus on Session 1 and then was flush with the front wall of the apparatus for the remainder of the experiment. When the sipper tube was retracted, another interval averaging 30 s (±15 s) was started. At the end of this interval, animals were returned to their home cages, boxes were wiped down with a damp paper towel, and the next squad was placed in the conditioning boxes. These intervals before and after a session of continuous access to sucrose were interpolated to minimize the potential effects of the handling on consummatory behavior.

Group 32–4 received 32% sucrose in even-numbered sessions and 4% sucrose on odd-numbered sessions. Sucrose solutions were prepared w/w by mixing 32 g (4 g) of sucrose for every 78 g (96 g) of distilled water. Animals were assigned to a given squad and a given conditioning box for the duration of the experiment. The order in which squads were run changed randomly across days. Animals were fed in the colony room after the last squad of the day was run (7 days/week). Therefore, postsession feeding was administered at variable intervals across days since the end of the session; such intervals ranged between 15 and 45 min.

Goal-tracking times were transformed to seconds for plotting and analysis purposes. Standard analysis of variance, with $p < 0.05$, was used to analyze the main data (IBM SPSS Statistics 21). For brevity, only significant results are reported in these experiments.

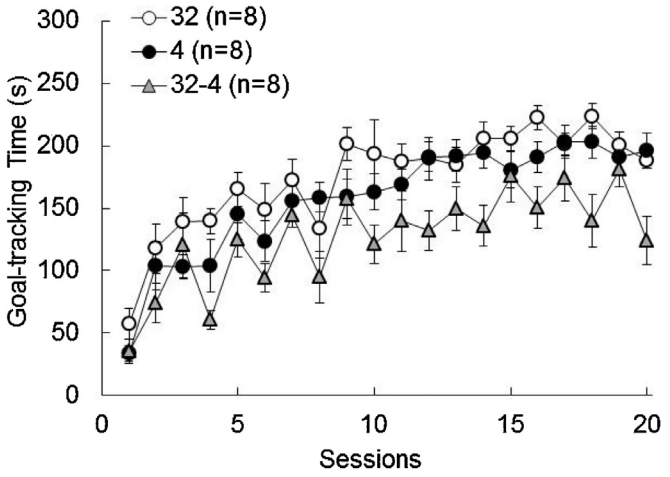

Fig. 1. Mean (±SEM) goal-tracking time of groups given access to 32% sucrose (32) or 4% sucrose (4) across 20 sessions, of single alternation access to 32% and 4% sucrose across sessions (32–4). Results from Experiment 1.

2.2. Results

Fig. 1 shows the main results of the experiment. Several features are noteworthy. First, animals given access to 32% sucrose increased their goal-tracking times somewhat faster than those receiving 4% sucrose, but the difference, if any, was transient and disappeared late in training. A Sucrose (32%, 4%) × Session (1–20) analysis of Groups 32 vs. 4 yielded only a significant session effect, $F(19, 266) = 25.54$, $p < 0.001$. Group 32-4's single alternation access to 32% and 4% sucrose produced a sharp tendency for goal-tracking times to go up (in odd-numbered sessions) and down (in even-numbered session) early (Sessions 3–10) and late in training (Sessions 17–20), but it was not present at the outset of training (Sessions 1–3) or during the middle portion of training (Sessions 10–14). A repeated-measure analysis of the times produced by this group only in these two types of sessions indicated a significant type of session by session interaction, $F(9, 63) = 4.65$, $p < 0.001$. The session effect was also significant, $F(9, 63) = 7.36$, $p < 0.001$, but the difference between 32% and 4% trials did not reach a significant level, $F(1, 7) = 4.49$, $p < 0.08$.

The main results were comparisons between each of the unshifted controls with the corresponding sessions of the alternating group. Thus, a comparison between Groups 32 and 32–4 only on the ten sessions in which both groups received access to 32% sucrose indicated an effect of session, $F(9, 126) = 24.73$, $p < 0.001$. Interestingly, the main effect of contrast was marginally nonsignificant, $F(1, 14) = 4.29$, $p < 0.06$, but the effect would have been in the opposite direction to that of a cSPC effect, namely, lower performance in the upshifted compared to the unshifted control—a reversed cSPC effect. Unlike the upshift comparison, an assessment of Groups 4 and 32–4 on the ten sessions in which both groups received access to 4% sucrose revealed a significant cSNC effect, $F(1, 14) = 11.57$, $p < 0.005$. There was also a session effect, $F(9, 126) = 15.41$, $p < 0.001$, but a negligible interaction, $F < 1$.

Thus, these results replicated those reported by Flaherty et al. (1983) using a similar procedure in terms of the cSNC effect, but not in terms of the cSPC effect. Flaherty et al. attributed the reduced size of the cSPC effect across sessions to a ceiling effect, an explanation that cannot be applied to the current data. As shown in Fig. 1, the performance of Group 32 was rather low initially and still the cSPC effect did not occur. In fact, none of the sessions yielded evidence of increased consummatory performance in upshifted animals relative to their unshifted controls. This evidence suggests that whereas relative reward value affected

behavior during downshifted sessions, using these parameters, it was the absolute value that influenced behavior during upshifted sessions.

Why was there a discrepancy between our findings and those reported by Flaherty et al. (1983) in terms of reward upshift, but not in terms of reward downshift? There were several procedural differences between these experiments that might account for the discrepant results. First, Flaherty et al. (1983) used Sprague-Dawley rats whereas we used Wistars. There is no evidence of differences in the strength of the cSNC effect with commercially available rat strains (Flaherty, 1996, pp. 44–45), Moreover, we have reported in different experiments from our lab, reliable cSNC effects with Sprague-Dawley, Long-Evans, and Wistar rats (e.g., Glueck et al., 2015; Wood et al., 2005). However, perhaps there are strain differences in the response to reward upshift that have not yet been studied. Second, Flaherty et al. (1983) used lick frequency as a dependent variable, whereas goal-tracking time was used in Experiment 1. As stated previously, both measures have yielded similar outcomes with respect to cSNC across a variety of manipulations. Although it seems unlikely that these two measures would not covary significantly, some experiments in this series were designed to measure lick frequency and, as will be shown below, the results were consistent across measures. Third, rats in Flaherty et al.'s (1983) experiment received their daily ration of food 15 min after the sessions, whereas our animals received their supplemental food after a variable period ranging between 15 and 45 min after the session. Research on time horizons suggests that, depending on the conditions of the experiment, postsession feeding episodes occurring 4 and 16 min after a session, but not 32 min after, may affect behavior during the session (Lucas et al., 1988). While it is difficult to determine whether the intervals used in the present experiments had an effect on session performance, the fact that Flaherty et al. (1983) used a shorter period and still were able to observe both cSPC and cSNC suggests that this was probably not a relevant factor in the present experiments. Finally, Flaherty et al. (1983) started their single-alternation training with access to 32% sucrose, whereas Experiment 1 started with access to 4% sucrose. However, Experiments 2 and 3, both also involving single-alternation training, started with the large reward (48% and 24% sucrose, respectively) and still produced no evidence of cSPC. Thus, there seem to be no strong reasons to believe that the failure to obtain evidence of cSPC was due to a procedural difference between Flaherty et al.'s (1983) experiment and Experiment 1 in this series.

3. Experiment 2

An important shortcoming of the previous results is that there was no statistical evidence that unshifted animals responded differently to 32% and 4% sucrose, although the presence of cSNC in several trials suggests that animals did differentiate the solutions. However, it is possible that negative discrepancies are detected at lower disparities between solutions, but positive discrepancies require greater disparities—a possibility consistent with negativity bias. In Experiment 2, animals were exposed to 48% and 4% sucrose solution, a 12:1 ratio (compared to an 8:1 ratio in Experiment 1). In a first phase (Sessions 1–10), the conditions of training were similar to those enforced in the previous experiment, except for the higher sucrose concentration. Because 48% sucrose has the potential to induce substantial satiety within a 300-s session, a second phase involved 100-s sessions (Sessions 11–20) under the same conditions of training. Finally, in a third phase (Sessions 21–30), all animals were exposed to 48% sucrose in an attempt to demonstrate cSPC under more conventional conditions.

