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Short report

# Consummatory suppression due to incentive downshift is not a consequence of enhanced search behavior

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ABSTRACT

Rats shifted from 32% to 4% sucrose solution consume less from the 4% solution than rats that experience only the 4% solution. This consummatory suppression, a phenomenon known as consummatory successive negative contrast (cSNC), is accompanied by an increase in other behaviors such as rearing, nose-down locomotion, ambulation, sampling new sources and grooming. Despite a large body of studies on the cSNC, it remains to be determined whether reduced consumption is part of the direct response to the reward downshift or a byproduct of the increase in alternative competing behaviors. The objective of the present study was to determine if consummatory suppression would occur when most competing behaviors are prevented from occurring. Rats were trained either with 32% or 4% sucrose solution for ten days in restrainers that limited almost all movement. On the next five days, all subjects received the 4% sucrose solution and a robust suppression in drinking in the downshifted animals was observed. These results suggest that consummatory suppression is a direct consequence of incentive downshift and not a byproduct of the increase in competing behaviors.

## 1. Introduction

Rats exposed to a high-value reward (e.g., 32% sucrose) consume significantly less when given a low-value reward (e.g., 4% sucrose) than those exposed only to the low-value reward. This consummatory suppression is accompanied by an increase in behaviors that prevent the performance of consummatory behavior (known as alternative behaviors); including rearing, nose-down locomotion, ambulation, and sampling of new sources of reward (Flaherty et al., 1979; Pecoraro et al., 1999; Pellegrini and Mustaca, 2000). After the initial suppression, animals eventually recover their intake, matching the level observed in the control group. The recovery is accompanied by a decrease of the alternative behaviors. As most studies focus on consummatory behavior, this effect is known as the consummatory successive negative contrast (cSNC) effect. To avoid confusion, we are going to refer to consummatory suppression and alternative behaviors rather than to cSNC. The role of each response is still not clear and a basic question remains unanswered: Whether consummatory suppression stems from the active reduction of intake or is a byproduct of the increase of alternative behaviors. This question is of theoretical and methodological relevance. Theoretically, it helps to discern among competing theories of cSNC. Methodologically, the choice of intake as dependent variable would be warranted if consummatory suppression stemmed from the active reduction of intake but not if it turned out to be a byproduct of the increase of alternative behaviors. If the latter was the case, then it would be necessary to identify and understand the target behaviors.

Flaherty (see 1991, 1996) proposed that the first reaction to reward reduction is searching and that an emotional component is triggered afterwards. Briefly, the animals search for the missing reward and collect information about alternative sources of nutrition. The failure to find better or equal sources triggers a stress response. According to this model, consummatory suppression can be interpreted as a byproduct of increased alternative behaviors incompatible with consumption. In other words, those other behaviors steal time available for consumption. Consistently, situations that increase the occurrence of alternative behaviors also prolong the duration of the suppression. For instance, rats downshifted in complex contexts, such as an eight-arm radial maze (Flaherty, 1991) or an open field (Flaherty et al., 1979), suppressed consumption for more days than rats downshifted in the small standard apparatus. However, this is a comparison between experiments and a mechanism for consummatory suppression could be acting

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in conjunction with the one increasing search behavior. A better test to evaluate whether consummatory suppression is a byproduct of alternative behaviors would be to prevent the animals from searching and performing other alternative behaviors, and to then evaluate if the cSNC still occurs. According to the byproduct hypothesis, no suppression is expected under such conditions.

Flaherty (1991) also suggested that animals might be actively inhibiting licking during reward reduction. Adding a novel tone coincidently with the downshift reduces the degree of consummatory suppression (i.e., increases consumption), an effect that resembles Pavlovian disinhibition and was interpreted as supporting the inhibitory view of consummatory suppression (Lombardi and Flaherty, 1978). This mechanism should elicit suppression independently of the occurrence of the alternative behaviors. However, the dishinibition effect is apparent only starting on the second post-shift trial (Lombardi and Flaherty, 1978) and is limited to a particular type of stimuli (Flaherty et al., 1990b), suggesting that is not the cause of the initial suppression.

