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Effects of shifts in food deprivation on consummatory successive negative contrast

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ABSTRACT

Rats exposed to a downshift from a large reward (32% sucrose) to a small reward (4% sucrose) show less consummatory behavior than unshifted rats always exposed to the small reward—an effect called consummatory successive negative contrast (cSNC). Four experiments studied the effects of shifts in deprivation level between preshift and postshift sessions on the size of the cSNC effect. This manipulation is designed to test the general proposition that the cSNC effect depends not only on external factors (e.g., reward disparity), but also on the internal state of the organism either at the time it first experiences the rewards (incentive learning), at the time of reward downshift (reward need), or as a function of the transition of states from pre- to postshift sessions (state dependency). Experiments 1–2 adjusted deprivation level during a 10-day interval between the last preshift and first postshift sessions. During this interval, food deprivation was either maintained or changed (increased or reduced) relative to preshift sessions. Experiments 3–4 maintained all animals at 81–85% of their ad lib weight during the entire experiment, but they were either fed before each session (nondeprivation condition) or fed after the session (deprivation condition). This procedure avoided the 10-day interval used in previous experiments. In three of the four experiments, the size of the cSNC effect increased when animals were deprived while exposed to the large reward (32% sucrose) during preshift sessions, independently of postshift deprivation conditions. The remaining experiment yielded inconclusive results. Of the three tested hypothesis, the incentive learning view received the strongest support. According to this view, the incentive value of the large reward is partly determined by the deprivation state of the organism at the time of learning.

Animals exposed to reward devaluation show an abrupt reduction or disruption in instrumental (Elliot, 1928) or consummatory (Vogel, Mikulka, & Spear, 1968) behavior beyond the response level of unshifted controls (Flaherty, 1996). A typical consummatory procedure involves a downshift from 32% sucrose to 4% sucrose leading to a suppression of consummatory behavior (fluid intake, licking, or time of contact with the drinking spout), compared to animals that always receive 4% sucrose solution (Flaherty, 1996). This effect, known as consummatory successive negative contrast (cSNC), can activate an

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aversive state and elicit negative emotion with behavioral, neurobiological, and hormonal consequences (Papini, Fuchs, & Torres, 2015).

What determines the high incentive value of the large reward? A simple answer would be its absolute value, that is, its intensity or magnitude. The cSNC phenomenon itself shows that rewards also have relative incentive value, that is, a value dependent on that of other rewards previously presented in the situation (Flaherty, 1996). But is reward relativity dependent only on the value of external rewards? Or can the animal's internal state also contribute to the incentive value of a reward? The present research is concerned with the hypothesis that the internal motivational state at the time the animal receives a reward also determines its incentive value. Similar research has been published in a variety of incentive contrast situations (e.g., Flaherty & Kelly, 1973; Shanab & Ferrell, 1970; Weatherly, Arthur, & Tischart, 2003); this article centers on the issue of incentive value as it applies to the cSNC effect.

A few studies evaluated the effects of motivational factors on the cSNC preparation. Riley and Dunlap (1979) compared deprived (D; 80% of ad libitum body weight) and nondeprived (ND) animals. They reported that the cSNC effect diminished over the four postshift days in the D group, but persisted over the entire test period in ND animals. Similar results were reported by Dachowski and Brazier (1991). The longer-lasting suppression of consummatory behavior in free-fed animals appears to be related to caloric need. Thus, a downshift from 32% sucrose to 0.15% saccharin, which lacks caloric content, yields a long-lasting cSNC effect (Flaherty, 1996 p. 39). Vice versa, inducing a need for sugar with exogenous insulin eliminates the cSNC effect based on sucrose intake (Flaherty, McCurdy, Becker, & D'Alessio, 1983). Although ND rats may exhibit substantial suppression during the downshift, their licking behavior is different from that of D rats. Unlike D rats, consummatory suppression in ND rats is mainly due to an increase in the interval between successive lick bursts (Grigson, Spector, & Norgren, 1993). ND rats also respond different than D rats to the effects of anxiolytic benzodiazepines. Whereas chlordiazepoxide reduces the cSNC effect during the second postshift session, but has no effect when administered before the first postshift session in D rats (Flaherty, Grigson, & Rowan, 1986; Ortega et al., 2014), this drug eliminates the cSNC effect in ND rats during the first and second downshift session (Flaherty, Coppotelli, & Potaki, 1996).

These studies show that the internal state of the animal determines the course of recovery from reward devaluation, modifies the structure of licking behavior, and enhances the contrast-reducing effects of benzodiazepines. Unfortunately, a constant motivational state throughout the experiment, as used in the experiments described above, does not answer the main question raised in this article, namely, whether the animal's motivational state contributes to set the incentive value of the reward downshifted in cSNC experiments. To answer this question, the motivational state needs to vary within a single experiment from preshift to postshift sessions.

Such motivational shifts may affect consummatory behavior in at least three ways. First, deprivation level may set the value of the preshift incentive consequently affecting the size of the cSNC effect. D animals exposed to 32% sucrose may value that reward relatively more than ND animals. Thus, for D animals the 32–4% sucrose downshift would involve a greater reward disparity than that suggested by the nominal values of sucrose concentrations. This will be referred to as the incentive learning hypothesis (Balleine & Dickinson, 1991, 1998). Second, the postshift reward may be valued less by ND rats than by D rats because ND rats have less demand for calories. Caloric content supports the development of a conditioned preference for a flavor (Mehiel & Bolles, 1984; Tarner, Frieman, & Mehiel, 2004). This will be referred to as the reward need hypothesis (Flaherty et al., 1983). The most important difference between these two hypotheses resides in the moment during the experiment in which the deprivation state is critical to the cSNC effect. According to the incentive learning hypothesis, response to the 4% sucrose in postshift sessions depends on the deprivation condition enforced during exposure to 32% sucrose in preshift sessions. According to the reward need hypothesis, the key determinant of the cSNC effect is the deprivation state present in postshift sessions.