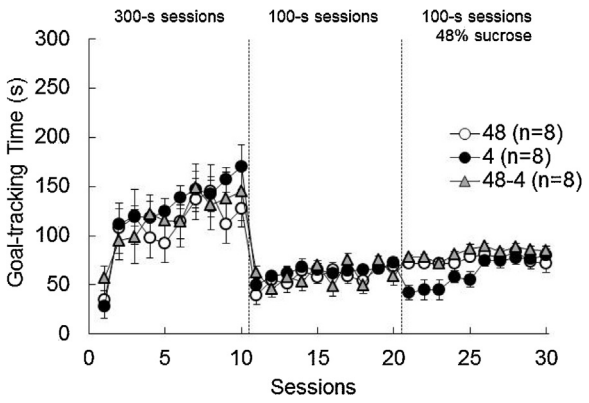

Fig. 2. Mean (±SEM) goal-tracking time for groups receiving access to 48% sucrose in every session (Group 48) and 4% sucrose in every session (Group 4). Group 48–4 received single alternation of 48% and 4% sucrose on Sessions 1–20, followed by access to 48% sucrose in every session thereafter. Sessions were 5-min long (left panel) and 100-s long (middle and right panels). Results from Experiment 2.

3.1. Method

3.1.1. Subjects and apparatus

Subjects were 24 male Wistar rats, experimentally naive. Animals were bred and maintained as described in Experiment 1, including the 81–84% deprivation criterion. Ad libitum weights at approximately 90 days of age ranged between 397 and 616 g. The same conditioning boxes and maintenance conditions described in Experiment 1 were used here.

3.1.2. Procedure

Animals were matched by ad libitum weight and randomly assigned to one of three groups ($n = 8$): Group 48–4 (single alternation of 48% and 4% sucrose across days), Group 48 (48% sucrose in every session), or Group 4 (4% sucrose in every session). Animals were weighed prior to each session (7 days/week). The Group 48 received 48% sucrose throughout the study (Sessions 1–30), whereas animals in Group 4 received 4% sucrose on Sessions 1–20 and then were upshifted to 48% sucrose on Sessions 21–30. Animals in Group 48-4 received 48% sucrose on odd-numbered sessions (Sessions 1–20) and 4% sucrose on even-numbered sessions (Sessions 1–20). Group 48-4 was then upshifted to 48% sucrose during Sessions 21–30. Sessions 1–10 were 300 s in duration; for the remaining sessions (11–30), session duration was reduced to 100 s. Solutions were prepared w/w, as described above. All other procedural conditions were as described in Experiment 1.

3.2. Results

Fig. 2 shows the three phases of this experiment. Sessions 1–10 were 5-min long—the usual duration in these experiments. There was no evidence of either a differentiation of goal-tracking times as a function of sucrose concentration between unshifted groups (48% vs. 4%) or an alternating behavioral pattern in the group exposed to both concentrations in a single alternation schedule. We replicated the same four analyses that were computed in Experiment 1 for the results of this initial phase and obtained only a session effect in each of them, $Fs > 5.67$, $ps < 0.002$. Thus, increasing the disparity between the two rewards yielded none of the expected results and, in particular, no evidence of either cSPC or cSNC effects.

Fig. 2 also shows the results obtained on Sessions 11–20 with a reduction in the duration of the sessions to 100 s. There still was no apparent differentiation between animals exposed to 48% and 4% sucrose and no evidence of either cSPC or cSNC effects in these results. These analyses yielded only significant session effects,

Fs > 3.76, *ps* < 0.01. However, there was significant behavioral alternation. A repeated-measure analysis of the performance of Group 48–4 indicated higher goal-tracking times under 48% sucrose than under 4% sucrose, $F(1, 7) = 11.94$, $p < 0.02$. This pattern of results (behavioral alternation and lack of incentive contrast) suggests that consummatory behavior was under the control of the absolute value of these rewards.

In the final phase of this experiment, Sessions 21–30, session length was kept at 100 s, but all the animals were given access to 48% sucrose. Thus, Group 4 experienced a 4-to-48% sucrose upshift after 20 preshift sessions, Group 48 served as an unshifted control, and the animals exposed to the single alternation schedule now received access only to 48% sucrose. Although we were anticipating a cSPC effect, the reward upshift yielded consummatory suppression relative to the unshifted control. A comparison of Groups 48, 4, and 48–4 (all receiving access to 48% sucrose) indicated a significant contrast by session interaction, $F(18, 189) = 2.16$, $p < 0.007$. There were also significant main effects for contrast, $F(2, 21) = 9.50$, $p < 0.002$, and sessions, $F(9, 189) = 6.81$, $p < 0.001$. To determine the source of the interaction effect, pairwise LSD comparisons were calculated with the error term derived from the main analysis. These comparisons indicated that upshifted animals (Group 4) were significantly more *suppressed* than unshifted controls (Group 48) on Sessions 21–23 and 25, *ps* < 0.02, and significantly more *suppressed* than the alternating group (Group 48–4) on Sessions 21–26, *ps* < 0.04. The performance of Groups 48 and 48-4 did not differ in any of the sessions.

The effect of a 4-to-48% sucrose upshift on consummatory behavior (Fig. 2, Sessions 21–30) appears visually more like the usual effect of a sucrose downshift, yielding a transient behavioral suppression, rather than an enhancement. Interestingly, the group that had received exposure to both 48% and 4% sucrose in single alternation did not exhibit suppression, but rather a behavior similar to that of unshifted 48% controls. The transient nature of the behavioral suppression induced by reward upshift suggests a comparison between the current reward (48% sucrose) and the remembered preshift reward (4% sucrose).

4. Experiment 3

This experiment tests again the effects of single alternation with two modifications. First, lower concentrations of sucrose solutions were used, 24% and 3% sucrose. These concentrations produce an 8:1 disparity ratio. Pilot studies suggested that these concentrations would produce clear evidence of differential performance in unshifted controls, thus controlling for the possibility that the absence of cSPC was due to a failure to differentiate the solutions. Such differential performance was not observed in the first two experiments. Second, lick frequency was used as a dependent measure instead of goal-tracking time. Although there is evidence of the covariation of these two measures (Papini et al., 1988; Riley and Dunlap, 1979), this change brings the experiment closer to the original demonstrations of cSPC with the alternating schedule (Flaherty et al., 1983).

4.1. Method

The subjects were 29 male Wistar rats, all experimentally naïve, with ad libitum weights ranging between 397 and 567 g. Maintenance conditions and apparatus were as described in Experiment 1, including the 81–84% deprivation criterion. Animals were matched in terms of ad libitum weights and randomly assigned to one of three groups: Group 24 ($n = 10$), Group 3 ($n = 9$), or Group 24–3 ($n = 10$). The procedure was the same as that described for Experiment 1, except for the following. First, there were 10 sessions of training. Second, 24% and 3% sucrose solutions were used. The solutions were prepared w/w as described above. Third, lick frequency (the number of licks recorded in a 5-min session) was the dependent variable. It was recorded based on the same circuit described earlier for goal-tracking time. As noted above, goal-tracking time and lick frequency correlate with each other (Mustaca et al., 2002), and tend to produce results similar to those observed with amount of fluid intake (Manzo et al., 2015). Despite evidence to the contrary, it seemed possible that a different dependent variable could potentially provide new evidence of the effects of reward upshift on consummatory behavior. Fourth, in the present experiment and all that follow in this series, there was no need to apply the rule of repeating the first session as all the animals show evidence of consummatory behavior.

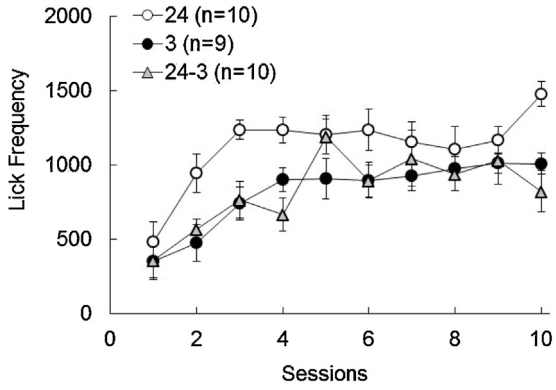

Fig. 3. Mean (±SEM) lick frequency for groups receiving access to 24% sucrose in every session (Group 24) and 4% sucrose in every session (Group 4). Group 24–3 received single alternation of 24% and 3% sucrose on Sessions 1–10. Results from Experiment 3.

4.2. Results

The results of this experiment were analyzed following the same procedures used for Experiment 1's data. The results are presented in Fig. 3. With these concentrations and dependent measure, it is clear that animals receiving access to 24% sucrose acquired the consummatory behavior faster than animals receiving access to 3% sucrose. A Sucrose (24%, 3%) × Session (1–10) analysis of Groups 24 vs. 3 yielded significant sucrose, $F(1, 17) = 9.60$, $p < 0.008$, and session effects, $F(9, 153) = 12.77$, $p < 0.001$. Single alternation in Group 24–3 did not produce a sharp difference between access to 24% and 3% sucrose. A repeated-measure analysis of lick frequency in these two types of sessions indicated a significant session effect, $F(4, 36) = 12.83$, $p < 0.001$, but the type of trial by session interaction fell short of significance, $F(4, 36) = 2.53$, $p = 0.057$. Similarly, an analysis of the upshift and downshift effects (Group 24-3 vs. either Group 24 or 3, respectively) indicated only significant changes across sessions, Fs > 10.76, ps < 0.001. Therefore, having a clear behavioral differentiation between the unshifted controls did not guarantee the emergence of either of the two contrast effects sought in this experiment. These results failed to replicate those reported by Flaherty et al. (1983) using the same dependent measure (lick frequency), but with different sucrose concentrations (24–3% rather than 32–4%).