Another theory that predicts consummatory suppression independently of the occurrence of alternative behaviors is the frustration theory (Amsel, 1992). According to this account, a reward downshift triggers an aversive emotional state and animals avoid the low value reward to minimize this reaction (Amsel, 1992; Papini, 2003; Wood et al., 2005). Frustration, the aversive emotional state, not only arises but also becomes associated to the feeder and areas where the unexpected downshift of a high value reward is experienced. These stimuli are also avoided to prevent or minimize frustration (Daly, 1969; Daly and McCroskery, 1973). Even if the animals are incapable of moving and escape those stimuli, they should still suppress their consumption to prevent the unconditioned reaction. The goal of the present study is to determine whether consummatory suppression is a motivational feature of the rat – as predicted by the frustration theory – or, rather, a byproduct of search and alternative behaviors. Consummatory suppression while the animals are severely restricted in their movement would support the frustration account; absence of suppression under restraint would support the byproduct account.

## 2. Methods

### 2.1. Subjects

The subjects were 16 adult male Wistar rats with a mean ad libitum body weight of 471 g (range, 273–473 g). All had served as controls in a cSNC experiment in which they received4% sucrose and testosterone injections in an apparatus different from the one used here. The animals had free access to food and water for 14 days before the beginning of the experiment. Subsequently, access to food was restricted as described below. The light–dark cycle (light from 07:00 to 19:00 h) and the temperature (21–22 °C) were artificially controlled in the colony room.

Ten days before training, animals were housed individually in wire-bottom cages and their weight was gradually reduced up to the 85% of their ad libitum weight by restricting the daily amount of food. During the experiment, rats were fed at least 20 min after the daily training session in the home cages where water remained continuously available.

### 2.2. Apparatus

The apparatus were three restrainers, made with black acrylic plastic plaques, in a half cylinder shape (see Fig. 1). Each one measured 22.5 cm in length, 6 cm in width, and 6.5 cm in height, and had holes on its sides to allow breathing. In the front and back of the half cylinder, removable walls were introduced to prevent the animal from escaping. Glass drinking spouts were inserted through a hole on the front wall and were fitted to graduated bottles. Sucrose solutions were prepared by mixing commercial grade cane sugar with tap water and administered at room temperature. The employed solutions were of 4%, w/w sucrose (4%) and 32%, w/w sucrose (32%).

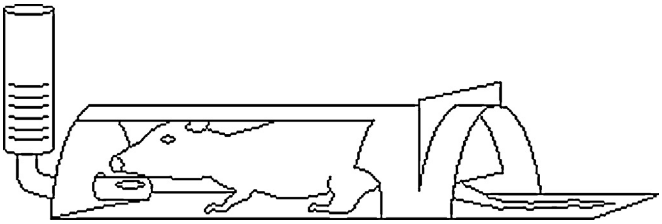

**Fig. 1.** Schematic view of a rat inside a restrainer.

### 2.3. Procedure

Rats were randomly assigned to two weight-matched groups ($n = 8$, in each group). Animals were randomly assigned into squads of three and each subject was assigned to a particular restrainer. For 3 days, the rats were habituated to being restrained by progressively increasing the time spent in the apparatus. Each daily trial lasted 1, 3, and 5 min respectively. Animals were placed with their heads inside the restrainer and were allowed to enter without being pushed. Then the device with the animal was positioned on a tray. At the end of the trial, the frontal wall was removed and subjects could exit the restrainer. Restrainers were wiped between animals and washed with hot water at the end of the day. For the next 15 days, daily trials lasted 5 min. The procedure in these trials was similar to the habituation. However, when the restrainer with the animal was placed on the tray, a drinking spout was introduced into the restrainer allowing the animal to drink. On trials 1–10, half the rats consumed 32% sucrose solution (Group 32) and the other half consumed 4% sucrose solution (Group 4). On trials 11–15, all rats received the 4% sucrose solution. Fluid intake was recorded to the nearest 0.5 ml and data were analyzed using analysis of variance (ANOVA).

## 3. Results

Data from two subjects (1 from Group 4 and 1 from Group 32) were discarded due to a failure to drink and an experimental mistake, respectively. Fig. 2 presents the mean fluid intake in each

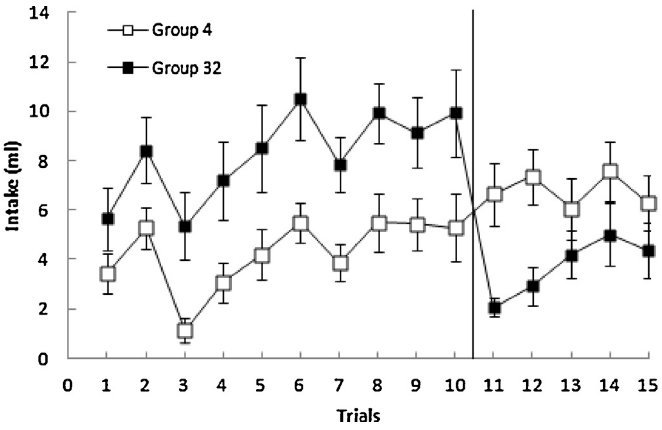

**Fig. 2.** Mean intake of sucrose solution in ml (±SEM) for shifted and unshifted groups (Groups 32 and 4, respectively) in successive daily trials. The vertical line between trials 10 and 11 marks when rats from Group 32 were shifted from the 32% to the 4% solution.