In the present experiments, animals were either kept under the same deprivation state across sessions or were shifted from one condition to another between preshift and postshift sessions. In each of four experiments, deprivation conditions during postshift sessions were kept constant across groups. Dissociating the deprivation states allows for an assessment of the extent to which the size of the cSNC effect depends upon the state of deprivation during preshift sessions (incentive learning) or during postshift sessions (reward need). The incentive learning hypothesis predicts that the size of the cSNC effect should increase when animals are exposed to 32% sucrose while deprived, independently of the postshift deprivation state. However, the reward need hypothesis predicts that the cSNC effect should be stronger in nondeprived animals during the postshift, independently of their state during preshift sessions. There is also a third possible explanation for the effects of deprivation shifts. Changing deprivation states across phases introduces state-dependent learning as a potential factor (Eich, 1980). Rats can use cues derived from their food deprivation level as signals in conditioning experiments (Davidson & Benoit, 1996), therefore giving plausibility to the idea that changing their internal state may cause generalization decrement and disrupt consummatory performance across phases. Results consistent with the state dependency hypothesis were reported in the instrumental SNC situation (iSNC) after a change in deprivation condition from pre- to postshift sessions. The iSNC effect was eliminated whether the deprivation state was increased or decreased (Capaldi, Smith, & White, 1977). Thus, state dependency predicts that deprivation changes, whether in one direction or the other, should interfere with memory reactivation of the 32% sucrose, thus attenuating the cSNC effect relative to groups kept under constant deprivation conditions. The predictions made by the three hypotheses considered here are summarized in Table 1.

Table 1
Predictions made by the three hypotheses considered here for the current manipulations.

Hypothesis	Predicted results	Predicted results	
		Exp 1 and 3	Exp 2 and 4
Incentive learning	(D–D) ~ (D–ND) > (ND–ND) ~ (ND–D)	D–D > ND–D	D–ND > ND–ND
Reward need	(D–ND) ~ (ND–ND) > (D–D) ~ (ND–D)	D–D ~ ND–D	D–ND ~ ND–ND
State dependency	(D–D) ~ (ND–ND) > (D–ND) ~ (ND–D)	D–D > ND–D	ND–ND > D–ND

Note. Shifts in motivation were achieved by food deprivation during a 10-day interval between the last preshift and first postshift session (Experiments 1–2) or by presession vs. postsession feeding (Experiments 3–4). D, Deprived or postsession feeding. ND, Nondeprived or presession feeding. >, Size of the cSNC effect is greater than. ~, Size of the cSNC effect is similar. For each condition (e.g., D–ND), the first corresponds to the condition during preshift sessions while the second corresponds to the condition during postshift sessions.

1. Experiment 1

Experiment 1 was designed to contrast D and ND conditions during preshift sessions, in rats tested under D conditions during postshift sessions. As Table 1 indicates, these three hypotheses make contrasting predictions. To change deprivation conditions (ND to D), a 10-day period was interpolated between the last preshift and first postshift sessions; this period allowed weights to be adjusted by food deprivation. D groups were maintained at the target level by a daily regime of food administration. Prior research suggests that interpolating a retention interval (without changes in deprivation condition) of up to 17 days between the last preshift session and the first postshift session does not interfere with the occurrence of the cSNC effect (see Flaherty, 1996 pp. 40–42). It is possible that sensitivity to the effects of a retention interval varies as a function of several factors. Thus, for example, whereas a 1- vs. 5-day interval does not affect the size of the cSNC effect in 3-month old rats (the age used in the present experiments), 14-month old rats exhibited an impaired cSNC effect when a 5-day interval was interpolated between Sessions 10 and 11 (Bentosela, D'Ambros, Mustaca, & Papini, 2006). A 10-day interval was chosen as a compromise between avoiding too fast a deprivation procedure afforded by a 5-day interval and a risk at disrupting the cSNC effect with an interval close to the 17-day interval suggested in the literature as a cut-off value.

1.1. Method

1.1.1. Subjects

The subjects were 48 male Wistar rats (ad lib weights: 363–505 g) bred at the TCU vivarium from breeders purchased at Harlan Laboratories (Indianapolis, NS), approximately 90 days old at the start of the experiment, and experimentally naïve. Rats were individually housed in wire-bottom cages with ad libitum water and rat chow. A dark red Plexiglas rodent retreat (BioServ, Frenchtown, NJ) measuring 15 × 9 × 9 cm (L × H × W) was placed inside the home cage as an enrichment device. During all experiments, animals were under a 12:12 h light:dark schedule (lights on at 07:00 h), with constant room temperature (22–23 °C) and humidity (40–65%). When animals were 90 days old, ad libitum body weights were measured and half of the animals were deprived during 8 days until reaching 81–85%, while the others were maintained at 100% of the ad lib weight.

1.1.2. Apparatus

Behavioral training was conducted in eight conditioning boxes (MED Associates, St. Albans, VT) made of aluminum and Plexiglas (29.4 × 28.9 × 24.7 cm, L × H × W). The floor of each box consisted of steel rods. A tray with corncob bedding was placed below the floor to collect feces and urine. A hole in the feeder wall (2 × 1 cm, H × W, and 4 cm from the floor) allowed the insertion of a sipper tube (1 cm in diameter). When fully inserted, the sipper tube was slightly inside the box during the initial two sessions and flush against the wall thereafter. This facilitated the initial development of licking. Diffuse light was provided by a house light located in the upper part of a wall opposite to the sipper tube. A computer controlled the presentation and retraction of the sipper tube and recorded the rat's contact with it. When the animals made contact, a circuit involving the steel rods in the floor and the sipper was closed, and the signal was recorded by the computer. This provided a measure of cumulative contact, called goal-tracking time and measured in 0.01-s units. Goal-tracking time correlates positively and significantly with fluid intake for both 32% and 4% sucrose concentration (Mustaca, Freindín, & Papini, 2002). Previous experiments have also provided essentially the same results using goal-tracking time and lick frequency simultaneously in rats (Riley & Dunlap, 1979). 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. Sucrose solutions were prepared by weight, mixing 32 g (4 g) of sucrose for every 68 g (96 g) of distilled water.