5. Experiment 4

Experiment 4 introduced several procedural modifications in an attempt to look for evidence of cSPC under different conditions relative to the previous three experiments. First, Experiment 4 explored the effects of a regular reward upshift as well as single alternation

using lower sucrose concentrations. Pilot experiments suggested that lower concentrations produce extreme differences in consummatory behavior, a fact that may be required to induce cSPC. Second, a small number of preshift sessions was used. Experiments on negative contrast usually involve 10 preshift sessions (Flaherty, 1996), but rather than extrapolating this number to the case of reward upshift, we decided to run 6 preshift sessions. If a ceiling effect is an important factor in the detection of cSNC (cf. Flaherty et al., 1983), then the reward upshift should occur before consummatory behavior reached its asymptote with a fewer number of preshift sessions. Third, female rats were used in this experiment and, although there is no evidence of sexual differences in cSNC (cf. Flaherty, 1996), the issue was not addressed for cSPC, as far as the authors know. An explicit sex comparison within a single experiment was planned for a subsequent experiment provided that using females would result in strong evidence of cSPC. By modifying several training parameters at the same time we are prioritizing the potential to detect evidence of cSPC at the expense of determining which factor is responsible for the effect. It was assumed that once evidence was detected, subsequent experiments would help determine the actual parameters that were responsible for the finding.

5.1. Method

The subjects were 32 female Wister rats, experimentally naïve, and with ad libitum weights ranging between 216 and 297 g. Animals were reared and maintained as described in Experiment 1, including the 81–84% deprivation criterion. The same 8 conditioning boxes were used for training. Animals were matched for ad libitum weights and randomly assigned to one of four groups ($n = 8$) differing in the sucrose concentration available during preshift sessions: 12%, 2%, 1%, or 0.5% sucrose. All sucrose solutions were mixed w/w with distilled water. These solutions were administered during Sessions 1–6. On Sessions 7–10, all animals received access to 12% sucrose; thus, three groups were upshifted, whereas Group 12 remained as the unshifted control. On Sessions 11–16, Groups 2–12, 1–12, and 0.5–12 alternated between the solution they had received during preshift sessions and 12% sucrose; three such alternating cycles were run. Group 12 remained as the unshifted control. Goal-tracking time was again used as the dependent measure. All other procedural details and statistical analysis were as described in previous experiments.

5.2. Results

The sucrose concentrations chosen for this experiment yielded distinct preshift functions ordered by concentration, as shown in Fig. 4, left panel. A Contrast (12, 2–12, 1–12, 0.5–12% sucrose) × Session (1–6) analysis indicated significant effects for the interaction, contrast, and session factors, $Fs > 4.44$, $ps < 0.001$. Pairwise LSD tests on the contrast factor revealed that all concentrations were different from each other during these sessions as a whole, $ps < 0.009$. As shown in the middle panel of Fig. 4, however, the upshift to 12% sucrose yielded no evidence of cSPC; rather, consummatory behavior remained ordered by sucrose concentration. Animals that received preshift exposure to 0.5% sucrose performed the lowest whereas those receiving 2% sucrose performed very close to the unshifted, 12% sucrose controls. A Contrast × Session (7–10) analysis provided only a significant main effect of contrast, $F(3, 28) = 5.49$, $p < 0.005$. Pairwise LSD tests based on the main effect of sucrose and derived from the main analysis indicated that whereas Group 0.5–12 differed from Groups 2–12 and 12, $ps < 0.008$, none of the other comparisons reached significance.

During a final phase involving single alternation training of each preshift concentration and 12% sucrose (e.g., 0.5-12-0.5-12-0.5. . .), there was again no evidence of cSPC. However, interestingly, groups were now closer to each other during sessions in which they all received access to 12% sucrose. A Sucrose × Session (11–16) analysis revealed large effects for all three factors, $Fs > 12.64$, $ps < 0.001$. Pairwise LSD comparisons now based on the interaction effect were computed to determine group differences on each session. The following results were observed for sessions with exposure to the preshift concentration (Sessions 11, 13, and 15): Groups 0.5–12 and 1–12 never differed from each other, but they were significantly more suppressed than Groups 2–12 and 12 on each of these sessions, $ps < 0.001$. Regarding sessions of exposure to 12% sucrose (Sessions 12, 14, and 16), Group 0.5–12 differed from Groups 2–12 and 12 on Session 12, $ps < 0.05$. None of the other comparisons yielded significant results.

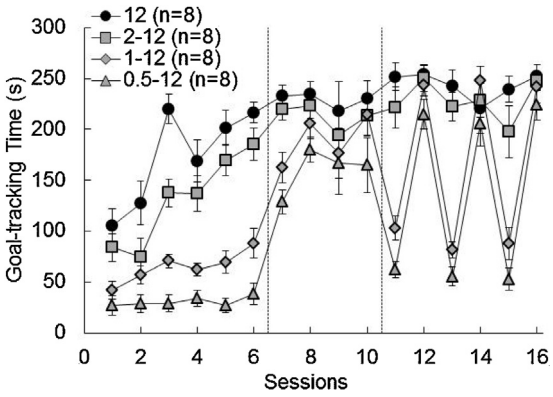

Fig. 4. Mean (±SEM) goal-tracking time during the preshift (Sessions 1–6, left panel), postshift (Sessions 7–10, middle panel), and single alternation training (Sessions 11–16, right panel) in groups receiving 12, 2, 1, or 0.5% sucrose during preshift sessions. During Sessions 7–10, all groups received access to 12% sucrose. During Sessions 11–16, groups alternated between whatever concentration they received during preshift sessions and 12% sucrose. Group 12 received access to 12% sucrose throughout training. Results from Experiment 4.

Clear preshift differences in performance were observed in this experiment and yet no evidence of cSPC. One aspect of the results of the upshift phase is noteworthy. The level of consummatory performance during these sessions was higher than during preshift session, but ordered according to the degree of disparity between the solutions. Thus, the greater the reward disparity between preshift and postshift concentrations, the lower the response level after the upshift—a reversed cSPC effect. These results suggest the concurrent influence of opposing factors on performance, one driving performance upward (an increase in reward value) and one driving the performance downward (a novelty-related factor, such as taste neophobia or generalization decrement). Consistent with this novelty hypothesis, differences between groups during access to 12% sucrose in the alternation phase dissipated toward the end of training.

6. Experiment 5

Experiment 5 replicated the conditions of the previous experiment with one important difference: Postshift sessions were 20-min long, rather than 5-min long. This change was introduced on the assumption that consummatory behavior would decrease over a relatively long session, thus minimizing a potential ceiling effect. In addition, if novelty is a factor in upshift experiments, then extending the session duration may allow its effects to dissipate, thus potentially uncovering the effects of reward upshift on consummatory behavior. This would be observed as a within-session crossing-over of functions between the upshifted and unshifted conditions.

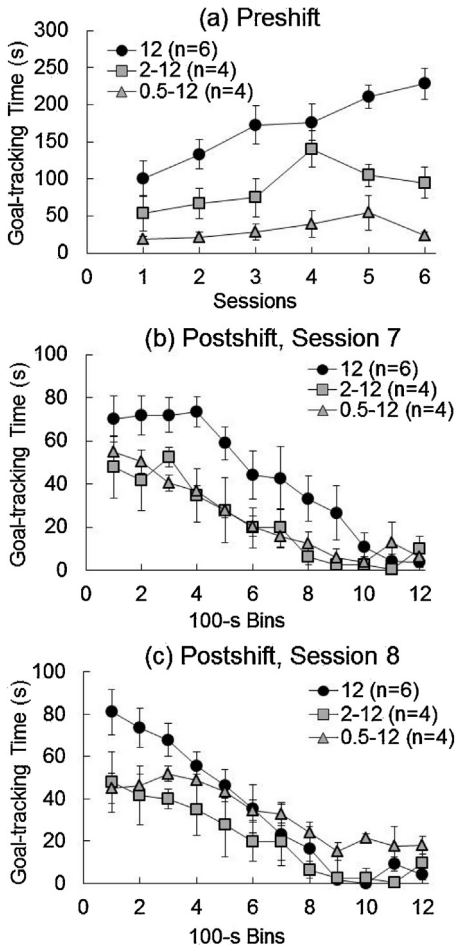

Fig. 5. Mean (±SEM) goal-tracking time during (a) preshift Sessions 1–6, between-session performance; (b) Postshift Session 7, within-session performance; and (c) Postshift Session 8, within-session performance. Within-session data are plotted against 100-s bins, for a total of 20 min. Groups are labeled according to the sucrose concentration received during preshift sessions: 12%, 2%, or 0.5% sucrose. All groups received access to 12% sucrose during postshift sessions. Results from Experiment 5.

