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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.