1.1.3. Procedure

The animals were randomly assigned to one of four groups ($n = 12$), matched in terms of ad lib weight differing in terms of the incentive magnitude (32% or 4% sucrose) and the deprivation state during preshift sessions (D: deprived or ND: not deprived). Two groups were deprived until reaching 81–85% of their ad lib. body weight, while the other groups were

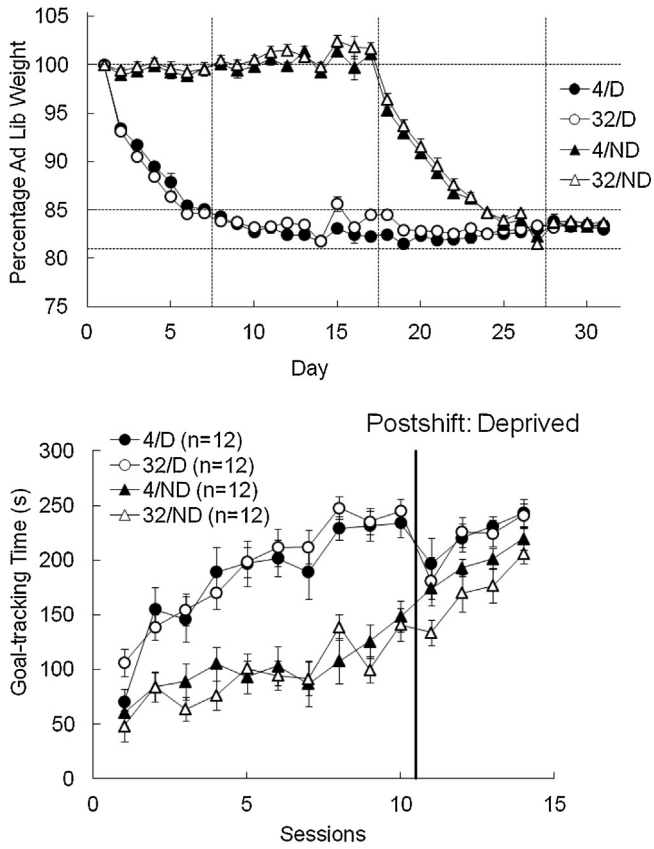

Fig. 1. Top: Mean (±SEM) deprivation level for each phase and group of the experiment. Dashed lines signal key deprivation levels (81, 85, and 100% of ad lib weight) and phases of the experiment (deprivation, preshift, 10-day retention interval, and postshift). Bottom: Mean (±SEM) goal-tracking time (in seconds) during preshift and postshift sessions for each group. The thick vertical line represents the 10-day retention interval used to adjust deprivation levels of animals in Groups 32/ND and 4/ND. Each group label also provides the sample size. In Experiment 1, all animals were deprived (D) during postshift sessions.

maintained at 100%. After 8 days, all animals received training during 10 daily preshift sessions each lasting 5 min starting with the first detected contact with the sipper tube. For two conditions (Groups 32/D and 32/ND), 32% sucrose was available during Sessions 1–10. For the other two conditions (Groups 4/D and 4/ND), 4% sucrose was available. After preshift sessions, an interval of 10 days was introduced to manipulate the animals' deprivation level. Previously deprived animals (Groups 32/D and 4/D) were maintained at the same level. Previously nondeprived animals (Groups 32/ND and 4/ND) were gradually reduced until they reached 81–85% of their ad lib weight. Postshift sessions started a day after. All animals received 4 postshift sessions of access to 4% sucrose.

Rats received training in squads of eight. Each animal was always in the same squad and trained in the same conditioning box, but the order of squad was randomized across days. Conditioning boxes were cleaned with a damp towel after each trial. Each trial started with a variable interval of 30 s (range: 15–45s). At the end of this interval, the sipper tube was automatically presented. A recording period started when a rat contacted the sipper tube and lasted 5 min. Retraction of the sipper tube was followed by a variable interval of 30 s (range: 15–45 s). These variable intervals were introduced to minimize the effects of handling on consummatory behavior.

Goal-tracking times were subjected to factorial analysis of variance. Where interactions were significant, pairwise LSD tests with the error term derived from the main analysis were computed to identify their source. In every experiment, additional analyses were computed to compare separately the performance of downshifted vs. unshifted groups for each deprivation condition during postshift trials (e.g., Groups 32/D vs. 4/D). All statistics reported in this article were calculated with SPSS v. 21 using a 0.05 alpha level.

1.2. Results and discussion

Fig. 1 (top) shows changes in percentage deprivation across the experiment. The target deprivation levels were achieved for each phase of the experiment. Fig. 1 (bottom) shows the behavioral results. During preshift sessions, there was a strong effect of deprivation condition, with deprived animals performing above nondeprived animals, but no effect of sucrose

condition. A contrast (32%, 4%) × deprivation (D, ND) × session (1–10) analysis indicated a significant interaction between deprivation condition and session, $F(9, 396) = 5.04$, $p < 0.001$, $\eta^2 = 0.1$, and also a significant main effect of deprivation, $F(1, 44) = 75.70$, $p < 0.001$, $\eta^2 = 0.63$. The increase in goal-tracking times across sessions was also significant, $F(9, 396) = 35.88$, $p < 0.001$, $\eta^2 = 0.45$. None of the other effects was significant, Fs < 1.38, ps > 0.19 $\eta^2 < 0.03$.