6.1. Method

The subjects were 28 female Wistar rats, experimentally naïve, and maintained as described in Experiment 1. Ad libitum weights at approximately 90 days of age ranged between 209 and 257 g. The same conditioning boxes and maintenance conditions described in Experiment 1 were used here, including the 81–84% deprivation criterion. The training procedure was the same used in Experiment 4 with the following exceptions. First, only 12%, 2%, and 0.5% sucrose solutions were used here. Second, the two postshift sessions (Sessions 7 and 8) were 20-min long. Within-session performance was recorded in twelve 100-s bins.

6.2. Results

As shown in Fig. 5, top panel, the preshift performance of these groups was similar to their homonyms from Experiment 4 (Fig. 4). Consummatory behavior was differentially affected by sucrose concentration, yielding distinct functions for each group. A Contrast by Session (1–6) analysis indicated significant effects for all three factors, $Fs > 3.12$, $ps < 0.004$. Pairwise tests on the main effect of contrast revealed that all groups were different from each other, $ps < 0.009$.

Fig. 5 also shows the postshift performance in the middle and lower panels. Clearly, unshifted controls performed above the two upshifted groups on almost all bins during Session 7. An analysis confirmed a significant group effect, $F(2, 11) = 5.87$, $p < 0.02$, and a significant decrease across bins, $F(11, 121) = 21.25$, $p < 0.001$, but a nonsignificant interaction. The source of the contrast effect was the difference between Group 12 and Groups 2–12 and 0.5–12, $ps < 0.03$, which did not differ from each other. The first upshift session thus produced evidence of a reversed cSPC effect, with upshifted groups performing below unshifted controls.

In Session 8, however, these differences were reduced and, interestingly, Groups 12 and 0.5–12 crossed in the middle of the session. Although the initial difference between these groups points to a suppressive effect of the upshift on consummatory behavior, the subsequent crossing over is consistent with a cSPC effect. Animals upshifted from 0.5% to 12% sucrose (but not those upshifted from 2% to 12% sucrose) took longer to reach lower performance levels by the end of the 20-min session. A Contrast × Bin analysis of Session 8 data yielded a marginally nonsignificant interaction effect, $F(22, 121) = 1.63$, $p = 0.051$. The bin effect was significant, $F(11, 121) = 19.56$, $p < 0.001$, but the contrast effect was nonsignificant. To focus on the two groups that showed a crossing over in the course of Session 8, goal-tracking times from Groups 12 and 0.5 were selected for a follow-up analysis. In this case, the interaction effect was significant, $F(11, 88) = 2.47$, $p < 0.02$. Pairwise LSD tests determined that while Group 12 was significantly above Group 0.5–12 on Bins 1–2, $ps < 0.02$, they were reversed on Bin 10, $p < 0.04$. Therefore, this experiment provided the only evidence consistent with cSPC, but it was rather weak.

7. Experiment 6

Some results suggest that both iSPC and cSPC may be more easily observed under conditions of low deprivation (Shanab and Ferrell, 1970; Panksepp and Trowill, 1971). To explore this possibility, Experiment 6 used a design similar to that of the previous experiment, but with animals maintained at a 100% level of deprivation (i.e., at a weight similar to that of the animal's ad libitum weight assessed before the start of training).

7.1. Method

The subjects were 22 female Wistar rats, experimentally naïve, and kept under the same conditions described in Experiment 1. Ad libitum weights recorded approximately at 90 days of age varied between 212 and 261 g. There two novel features in this experiment, relative to the previous one. First, animals were kept at ±4% of the ad libitum weight measured at 90 days of age (i.e., a 96–104% deprivation criterion) for the duration of the experiment by giving them extra food after the training session as described in Experiment 1. In this experiment, animals are said to be "nondeprived," although it is acknowledged that rats tend to increase their weight continuously during this age period. Second, three upshift sessions, rather than two, were included (Sessions 7–9). Otherwise, the present experiment used the same procedure described in Experiment 5, including the conditioning boxes.

7.2. Results

The preshift performance of nondeprived rats was considerably depressed relative to what was observed in Experiments 4–5 with food-deprived animals, but the groups still segregated according to sucrose concentration (Fig. 6). A Contrast × Session (1–6) analysis indicated a significant contrast effect, $F(2, 19) = 17.72$, $p < 0.001$; the session effect was also significant, $F(5, 95) = 3.79$, $p < 0.005$, but the interaction was not significant. Pairwise LSD tests based on the

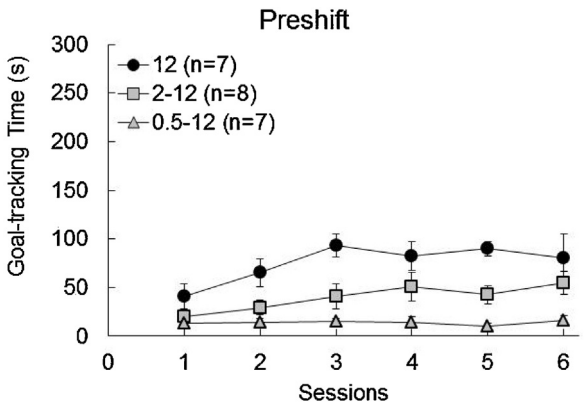

Fig. 6. Mean (±SEM) goal-tracking time during preshift Sessions 1–6 for groups given access to 12, 2, or 0.5% sucrose. Results from Experiment 6.

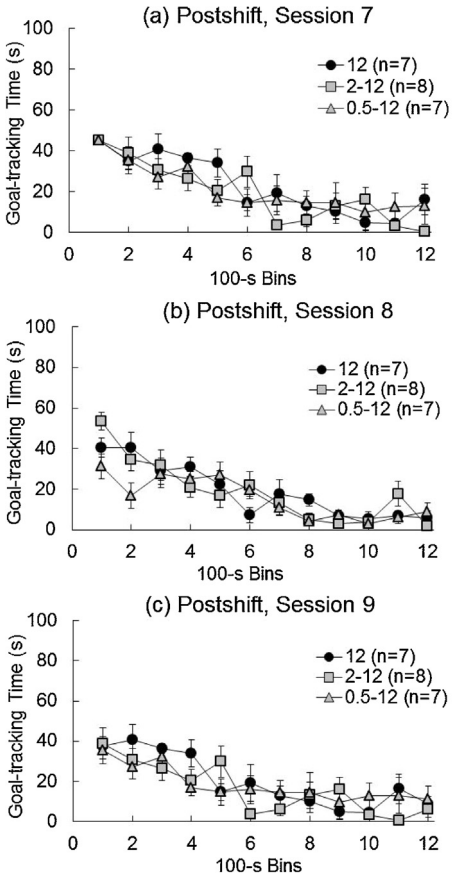

Fig. 7. Mean (±SEM) goal-tracking time during postshift Sessions 7 (top), 8 (middle), or 9 (bottom) for groups given access to 12, 2, or 0.5% sucrose and across 100-s bins (i.e., within-session performance). Results from Experiment 6.

main contrast effect indicated that all gorups were different from each other, $ps < 0.02$.

Fig. 7 shows the within-session performance for the three postshift sessions. The bin effect was significant on Sessions 7–9, $Fs(11, 209) > 11.77$, $ps < 0.001$. However, the sucrose by bin interaction was significant only on Session 8, $F(22, 209) = 2.07$, $p < 0.006$. Pairwise LSD comparisons indicated that the source of this interaction effect was the occasional crossing over of groups. Thus, Group 0.5–12 was significantly *below* Group 12 on Bins 2 and 8, $ps < 0.03$, and Group 2–12 was significantly *above* Group 12 on Bin 6, but *below* it on Bin 8, $ps < 0.05$. Thus, these differences were neither consistent nor large.

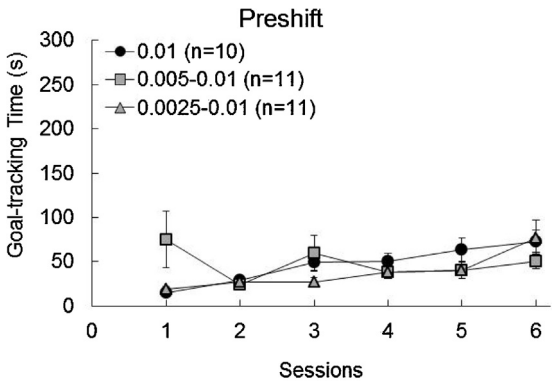

Fig. 8. Mean (±SEM) goal-tracking time during preshift Sessions 1–6 for groups given access to 0.01, 0.005, or 0.0025 M saccharin. Results from Experiment 7.