phase of training for Group 32 and 4. The data meet ANOVA assumptions. These results were subjected to a Group by Trial analysis, with the latter as a repeated-measure factor. Animals in both groups increased consumption across the first ten trials [$F(9, 108) = 10.95$, $p < .001$]. Further, rats presented with 32% consumed more than those receiving 4% sucrose [$F(1, 12) = 7.08$, $p < .021$]. The interaction between these two factors was not significant [$F(9, 108) = .72$, $p < .689$]. After the downshift from 32% to 4% sucrose, subjects in Group 32 consumed less of the 4% solution than animals in Group 4. An analysis of consumption in the 5 trials of the post-shift phase showed significant effects for Group, $F(1, 12) = 5.02$, $p < .045$, Trial, $F(4, 48) = 3.52$, $p < .013$, and the Group by Trial interaction, $F(4, 48) = 3.30$, $p < .018$. Significant post-shift differences between groups were obtained only in trials number 11, $F(1, 12) = 11.85$, $p < .005$, and number 12, $F(1, 12) = 10.62$, $p < .007$.

## 4. Discussion

This experiment shows a consummatory suppression even when animals are severely restricted in their movement. The suppression of fluid intake under these conditions suggests that consummatory suppression is part of the direct response to incentive devaluation and not a byproduct of enhanced non-consummatory activities elicited by the downshift. This finding is consistent with other findings that show that animals suppress consumption even when they are not occupied with other activities. For example, free moving rats spend between 15 and 20% of the time motionless when downshifted from a high to a low value reward (Flaherty et al., 1978, 1979). Similarly, starlings spend on average 60% of their time sitting on perches or at the bottom of the cage when facing similar circumstances (Freidin et al., 2009).

There are two issues with the present experiment. First, the animals had previous experience with the 4% sucrose solution. However, previous experience with a low value reward is known to *reduce* the degree of cSNC (Flaherty et al., 1990a); if anything, this suggests the degree of consummatory suppression observed in our experiment is an underestimate of the effect on naïve animals. Second, physical restraint causes stress that can lead to hypophagia (Buynitsky and Mostofsky, 2009). In the present experiment, animals were habituated and allowed to enter voluntarily to the restrainers to minimize the averseness of the procedure. Also, the duration of our trials was shorter than the duration of the trials used for inducing stress (Buynitsky and Mostofsky, 2009). Furthermore, access to sucrose solutions reduces the effects of restraint-induced stress (Foster et al., 2009; Martin and Timofeeva, 2010; Ulrich-Lai et al., 2007). In the cSNC procedure, physical stress (induced by tissue damage) does not affect the magnitude of the effect of the initial suppression of rats downshifted from 32% to 4%, although it does prolong the recovery process (Ortega et al., 2011). Together, these data suggest that stress might have affected the result of the test but by itself is unlikely to have caused the consummatory suppression.

Of the theories reviewed in the Introduction, only the frustration theory can explain these results. According to this view, animals reject the low value reward to minimize an aversive emotional state. The theory also suggests that animals avoid stimuli previously associated with high value rewards because they elicit an aversive state when paired with low value rewards. However, even when downshifted animals suppress their consumption, they do not always avoid feeders, surrounding areas, and flavors paired with the high value reward when given alternative options (Flaherty et al., 1979; Freidin et al., 2009; Lopez Seal et al., 2010; Pecoraro et al., 1999). A new comprehensive theory is needed.

In conclusion, rats reject devaluated rewards. This confirms the existence of a cSNC effect that is independent of alternative behavior and validates the use of consummatory suppression as a dependent variable for the study of incentive relativity. In the future, it would be interesting to study whether the alternative behaviors influence the magnitude and duration of cSNC in standard experimental settings. This can be achieved by comparing the cSNC in restrained vs. free moving rats. Also, this study provides an experimental paradigm that it is potentially useful for pharmacological testing and brain lesion studies because it reduces the effect of gross movement impairments by confining the animal in one location.

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