After the 10-day interval, the performance of D animals (which continued to be deprived) showed a reduction followed by a recovery to preshift levels, whereas ND animals (which were food deprived during the interval) showed an increase in performance relative to preshift levels. To detect the combined effects of the 10-day interval and the change in deprivation state, an analysis of data from sessions 10–11 was computed. There was a significant interaction between deprivation and session, $F(1, 44) = 9.14$, $p < 0.005$, $\eta^2 = 0.17$. D animals still performed above animals previously trained under ND conditions, even though all animals were similarly deprived during these sessions. A contrast × deprivation × session (11–14) analysis yielded main effects for deprivation, $F(1, 44) = 10.47$, $p < 0.003$, $\eta^2 = 0.19$, and sessions, $F(3, 132) = 26.79$, $p < 0.001$, $\eta^2 = 0.38$. All other effects were nonsignificant, Fs < 1.86, ps > 0.17, $\eta^2 > 0.04$. Independent contrast × session (11–14) analyses were computed to compare downshifted vs. unshifted groups for each deprivation condition. The group effect was nonsignificant for D groups, $F < 1$, $\eta^2 < 0.01$, but marginally so for ND groups, $F(1, 22) = 3.75$, $p = 0.066$, $\eta^2 = 0.15$. The interactions were both nonsignificant, Fs < 1, and the increase across sessions was significant in both cases, Fs(3, 66) > 10.99, ps < 0.001, $\eta^2 > 0.33$. Analyses restricted to session 11 indicated that, consistent with Fig. 1, the difference between Groups 32/D and 4/D was negligible, $F < 1$, $\eta^2 = 0.01$, but Group 32/ND performed significantly below Group 4/ND, $F(1, 22) = 6.98$, $p < 0.02$, $\eta^2 = 0.24$.

These results showed that a cSNC effect was stronger in animals shifted from ND to D during the 10-day interval between preshift and postshift sessions than in D–D animals (i.e., ND–D > D–D). None of the three hypotheses described in Table 1 predicted this effect; all of them predict that the cSNC effect would be attenuated by a shift in internal conditions from ND to D. Discussion of these results is resumed in the final section of this article. Unexpectedly given prior results (e.g., Ciszewski & Flaherty, 1977; Flaherty, Capobianco, & Hamilton, 1973), the 10-day interval introduced to adjust the deprivation state of the animals did affect cSNC in D–D animals whose internal state was not shifted. A variety of parameters differentiate the experiments just cited and the present one (e.g., dependent variable, retention interval), so it is difficult to speculate as to the reason for this discrepancy.

2. Experiment 2

Experiment 2 followed the same general procedure, but explored the effects of a transition from D to ND conditions. As in the previous experiments, the three hypotheses make contrasting predictions for this case (Table 1).

2.1. Method

2.2.1. Subjects and apparatus

The subjects were 38 male Wistar rats (ad lib weights: 321–488 g), about 90 days old at the start of the experiment, and experimentally naïve. The conditions of maintenance, deprivation, and housing, as well as the conditioning boxes used were as described in Experiment 1.

2.2.2. Procedure

Except for the deprivation state enforced during postshift sessions, the general procedure used was as described in Experiment 1. Unlike in the previous experiment, all animals were nondeprived during postshift sessions in the present experiment. Animals were randomly assigned to one of four groups as a function of the reward received (32% or 4% sucrose) and the deprivation state (D or ND) during preshift sessions: Groups 32/D ($n = 10$), 32/ND ($n = 9$), 4/D ($n = 10$), and 4/ND ($n = 9$).

2.2. Results and discussion

One animal in Group 32/ND did not acquire drinking behavior and was therefore excluded from the experiment. Fig. 2 (top) shows that the target deprivation levels were achieved for each phase of the experiment. Fig. 2 (bottom) shows the behavioral results of this experiment. A contrast (32%, 4%) × deprivation (D, ND) × session (1–10) analysis confirmed that during the preshift sessions (1–10), there was a strong effect of deprivation condition, but no effect of sucrose concentration. There was an interaction between deprivation and sessions, $F(9, 306) = 4.69$, $p < 0.001$, $\eta^2 = 0.12$, and a main effect of deprivation, $F(1, 34) = 141.47$, $p < 0.001$, $\eta^2 = 0.81$. The change across sessions was also significant, $F(9, 306) = 42.94$, $p < 0.001$, $\eta^2 = 0.56$. None of the other factors was significant, Fs < 1.03, ps > 0.41, $\eta^2 < 0.03$.

A decremental effect of the 10-day interval similar to that described in Experiment 1 was also observed in the deprived groups, 32/D and 4/D. The performance of 4/D animals (which also experienced a change in deprivation or reward conditions) showed a reduction maintained during postshift sessions. A similar effect was observed in 32/D animals, but the reduction in consummatory behavior was much more pronounced given the downshift. However, the 10-day interval did not seem to affect nondeprived animals (which experienced no change in deprivation condition). An analysis restricted to sessions 10–11 detected these differential effects of the 10-day interval, the 32–4% sucrose downshift, and the change in deprivation in terms of a marginal, but nonsignificant, triple interaction, $F(1, 34) = 3.72$, $p < 0.06$, $\eta^2 = 0.1$.