8. Experiment 7

Rabiner et al., 1988 reported that an upshift in saccharin concentration from 0.0025 to 0.01 M solutions yielded evidence of an iSPC effect. Indeed, the effect was not only present, but was undiminished during ten postshift sessions. Experiment 7 sought a demonstration of cSPC using the same concentrations plus an intermediate one, 0.005 M saccharin, but with 20-min long postshift sessions to minimize a potential ceiling effect.

8.1. Method

The subjects were 22 female, 90-day old Wistar rats, all experimentally naïve and maintained as described in Experiment 1, including the 81–84% deprivation criterion. Ad libitum weights varied between 212 and 261 g. The conditioning boxes were those described above. This experiment replicated the procedure used in Experiment 5, except for the following. Animals were assigned to a group with access to different concentrations of saccharin during Sessions 1–6: Group 0.01 ($n = 10$), Group 0.005–0.01 ($n = 11$), or Group 0.0025–0.01 ($n = 11$). All groups had access to the 0.01 M saccharin solution during Sessions 7–9.

8.2. Results

Consummatory behavior was not affected differentially by different saccharin concentrations. Moreover, saccharin supported relatively low levels of goal-tracking time (e.g., all group means were below 100 s; Fig. 8). A statistical analysis of preshift performance identified a significant contrast by session interaction, $F(10, 145) = 2.19$, $p < 0.03$, and a significant change across sessions, $F(5, 145) = 3.54$, $p < 0.006$. However, pairwise LSD tests indicated that these effects were probably due only to significantly higher goal tracking in Group 0.005 than in the other two groups on Session 1, $p < 0.05$. For postshift Sessions 7–9 (Fig. 9), the bin effect was significant in all three sessions, $Fs(11, 319) > 26.86$, $ps < 0.001$, but the only other effect reaching significance was the contrast by bin interaction on Session 9, $F(22, 319) = 1.68$, $p < 0.04$. Pairwise LSD tests indicated that this was caused by Group 0.01 (the unshifted controls) having higher goal-tracking times than Group 0.0025–0.01 on Sessions 3 and 7, and higher than Group 0.005-0.01 on Session 7, $ps < 0.05$. As with nondeprived rats (Experiment 5), using saccharin produced neither consistent nor substantial evidence of either cSPC or reversed cSPC.

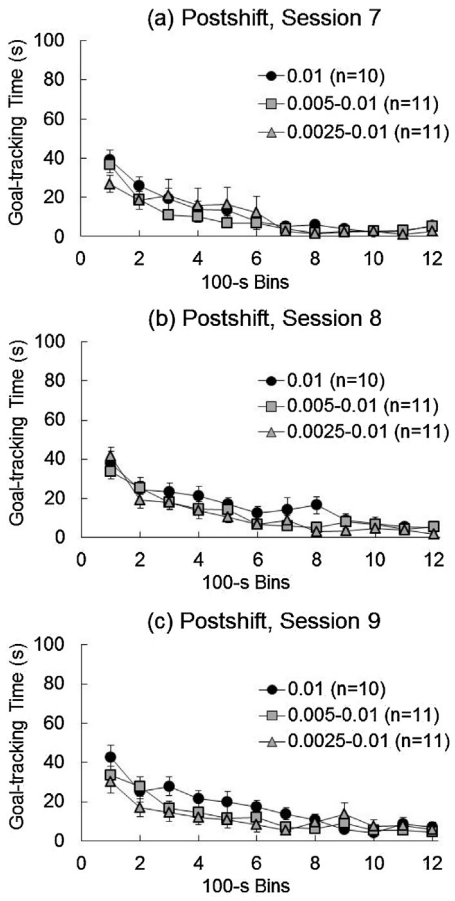

Fig. 9. Mean (±SEM) goal-tracking time during postshift Sessions 7 (top), 8 (middle), or 9 (bottom) for groups given access to 0.01, 0.005, or 0.0025 M saccharin. Results are displayed in 100-s bins (i.e., within-session performance). Results from Experiment 7.

9. Experiment 8

Two conclusions follow from the results of previous experiments. First, the upshift manipulation resulted in a level of consummatory behavior inversely related to the reward disparity (e.g., Fig. 4, middle panel), suggesting a connection with a factor derived from novelty. Second, the single alternation manipulation (e.g., Fig. 4, right panel) showed a tendency for that inverse relationship to be reduced and eventually eliminated. Two potential mechanisms could produce a transient suppression that is reduced after periodic exposure to the postshift solution: taste neophobia and stimulus generalization decrement. Taste neophobia refers to a reluctance to consume novel foods (Alley and Potter, 2011). Although 12% sucrose is not completely novel to animals that consumed solutions of lower concentrations, the shift in sweetness intensity may promote neophobia, making the animals less likely to consume the food. Taste neophobia is reduced as the animal becomes more familiar with the upshifted solution, leading to a gradual increase in food consumption (e.g., De la Casa and Díaz, 2013). The present results also tend to show an increase in consummatory behavior directed at 12% sucrose during later sessions (e.g., Fig. 4, right panel). Stimulus generalization decrement refers to behavioral disruption caused by novel stimulus conditions, relative to previous conditions in the same situation (Bitterman, 1979). Thus, animals trained with one sucrose solution could show a decrement in responding to a new solution simply because it is different. The present experiment was designed to test the effects of novelty on reward upshift in general, without distinguishing between taste neophobia and stimulus generalization decrement. As it was the case with previous experiments, the assumption was that evidence of cSPC under these conditions would later lead to a systematic manipulation of reward novelty.

In addition to these decremental effects of novelty on reward consumption, there is obviously an incremental effect during upshift sessions. That is, animals are not simply rejecting the upshifted solution; they are drinking less than unshifted controls, but more than they used to drink during preshift sessions. Two mechanisms could increase reward consumption in these experiments, namely, absolute and relative incentive value. An upshift in absolute incentive value should lead to levels of consummatory behavior similar to those of unshifted controls. An upshift in relative incentive value should lead to higher behavioral levels than those displayed by unshifted controls (i.e., cSPC).

Experiment 8 sought to test for the decremental effects of novelty by preexposing animals to either 12% sucrose or water in their cage before the start of the experiment. Such preexposure would familiarize animals with the upshift reward, thus reducing the intensity of neophobia and/or generalization decrement. Thus, animals preexposed to 12% sucrose were expected to exhibit less suppression during upshift sessions than animals preexposed to water.

9.1. Method

The subjects were 37 female, 90-day old, experimentally naïve Wistar rats, maintained as described in Experiment 1, including the 81–84% deprivation criterion. Ad libitum weights varied between 265 and 375 g. The conditioning boxes were those described above. This experiment used again the same procedure described in Experiment 5, except for the following. Once the animals reached the target deprivation weight, they received the preexposure treatment. For 3 days animals were preexposed to 10 ml of either 12% sucrose ($n = 19$) or water ($n = 18$) in their cage. Bottles with the appropriate fluid were placed in each cage at 10:00 h each of these days and replenished the following day at the same time. During these preexposure days, animals also had free access to water, as they did during the entire experiment. Then, animals in each preexposure condition were randomly assigned to one of two groups. Groups W/12 ($n = 9$) and S/12 ($n = 10$) received access to 12% sucrose in each of 9 sessions. Groups W/0.5–12 ($n = 9$) and S/0.5-12 ($n = 9$) received access to 0.5% sucrose on Sessions 1–6 and then access to 12% sucrose on Sessions 7–9. As in Experiment 3, the dependent variable was lick frequency. Other aspects of the training procedure were as described in Experiment 5.

9.2. Results

All animals consumed the fluid (12% sucrose or water) during the three preexposure days. Lick frequency for the four groups of this experiment during preshift sessions is plotted in Fig. 10. A Contrast (12%, 0.5%) × Preexposure (sucrose, water) × Session (1–6) analysis indicated a significant contrast by session interaction, $F(5, 165) = 11.93$, $p < 0.001$, and significant main effects for contrast and session, $Fs > 11.20$, $ps < 0.001$. None of the factors involving the preexposure manipulation had an effect on preshift performance.

