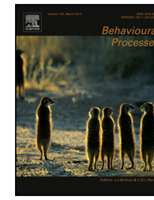
Behavioural Processes 129 (2016) 54–67

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Complex effects of reward upshift on consummatory behavior

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ARTICLE INFO

Article history:
Received 25 February 2016
Received in revised form 9 May 2016
Accepted 9 June 2016
Available online 11 June 2016

Keywords:
Consummatory successive positive contrast
Neophobia
Generalization decrement
Incentive relativity

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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http://dx.doi.org/10.1016/j.beproc.2016.06.006
0376-6357/

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.