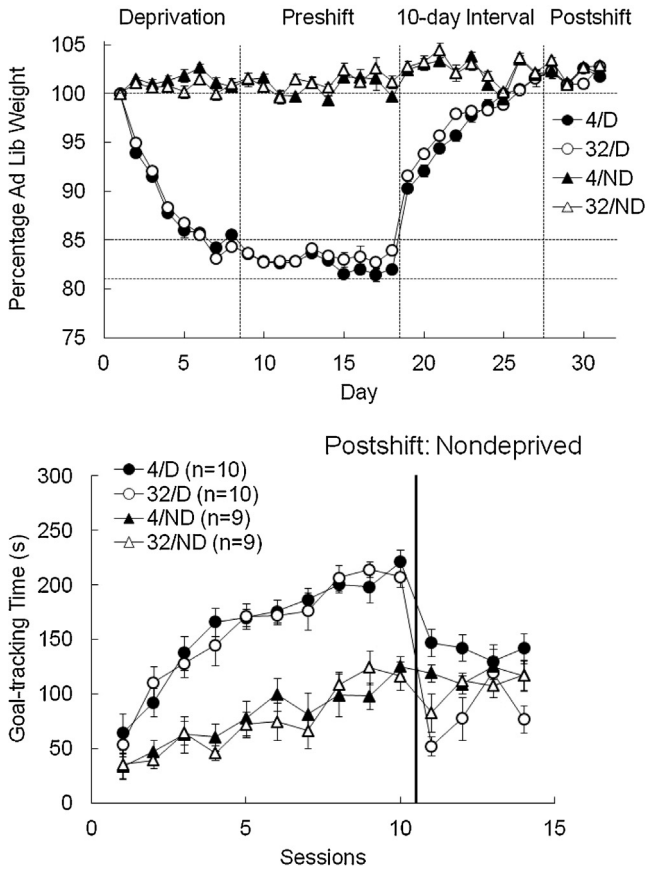

Fig. 2. Top: Mean (±SEM) deprivation level for each phase and group of the experiment. Dashed lines signal key deprivation levels (81, 85, and 100% of ad lib weight) and phases of the experiment (deprivation, preshift, 10-day retention interval, and postshift). Bottom: Mean (±SEM) goal-tracking time (in seconds) during preshift and postshift sessions for each group. The thick vertical line represents the 10-day retention interval used to adjust deprivation levels of animals in Groups 32/D and 4/D. Each group label also provides the sample size. In Experiment 2, all animals were nondeprived (ND) during postshift sessions.

The postshift results also shown in Fig. 2 suggest that the cSNC effect was larger in groups that were food deprived during preshift sessions than in groups that were nondeprived. This was reflected in a significant interaction between contrast and deprivation, $F(1, 34) = 6.62$, $p < 0.02$, $\eta^2 = 0.16$. There was also a contrast by session effect, $F(3, 102) = 3.52$, $p < 0.02$, $\eta^2 = 0.09$, and a main effect of contrast, $F(1, 34) = 15.76$, $p < 0.001$, $\eta^2 = 0.32$. None of the other effects reached significance, $Fs < 2.40$, $ps > 0.07$, $\eta^2 < 0.06$, although the triple interaction was marginally nonsignificant, $p < 0.07$, $\eta^2 = 0.07$. Because the triple interaction was not significant, we calculated pairwise effects on the overall postshift performance based on the contrast by deprivation interaction. A comparison of Groups 32/ND vs. 4/ND did not show a cSNC effect, $F < 1$, whereas a strong effect was observed between Groups 32/D vs. 4/D, $F(1, 34) = 22.60$, $p < 0.001$. Moreover, independent contrast × session analyses for deprived and nondeprived groups indicated a significant interaction, $F(3, 54) = 4.40$, $p < 0.01$, $\eta^2 = 0.2$, and highly significant contrast effect, $F(1, 18) = 19.04$, $p < 0.001$, $\eta^2 = 0.51$, for deprived animals. No effect was significant for nondeprived animals, $Fs < 1.37$, $ps > 0.26$, $\eta^2 < 0.08$.

These results provide support for the incentive learning hypothesis and contradict predictions derived from the reward need and state dependent hypotheses (Table 1). Animals exposed to 32% sucrose while under food deprivation exhibited a substantially stronger cSNC effect when downshifted to 4% sucrose than animals exposed to 32% sucrose while nondeprived. These results are also generally consistent with previous experiments with deprivation conditions held constant during pre- and postshift sessions, showing that ND animals (Groups 32/ND and 4/ND in Experiment 2) tend to show a stronger cSNC effect than D animals (Groups 32/D and 4/D in Experiment 1; e.g., Riley and Dunlap, 1979). As in the previous experiment, the 10-day interval used to adjust deprivation level had an effect on the retention of preshift performance.

3. Experiment 3

In the previous two experiments, the results of a shift in deprivation condition were compromised by an unexpected (i.e., based on prior research; Flaherty, 1996) performance disruption apparently related to the use of a 10-day interval.

This value was chosen as a compromise designed to minimize the deleterious effects of a rapid change in deprivation and a long retention interval between preshift and postshift sessions. However, the observed disruption suggested that a different approach was needed. In Experiments 3 and 4, animals were kept at 81–85% of the weight exhibited before training, but their motivational level was manipulated by given them access to additional food either before (experimental condition) or after (control) the consummatory session. Presession feeding has been used as a reward devaluation technique in studies of instrumental learning (e.g., Corbit, Janak, & Balleine, 2007). Usually the food administered before and during the training session is the same. In the present experiments, however, these rewards were different: food pellets vs. sucrose solutions. We reasoned that since animals were not explicitly deprived of water, but only of food, the main motivational condition underlying their sucrose feeding was hunger rather than thirst. In addition, a different reward (food pellets) from that used in the consummatory session was chosen because of the strong satiating effects of consuming even small amounts of sucrose solutions in the cSNC situation (e.g., Pellegrini, Muzio, Mustaca, & Papini, 2004). Finally, Pavlovian-to-instrumental transfer studies show that the presentation of a signal previously paired with one reward (e.g., food pellets) can enhance responding reinforced with another reward (e.g., 20% sucrose); furthermore, this effect is eliminated in animals given presession feeding with their maintenance diet (Corbit et al., 2007).