Fig. 11 presents the results of the three postshift sessions in which all animals received access to 12% sucrose. Two outcomes are noteworthy, both transient, occurring only on Session 7. First, there was a sharp reduction in licking during the early bins of Session 7 for upshifted animals preexposed to water, but not for upshifted animals preexposed to 12% sucrose. Second, upshifted animals in Group W/0.5–12 ended Session 7 at a higher response level than unshifted controls in Group W/12. Such crossing-over is consistent with a cSPC. On Session 8 there was also a weak trend for upshifted

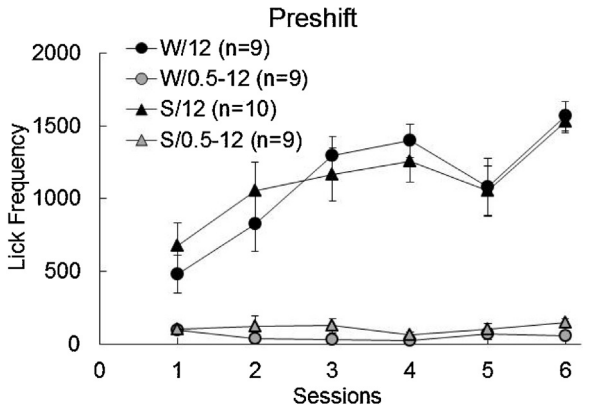

Fig. 10. Mean (±SEM) lick frequency during preshift Sessions 1–6 for groups preexposed to either 12% sucrose (S) or water (W) in their cages before the start of the experiment. Groups received access to 12% or 0.5% sucrose. Results from Experiment 8.

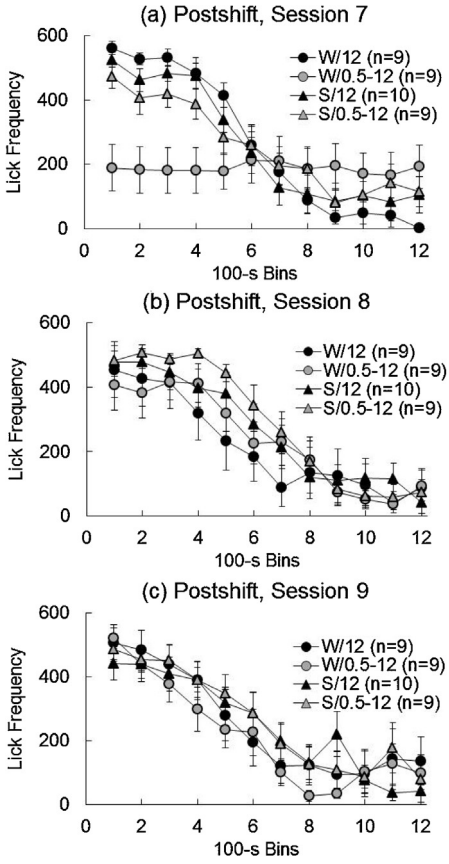

Fig. 11. Mean (±SEM) lick frequency during postshift Sessions 7 (top), 8 (middle), or 9 (bottom) for groups given preexposure to 12% sucrose (S) or water (W) followed by preshift access to 12 or 0.5% sucrose. During these postshift sessions, all groups received access to 12% sucrose. Performance was recorded in 100-s bins (i.e., within-session performance). Results from Experiment 8.

groups to lick at a higher frequency than the unshifted controls. These results receive statistical support.

A Contrast × Preexposure × Bin analysis of Session 7 data (Fig. 11, top panel) indicated a significant triple interaction, $F(11, 363) = 4.27$, $p < 0.001$. Also significant were the bin by contrast interaction and the bin effect, $Fs > 9.37$, $ps < 0.001$. All other effects were nonsignificant. Pairwise LSD tests were computed independently as a function of preexposure condition and contrast condition to determine the source of the triple interaction. For groups preexposed to water, Group W/12 showed higher lick frequency than Group W/0.5–12 on Bins 1–5, $ps < 0.002$. However, the order was reversed on Bins 9 and 12, $ps < 0.04$. This result confirms that the crossing-over mentioned above was significant. Group preexposed to 12% sucrose did not differ at any point during Session 7. For groups exposed to a 0.5-to-12% sucrose upshift, Group S/0.5–12 was significantly above Group W/0.5–12 on Bins 1–4, $ps < 0.004$, whereas Groups S/12 and W/12 did not differ in any of the bins.

Similar analyses for Sessions 8–9 (Fig. 11, middle and bottom panels) indicated only significant bin effects, $Fs(11, 363) > 31.30$, $ps < 0.001$. None of the other effects reached significance, including the apparently higher lick frequency of upshifted groups relative to their respective unshifted controls on Session 8.

10. Experiment 9

The lowest nonshifted sucrose solution used in these experiments, 12% sucrose, tended to produce just as high goal-tracking time or lick frequency as solutions of higher concentration. This may introduce a response ceiling preventing cSPC from emerging. The present experiment used a still lower concentration, 2% sucrose, as the unshifted reward. Two groups were exposed to an upshift treatment from 0.5% and 1% sucrose. In addition, this experiment included a downshift manipulation. Groups exposed to 4% and 8% sucrose were devalued to 2% sucrose. These values were chosen to be consistent with the upshift manipulation in terms of the preshift-to-postshift ratios. Thus, a 1-to-2% sucrose upshift and a 4-to-2% sucrose downshift represent 2:1 ratios. In the downshift cases, and based on previous research (Papini and Pellegrini, 2006), a 2:1 ratio was not expected to induce cSNC, but to lead to either a higher or equal performance level as that of controls. Theoretically, a level of responding equal to that of unshifted controls would demonstrate control by absolute reward magnitude. A higher level of consummatory behavior in downshifted groups relative to the unshifted controls (a reversed cSNC effect) would have two implications. A practical implication is that it would demonstrate within a single experiment that a ceiling effect is not constraining behavior in upshifted animals (see Campbell et al., 1970). However, a theoretical implication is that the level of responding previously trained carries over to the downshifted phase, at least when the reward disparity is not strong enough to produce a contrast effect. Such carry-over effect might reflect a number of processes, including resistance to change (Berry and Odum, 2014) and habitual behavior (Adams and Dickinson, 1981). Whatever the case, this may have implications for the upshift case, in which the increase in behavior has not been to the level of the unshifted controls.

10.1. Method

The subjects were 43 female, 90-day old, experimentally naïve Wistar rats, maintained as described in Experiment 1, including the 81–84% deprivation criterion. Ad libitum weights varied between 228 and 354 g. The conditioning boxes were those described previously. This experiment used the same preexposure procedure described in Experiment 8 after the animals reached the target deprivation weight, except that animals were not preexposed to the postshift solution in their cage. Animals were randomly assigned to one of five groups: 8–2 ($n = 8$), 4–2 ($n = 8$), 2 ($n = 9$), 1–2 ($n = 9$), or 0.5–2 ($n = 9$). The group label refers to the sucrose concentration received during each of 6 daily preshift sessions. On Sessions 7–9, all animals received 2% sucrose. Therefore, Groups 8–2 and 4–2 were downshifted, Groups 0.5–2 and 1–2 were upshifted, whereas Group 2 remained as the unshifted control. As in Experiment 3, the dependent variable was lick frequency. Other aspects of the training procedure were as described in Experiment 5.

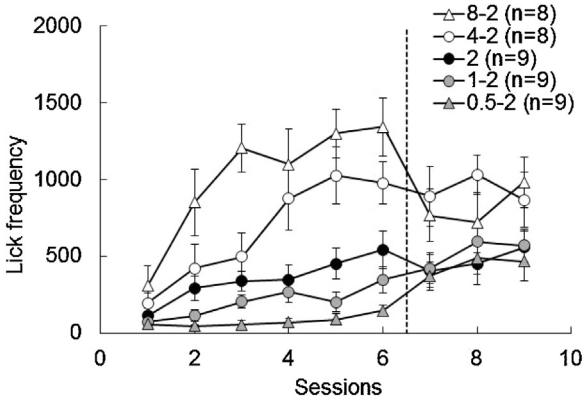

Fig. 12. Mean (±SEM) lick frequency for groups given preexposure to 0.5, 1, 2, 4, or 8% sucrose, followed by postshift exposure to 2% sucrose for all animals. Results from Experiment 9.

10.2. Results

Fig. 12 shows the results of the experiment. Several aspects are worthy of note. First, consummatory behavior during preshift sessions differentially reflected the concentration of sucrose received by the animals. Second, the behavior of the two upshifted groups was similar to that of the unshifted controls, yielding no evidence of either a relative incentive effect (cSPC) or a novelty effect. Third, the consummatory behavior of downshifted groups was somewhat above that of unshifted controls (i.e., no evidence of cSNC), thus providing direct evidence within a single experiment that a ceiling effect is not the cause of the failures to observe the cSPC effect.

Statistical analyses provided support for these observations. A Concentration (0.5, 1, 2, 4, and 8% sucrose) × Session (1–6) analysis of preshift performance indicated that all three factors were significant, $Fs > 3.74$, $ps < 0.001$. LSD pairwise comparisons based on the main effect of sucrose concentration indicated the following pattern: Group 0.5–2 was lower than Groups 2, 4–2, and 8–2, $ps < 0.02$, Group 2 was lower than Groups 4–2 and 8–2, $ps < 0.001$, and Group 4–2 was lower than Group 8–2, $p < 0.005$.