3.1. Method

3.1.1. Subjects

The subjects were 40 male Wistar rats (ad lib weights: 334–445 g) bred at the vivarium of the Instituto de Investigaciones Médicas Lanari (University of Buenos Aires), approximately 90 days old at the start of the experiment, and experimentally naïve. Rats were individually housed in wire-bottom cages with ad lib water and standard rat chow. The amount of food was gradually reduced over days until each animal reached 81–85% of its ad lib weight. This level of deprivation was maintained throughout the experiment for all the subjects, as described below. Animals were kept in a 12:12 h daily light:dark cycle (lights on at 07:00 h). The housing and testing rooms were maintained at a constant temperature (around 22 °C) and humidity (around 60–70%).

3.1.2. Apparatus

Training was carried out in 5 conditioning boxes (MED Associates, St. Albans, VT). The general features of the boxes were as described in Experiment 1, with the following exceptions. In the center of a lateral wall, there was a 5 cm hole, 3.5 cm deep, 1 cm above the floor level, through which a sipper tube could be manually introduced from the outside. When fully inserted, the sipper tube protruded 2 cm into the box. A photocell was located just in front of the tip of the sipper tube, inside this hole. Goal-tracking time (measured in 0.01 s units) was automatically recorded by a computer that measured the cumulative amount of time that the photocell was activated during the trial.

3.1.3. Procedure

Animals were randomly assigned to one of four groups ($n = 10$) counterbalanced by their ad lib weight and differing in terms of the incentive magnitude (32% or 4% sucrose) and whether they were fed after the session (deprived, D) or fed before the session (nondeprived, ND). In this experiment, D and ND conditions refer to preshift treatments; all animals were deprived during postshift sessions (i.e., fed after postshift sessions). Groups were labeled 32/D, 32/ND, 4/D, and 4/ND. Training started after animals reached the target deprivation state; deprivation was completed in 8 days. Animals were randomly assigned to two groups differing in terms of whether or not they received presession food. Half the animals (Groups 32/ND and 4/ND) had access to food 2 h before each preshift session, whereas the other half (Groups 32/D and 4/D) had access during 2 h at least 20 min after the end of the session. Since all the animals were equally deprived in this experiment, no retention interval between pre- and postshift sessions was introduced. In postshift sessions 11–14, none of the animals was fed before each session (i.e., D animals) and, as in previous experiments, all the animals had access to 4% sucrose. All other aspects of the procedure, including statistical analyses, were as described in Experiment 1.

3.2. Results and discussion

Table 2 summarizes the deprivation level for the entire experiment. Weights were recorded each day before any manipulation, whether presession feeding or training session. Although deprivation level was stable, it fluctuated around the lower boundary of the target 81–85% deprivation, occasionally dropping below it for some animals. Fig. 3 shows the behavioral results of this experiment. Two aspects of these results are different compared to Experiments 1–2. First, the absence of a time gap between phases produced no changes in behavior other than those related to contrast and motivational level. Second, preshift performance is different relative to previous experiments: The performance of Group 32/ND was similar to that of D groups, but the performance of 4/ND animals was considerably depressed. This pattern yielded a significant triple interaction between contrast, deprivation, and session, $F(9, 324) = 2.83$, $p < 0.004$, $\eta^2 = 0.07$. There were also significant contrast by deprivation, contrast by session, contrast, deprivation, and session effects, $Fs > 2.24$, $ps < 0.02$, $\eta^2 > 0.06$.

During postshift sessions there were cSNC effects in both conditions, but the difference between Groups 32/D and 4/D lasted longer than the difference between Groups 32/ND and 4/ND. This was captured by a significant interaction between contrast and deprivation, $F(1, 36) = 4.46$, $p < 0.05$, $\eta^2 = 0.11$. Subsequent pairwise LSD tests showed a significant difference

Table 2
Percentage deprivation averaged across the 14 sessions of training in Experiments 3 and 4.

Experiment	Group	*n* =	Means	SEMs
3	4/D	10	81.80	0.3
3	32/D	10	81.79	0.3
3	4/ND	10	80.62	0.3
3	32/ND	10	81.93	0.3
4	4/D	11	80.49	0.2
4	32/D	10	81.31	0.2
4	4/ND	10	81.29	0.2
4	32/ND	11	81.88	0.2

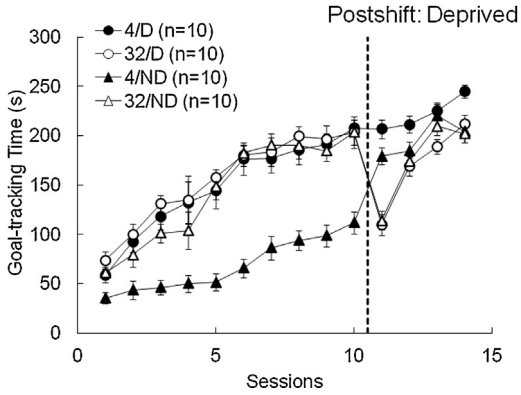

Fig. 3. Mean (±SEM) goal-tracking time (in seconds) during preshift and postshift sessions for each group, separated by a dashed vertical line. Groups differed in terms of whether extra feeding was administered after (D) or before (ND) the daily training session. Each group label also provides the sample size. In Experiment 3, all animals were deprived (D) during postshift sessions.

between groups receiving presession food, $F(1, 36) = 4.95$, $p < 0.04$, but a much higher significance for groups that were not fed before preshift sessions, $F(1, 36) = 27.16$, $p < 0.001$. The main analysis also produced significant results for the contrast by session interaction, deprivation by session interaction, and main effects for contrast and for session, $Fs > 3.84$, $ps < 0.02$, $\eta^2 > 0.1$. The triple interaction and the main deprivation effect were not significant, $Fs < 1.95$, $ps > 0.17$, $\eta^2 < 0.06$. Independent contrast × session (11–14) analyses for each pair of deprivation groups provided the following results. For animals receiving presession feeding (Groups 32/ND vs. 4/ND) there were significant interaction, $F(3, 54) = 7.60$, $p < 0.001$, $\eta^2 = 0.3$, contrast, $F(1, 18) = 4.58$, $p < 0.05$, $\eta^2 = 0.2$, and session effects, $F(3, 54) = 33.38$, $p < 0.001$, $\eta^2 = 0.65$. For animals receiving no presession feeding (Groups 32/D vs. 4/D), the effects were also significant, but at a higher level: interaction, $F(3, 54) = 10.23$, $p < 0.001$, $\eta^2 = 0.36$, contrast, $F(1, 18) = 29.54$, $p < 0.001$, $\eta^2 = 0.62$, and session effects, $F(3, 54) = 39.65$, $p < 0.001$, $\eta^2 = 0.69$.

Animals that were not fed before preshift sessions (D animals) exhibited a stronger cSNC effect than animal that were fed (ND animals), even though they were all fed after postshift sessions (D postshift condition). These results are consistent with both the incentive learning and state dependent hypotheses (Table 1). Moreover, to the extent that significant cSNC effects were observed in both conditions, it could be argued that they are also consistent with the reward need hypothesis. The present results are inconsistent with those observed in Experiment 1, although this discrepancy is attributable to the different motivational procedure used in these experiments (i.e., 10-day interval vs. presession feeding).

4. Experiment 4

This experiment applied the presession-vs.-postsession feeding procedure following a design otherwise analogous to that of Experiment 2. Unlike in that experiment, all animals received presession feeding (ND condition) during postshift sessions.

4.1. Method

4.1.1. Subjects and apparatus

The subjects were 42 male Wistar rats (ad lib weights: 305–470 g) bred at the vivarium of the Instituto de Investigaciones Médicas (Universidad de Buenos Aires), approximately 90 days old at the start of the experiment, and experimentally naïve. The conditions of maintenance, deprivation, and housing were as described in Experiment 1. The conditioning boxes were as described in Experiment 3.

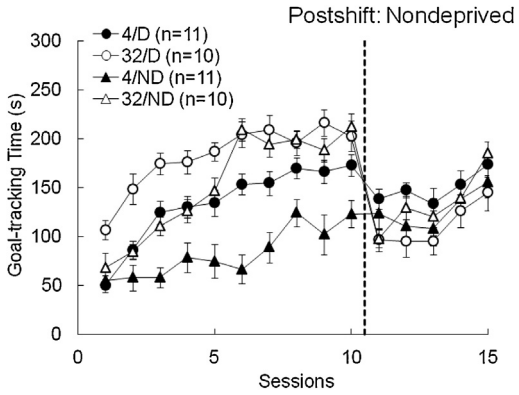

Fig. 4. Mean (±SEM) goal-tracking time (in seconds) during preshift and postshift sessions for each group, separated by a dashed vertical line. Groups differed in terms of whether extra feeding was administered after (D) or before (ND) the daily training session. Each group label also provides the sample size. In Experiment 4, all animals were nondeprived (ND) during postshift sessions.

Table 3
Summary of results.

Experiment	Observed result	Favored hypothesis
1	(ND–D) > (D–D)	None
2	(D–ND) > (ND–ND)	Incentive learning
3	(D–D) > (ND–D)	Incentive learning
	(But both cSNC effects significant)	State dependency Reward need?
4	(D–ND) > (ND–ND)	Incentive learning

4.1.2. Procedure

The training procedure was equal to that described in Experiment 3, except that all the animals were exposed to presession feeding during postshift sessions. Animals were randomly assigned to one of four groups in terms of the incentive magnitude (32% or 4% sucrose) and presession feeding (D or ND) during preshift sessions: Groups 32/D ($n = 10$), 32/ND ($n = 11$), 4/D ($n = 11$), and 4/ND ($n = 10$).

4.2. Results and discussion

Table 2 shows the average deprivation level for each group during the entire experiment. As in Experiment 3, deprivation level was around the lower boundary of the target 81-85% deprivation level. Fig. 4 shows the behavioral results of this experiment. The preshift performance of these groups is somewhat different from that observed in Experiment 3, especially between Groups 32/D and 4/D, and also during the initial sessions. A contrast × feeding × session (1–10) analysis yielded a significant triple interaction, $F(9, 342) = 4.90$, $p < 0.001$, $\eta^2 = 0.11$. Pairwise LSD tests indicated that Groups 32/D and 4/D differed on sessions 1–7 and 9, $Fs(1, 38) > 5.46$, $ps < 0.03$, whereas Groups 32/ND and 4/ND differed on sessions 3–10. On session 10, the performance of these four groups was similar to that observed in the previous experiment.

A global analysis of postshift performance yielded only a significant session effect, $F(3, 114) = 5.99$, $p < 0.002$, $\eta^2 = 0.14$. Visual inspection of Fig. 4 suggests that the cSNC effect was longer lasting in groups that had not been given presession food during the preshift than in groups receiving presession food. Separate analyses confirmed that Group 32/D was significantly suppressed relative to Group 4/D, $F(1, 19) = 7.04$, $p < 0.02$, $\eta^2 = 0.27$, whereas Groups 32/ND and 4/ND did not differ from each other, $F < 1$, $\eta^2 < 0.01$. The interaction effects were nonsignificant for both analyses, $Fs < 2.05$, $ps > 0.11$, $\eta^2 < 0.01$; the session effect was significant for prefed groups, $F(3, 57) = 3.35$, $p < 0.03$, $\eta^2 = 0.15$, but failed to reach significance for groups not given presession feeding, $F(3, 57) = 2.75$, $p = 0.051$, $\eta^2 = 0.13$.