A similar analysis for postshift sessions 7–9 indicated only a significant effect for concentration, $F(4, 38) = 3.43$, $p < 0.02$. LSD pairwise comparisons indicated that Group 2, the unshifted control, did not differ from Groups 0.5–2 and 1–2, but was significantly lower than Groups 4–2 and 8–2, $ps < 0.02$.

Although there was no evidence of either a novelty effect or a cSPC effect in the upshifted groups, downshifted groups showed higher consummatory behavior than unshifted controls. Such behavioral level shows within a single experiment that a higher performance is possible, thus restricting the validity of an explanation of the absence of cSPC in terms of a response ceiling. This effect also suggests the possibility that a shift in reward magnitude, whether positive or negative, must overcome a tendency of behavior to persist at the level developed during preshift trials. This effect may be understood in terms of the behavior's resistance to change in the face of a change in reward magnitude (Berry and Odum, 2014) or in terms of outcome-independent, habitual behavior (Adams and Dickinson, 1981). These factors could also interfere with the expression of a cSPC effect, as observed in the experiments reported in this series.

11. Experiment 10

Experiment 9 produced a hint of a cSPC effect in the 1-to-2% sucrose upshift (see Fig. 12, session 8). The present experiment sought to explore this upshift further by introducing a number of preshift sessions typical of experiments involving higher reward magnitudes. Two groups received access to 1% sucrose for either 10 or 18 preshift sessions and were then upshifted to 2% sucrose for 3 postshift sessions. The assumption was that more extensive preshift training would establish a firm expectation of the lower sucrose concentration thus increasing the salience of the upshift manipulation. Simultaneously, the use of a rather small reward disparity would discourage the suppressive effects of novelty observed with higher concentrations and reward disparities. However, the presence of a novelty-related factor would predict that the consummatory behavior of upshifted animals would still be lower than that of unshifted controls, at least during the first upshift session, independently of the number of preshift sessions.

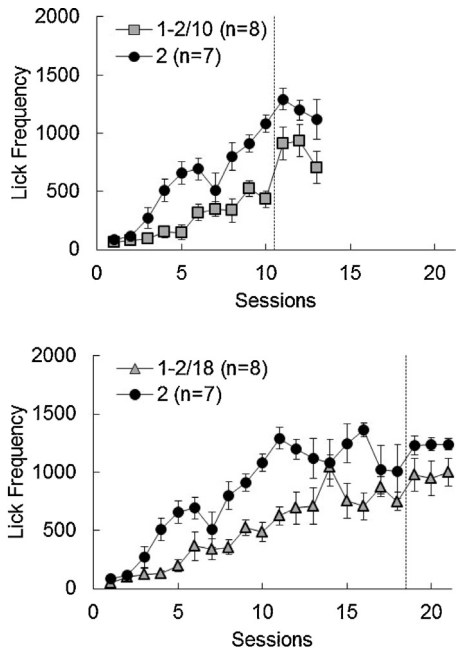

Fig. 13. Mean (±SEM) lick frequency for groups given preshift access to 1% sucrose, followed by postshift exposure to 2% sucrose for all animals. Groups differed in terms of the number of preshift sessions, either 10 (top) or 18 (bottom). The unshifted control group (the same in both panels) received access to 2% sucrose throughout the 21 sessions. Results from Experiment 10.

11.1. Method

The subjects were 23 female Wistar rats, 90-day old, experimentally naïve, and maintained as described in Experiment 1, including the 81–84% deprivation criterion. Free-food weights varied between 267 and 384 g. The conditioning boxes were those described previously. Animals were randomly assigned to one of three groups: 1–2/10 ($n = 8$), 1–2/18 ($n = 8$), or 2 ($n = 7$). The group label refers to the sucrose concentration received during preshift sessions (either 1% or 2% sucrose) and the number of preshift sessions (either 10 or 18). Group 2 received 2% sucrose during the entire experiment (unshifted control). As in Experiment 3, the dependent variable was lick frequency. Other aspects of the training procedure were as described in Experiment 5.

11.2. Results

When the reward upshift occurred after 10 preshift sessions (Fig. 13, top), there was a clear concentration effect in terms of both a contrast by session interaction, $F(9.117) = 4.87$, $p < 0.001$, and a main contrast effect, $F(1, 13) = 26.47$, $p < 0.001$. The session effect was also significant, $F(9117) = 25.82$, $p < 0.001$. LSD pairwise tests showed that Group 2 performed above Group 1–2/10 on sessions

4–6 and 8–10, $Fs(1, 13) > 8.92$, $ps < 0.02$. A similar analysis on data from the three postshift sessions only revealed a significant main effect of contrast, $F(1, 13) = 8.25$, $p < 0.02$. Thus, after 10 preshift sessions, consummatory behavior was lower in upshifted animals than in unshifted controls.

Similar results were obtained when the upshift was scheduled after 18 preshift sessions (Fig. 13, bottom). Again, consummatory behavior was higher with access to 2% sucrose than with 1% sucrose, both in terms of an interaction, $F(17, 221) = 2.07$, $p < 0.01$, and a main concentration effect, $F(1, 13) = 29.25$, $p < 0.001$. The sessions effect was also significant, $F(17, 221) = 21.06$, $p < 0.001$. LSD pairwise tests showed that 2% sucrose increased lick frequency above 1% sucrose on sessions 4–5, 8–12, and 15–16, $Fs(1, 13) > 4.77$, $ps < 0.05$, although the groups reached similar levels during the last two preshift sessions. Postshift performance yielded again only a significant main effect of contrast, $F(1, 13) = 5.00$, $p < 0.05$.

A comparison of the three groups in terms of their postshift sessions yielded only a significant main effect of contrast, $F(2, 20) = 5.63$, $p < 0.02$. LSD pairwise showed that 2% sucrose animals performed significantly above the two upshifted groups, $ps < 0.04$, which, in turn, did not differ from each other. The difference in the amount of preshift training made no difference in the outcome of the upshift manipulation. In agreement with a novelty hypothesis, an upshift resulted in lower lick frequencies relative to the unshifted control.

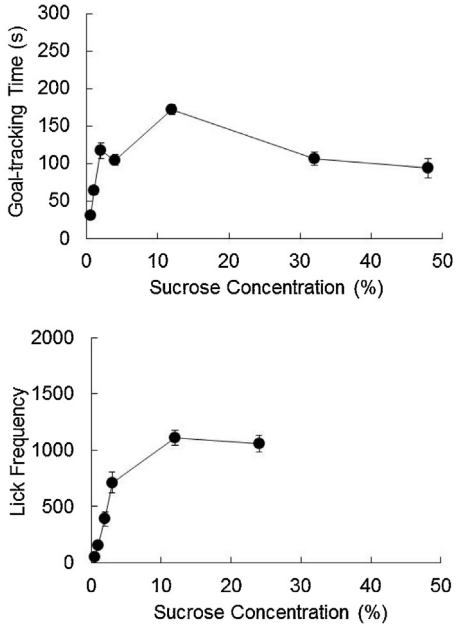

Fig. 14. Mean (±SEM) of goal-tracking time (top) and lick frequency (bottom) during the initial 6 sessions of training in the experiments reported in this article as a function of sucrose concentration.

12. General discussion

The aim of this series of experiments was to identify conditions that would produce the cSPC effect in a reliable manner. Training parameters were varied extensively to maximize chances of detecting such evidence. If a set of appropriate conditions were found, subsequent research would systematically vary these parameters to determine which among them were critical. The results, however, failed to show unequivocal evidence of cSPC. The strategy of extensive parameter variation then makes the absence of cSPC effects especially compelling. However, these experiments uncovered factors that produced significant effects and that might explain the unreliable (at best) nature of cSPC. The following discussion centers on five issues: (1) Evidence for cSPC, (2) Control by absolute reward value, (3) The role of novelty in upshift experiments, (4) Competing factors, and (5) The status of SPC as a phenomenon.