These results were consistent with the incentive learning hypothesis (Table 1). Animals that experienced 32% sucrose while relatively more deprived exhibited a stronger cSNC effect than animals that experienced the large reward after feeding on food pellets, even when tested under ND conditions in postshift sessions.

5. General discussion

In three of the four experiments reported here, animals exposed to a large reward during preshift sessions while either more deprived or not given presession access to food exhibited a stronger cSNC effect than animals that were either less deprived or given presession feeding exposure. These results are summarized in Table 3. The opposite pattern was observed only in Experiment 1, in which ND animals during preshift sessions actually showed a greater cSNC effect than D animals. One ad-hoc explanation of this result would attribute the absence of a cSNC effect in D animals to the disrupting effects of

the 10-day retention interval between pre- and postshift sessions. This is not an entirely satisfactory explanation because a similar interval did not prevent contrast from arising in Experiment 2. Moreover, prior research shows that more than 10 days are necessary to disrupt the cSNC effect (e.g., Ciszewski and Flaherty, 1977). Since the result was not replicated in the analogous design using presession feeding (Experiment 3), whereas the other two analogous Experiments (2 and 4) yielded comparable results, we suggest that this result should probably be dismissed as anomalous, at least for the moment.

Of the three hypotheses described in the introduction and in Table 1, the incentive learning hypothesis accounted for the results of three of the four experiments, whereas the reward need and state dependency hypotheses accounted for the results of only one of the four experiments. While it is possible that reward need and state dependency both play a role in situations involving reward devaluation, the explanatory role of these accounts for the present results seems limited. For example, the effects of reward need are highlighted by studies manipulating deprivation level and sucrose metabolism (Flaherty et al., 1983; Riley & Dunlap, 1979). These effects may be interpreted in the context of the approach-withdrawal conflict assumed to develop during the postshift sessions (Flaherty, 1996; Wood, Daniel, & Papini, 2005). Animals placed on free food and then experiencing a reward downshift may exhibit an extended cSNC effect because of the selective reduction of the approach tendency of the conflict by a reduced caloric need (Riley & Dunlap, 1979). Conversely, animals whose need for sucrose is increased by insulin administration may experience such an intense approach tendency that the cSNC is reduced or even eliminated (Flaherty et al., 1983). Although reward need seems to be a significant factor in cSNC experiments, its importance in situations involving deprivation shifts, as those implemented in the present studies, seems to be relatively weak. As for state dependency, this theoretical possibility was brought to bear on the present experiment on the assumption that changing stimulus conditions may induce generalization decrement. Flaherty (1996) considered generalization decrement as a factor in successive contrast experiments, both positive and negative contrast, and concluded that "the theory is more convincing than the results" (p. 25). The present results provide only limited support for such a factor in situations involving deprivation shifts.

In the present experiments, ND animals responded generally less than D animals, but did not show complete disruption of consummatory behavior, either during pre- or post- shift sessions. Indeed, ND animals (with the presession-feeding procedure) given access to 32% sucrose performed at the same level as D animals (see preshift performance of Group 32/ND in Figs. 3–4). Feeding to satiation in well-trained animals does not completely eliminate acquired responses (Capaldi & Myers, 1978; Morgan, 1974), a result that more recently has been interpreted in term of stimulus-response, habitual learning (Corbit et al., 2007). In habitual learning, behavior reflects stimulus strength without reference to the current value of the reward that supported the learning. This was first suggested by Thorndike (1911) and has since been found to account for behavior under some conditions, such as intense emotional distress (Packard & Goodman, 2012). Habitual learning is strikingly opposed to the cSNC effect, which clearly shows the importance of outcome representation in the control of consummatory behavior. However, these two forms of learning may coexist and exert simultaneous influence on behavior. This is shown, for example, by the relatively weak effects of reinforcer devaluation (usually by pairing the reward with a toxin), which typically show substantial residual performance despite reward rejection (Holand, 2008). Similarly, manipulations that reduce the value of the postshift incentive, as reviewed above (e.g., downshift from sucrose to saccharin; Flaherty, 1996 p. 39) and in ND animals of all the experiments reported here, lead to strong suppression of consummatory behavior, but substantial residual behavior is still observed. Thus, it seems plausible that consummatory behavior involves a degree of outcome-independent control by the stimulus conditions (stimulus-response learning), rather than by incentive expectations (stimulus-outcome learning). Still, the present results add to the notion that consummatory behavior is under substantial control by processes related to incentive learning.

As mentioned above, three of the four experiments reported here produced results consistent with the notion that the internal deprivation state of the animal contributes to determine the value of the reward received. In Experiments 2–4, the consummatory performance during the downshift was partially, but significantly, affected by the deprivation conditions prevailing during preshift sessions, when the value of the large reward was being acquired. This is at variance with the results of analogous experiments in the iSNC situation in which deprivation levels were adjusted during a 2-week retention interval between pre- and postshift sessions (Capaldi et al., 1977). In this case, the iSNC effect was eliminated when deprivation level was shifted, relative to unshifted deprivation conditions. Such differences between cSNC and iSNC are not entirely surprising; the two protocols are known to yield different results in response to the same factors, including type of reward and lesions of specific brain sites (e.g., Flaherty & Carpio, 1976; Leszczuk & Flaherty, 2000).

In conclusion, the results reported here suggest that the deprivation condition prevailing at the time the animal experiences access to the large reward is a significant determinant of that reward's incentive value. The effects of reward devaluation on consummatory behavior are thus increased by the memory of a large reward acquired when the animal was under a relatively high deprivation state, independently of the current deprivation state.

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University (Experiments 1–2) and Instituto de Investigaciones Médicas Lanari, Universidad de Buenos Aires (Experiments 3–4). Correspondence concerning this article may be addressed to M. R. Papini (m.papini@tcu.edu).

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