First, what can be concluded from the scanty and unreliable evidence of cSPC? Such evidence comes from some isolated 100-s bins in Experiment 5 (Session 8), Experiment 7 (Session 8), and Experiment 8 (Session 7). In all cases, the evidence took the form of a crossing-over of functions during a 20-min long session in which upshifted animals ended up exhibiting significantly higher consummatory behavior than unshifted controls. In two of these instances (Experiments 5 and 8), it could be argued that the crossing over was a simple product of relatively greater satiation in unshifted animals, which started at a higher consummatory level than upshifted animals. Notice, however, that this explanation cannot be applied in all cases. For example, in Experiment 5, Session 8 (Fig. 5), two upshifted groups (2% and 0.5% sucrose) started at the same level and should thus have been similarly satiated, but only the group that experienced the larger reward disparity (0.5-to-12% sucrose upshift) crossed over the unshifted controls. Some experiments had nondifferential preshift performance and, thus, it could be argued that cSPC failed to occur because the sucrose concentrations did not differentially affect behavior. However, in other experiments there was an orderly and differential preshift performance as a function of reward magnitude and still cSPC failed to occur. Moreover, several manipulations that had produced evidence of cSPC (or iSPC) in other labs, failed to do so consistently in our lab, including single alternation of reward magnitudes (Flaherty et al., 1983), low deprivation level (Shanab and Ferrell, 1970; Panksepp and Trowill, 1971), and access to saccharin solutions (Rabiner et al., 1988). At least in one case (Experiment 1), a failure to observe cSPC during single alternation did not prevent cSNC from emerging, and in another case (Experiment 2, third phase), reward upshift actually led to significant and transient consummatory suppression (i.e., an effect that superficially looks like arising from a downshift manipulation). These results were obtained despite extensive parameter variation, including dependent variables, sucrose concentrations, reward disparity, session length, and animal sex.

Second, was there evidence of control by absolute reward value? In most cases, given some minimum experience, there was evidence that consummatory behavior was under the control of absolute reward value. Thus, although the initial response to the upshifted solution may have been lower than that of unshifted controls, eventually upshifted and unshifted groups behaved similarly. Control by absolute reward value was also observed during preshift sessions with low sucrose concentrations, although not with higher values. Fig. 14 shows the average goal-tracking time (top) and lick frequency (bottom) for Sessions 1–6 in experiments with equivalent conditions of training, except for the sucrose concentration. In general agreement with previous data (Papini and Pellegrini, 2006), goal-tracking time and lick frequency peak somewhere between 10 and 20% sucrose and then tend to decline. This reduction with higher concentrations may in part be due to satiety as goal-tracking times have been observed to decrease within the 5-min session (Pellegrini et al., 2004). Notice also that the level of performance in groups receiving 4%, 32%, and 48% is comparable, which agrees with the lack of differentiation between these conditions during more extensive preshift training. These results suggest that the concentrations chosen for the upshift manipulations in most of the experiments (12–48% sucrose) may not have been the optimal concentrations for observing cSPC because they tend to produce the highest levels of consummatory behavior. Although there is nominally room in the session for either dependent variable to increase, a ceiling may be imposed by other processes (e.g., satiety). Experiment 9 tested this possibility by upshifting to a lower

concentration, 2% sucrose. In addition, it looked for evidence of a ceiling effect by introducing downshift conditions which, given the ratio of the concentrations used and based on previous research (Papini and Pellegrini, 2006), were not expected to yield cSNC. As expected, the consummatory behavior of downshifted rats was actually higher than that of unshifted controls. Such difference demonstrates that a ceiling effect is not the cause for the absence of a cSPC effect in upshifted groups because a higher behavioral level was possible, as shown by downshifted groups.

Third, what is the role of novelty in reward upshift experiments? As noted above, absolute reward value controlled consummatory behavior only after some experience with the upshifted solution. Initially, however, an upshift to a high concentration produced lower performance than that of animals trained with the high concentration from the outset. This initially lower consummatory behavior suggests an active suppressive process related to the novelty of the upshifted solution. At least two novelty-related mechanisms were noted previously, taste neophobia (Alley and Potter, 2011) and generalization decrement (Bitterman, 1979). For taste neophobia to be a factor, it is necessary to assume that a significant increase in sucrose concentration is capable of inducing rejection, even when the animal has had prior experience with sucrose, albeit at lower concentrations. In other words, it is not substance novelty per se, but a sudden increase in taste intensity that causes a rejection. For generalization decrement to be a factor, it is assumed that a change in reward magnitude interferes with consummatory behavior despite the fact that the new reward is surely preferred over the preshift magnitude (Sclafani and Nissenbaum, 1987). There was evidence also that the amount of suppression was directly related to the disparity of the two sucrose concentrations, a fact consistent with both novelty hypotheses—taste neophobia and generalization decrement. For example, in Experiment 4, Fig. 4, the upshift to 12% sucrose produced a level of lick frequency that was lowest after training with 0.5% sucrose, intermediate after 1% sucrose, and highest after 2% sucrose during preshift sessions.

Fourth, was there any evidence that behavior was influenced in opposite directions by different factors? Although upshifted animals consumed less than unshifted controls in early trials, they still generally consumed more than in preshift trials. For example (see Fig. 4), after a shift from 0.5% to 12% sucrose, upshifted animals generated a lower goal-tracking time than unshifted 12% sucrose animals (means: 129 s vs. 233 s), but more than the amount they were consuming in the previous session, when given access to 0.5% sucrose (means: 129 s vs. 39 s). Thus, the suppressive effects of novelty can only account for the difference between unshifted and upshifted values (i.e., 233 minus 129 s), but another process must be inferred to account for the increase in consumption (i.e., from 39 to 129 s). The implication is that more than one factor is at play during the initial encounter of a reward upshift. Whereas novelty accounts for the suppressive effects, the enhancement of consummatory behavior suggests that either absolute or relative incentive value is also at work. Given the scanty evidence in favor of incentive relativity in the present data, it is parsimonious to attribute the enhancing effect to the absolute value of the upshifted reward.

Finally, is SPC a real phenomenon? The weak, at best, evidence for SPC in these experiments is consistent with Spence's (1956) conclusion that only SNC needs an explanation. Building a case for the absence of an effect requires that the results of well-designed experiments are available for examination by those interested in the problem. The present series of experiments provides information from an extensive set of manipulations that consistently show both a failure to observe SPC and also a consistent suppressive effect of reward upshift on behavior. SPC has been reported occasionally in the literature, and has such potential theoretical and translational value to warrant careful consideration. However, as far as the authors can determine, there is nothing in the literature suggesting

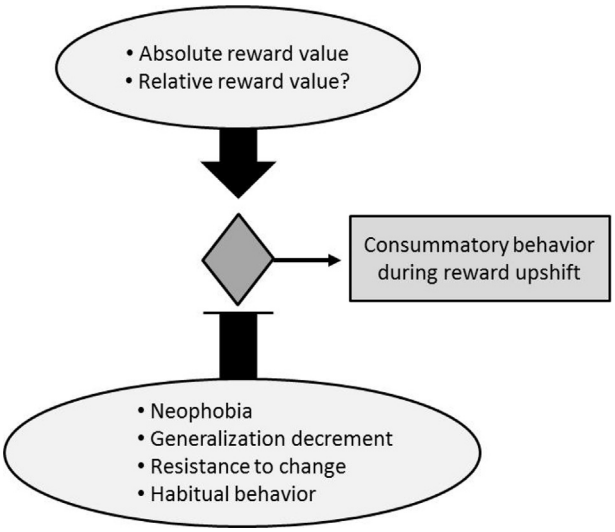

Fig. 15. A representation of the opposing influence of factors that increase (pointed arrow) and decrease (dashed arrow) consummatory behavior during an episode of reward upshift. The simple rule illustrated here assumes that consummatory behavior is the net result of the combination of these opposing factors. Thus, the expression of cSPC would be the result of a compromise between the relative strength of these factors.

a systematic and extensive research program consistently showing evidence of SPC, analogous, for example, to that observed in the case of SNC (e.g., Flaherty, 1996). One could argue that SPC occurs in rats only under a rather restricted set of conditions because the reward upshift manipulation activates a complex, interactive set of factors that work against each other, making it difficult to isolate the effect. Fig. 15 illustrates this hypothesis in terms of factors mentioned in this article. Of the two factors increasing consummatory behavior during a reward upshift event, the present experiments provide direct evidence for control by absolute value. In most experiments (e.g., Experiments 2, 4, and 9), the performance of upshifted rats eventually equated that of unshifted controls. As we have seen, evidence for relative reward value was not strong enough, so this factor is now questioned in the figure. As for the opponent factors, the effects of novelty (e.g., neophobia, generalization decrement) were confirmed in Experiment 8 by pretraining exposure to the upshifted sucrose solution, whereas the potential role of resistance to change and habit formation is reflected in most experiments, but perhaps most clearly in Experiment 9. In this experiment, both upshifted and downshifted groups failed to reach unshifted levels of consummatory behavior during the first session, but in each case responding was more in line with the level these groups were displaying before the reward shift (i.e., upshifted animals responded less than controls, but downshifted animals responded more than controls).

The diversity of conditions tested in the present experiments suggest that, at least in terms of consummatory behavior, perhaps it is time to abandon the attractive idea that symmetrical shifts in reward magnitude produce symmetrical contrast effects.

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