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Consummatory successive negative contrast in rats: Assessment through orofacial taste reactivity responses

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A B S T R A C T

Rats exposed to a downshift from a large reward (32% sucrose) to a small reward (4% sucrose) show an abrupt and transient reduction in consumption in comparison with animals that are always exposed to the small reward. This effect is called consummatory Successive Negative Contrast (cSNC) and involves negative affective consequences that lead to an aversive emotional, cognitive and behavioral state of frustration. There are few previous works that have investigated the hedonic alterations that undergo an unexpected incentive devaluation. The hedonic impact of fluids can be reliably assessed by examining the orofacial reactions of acceptance and rejection in the taste reactivity (TR) test. This study addressed in male adult Wistar rats the hedonic impact of incentive devaluation in an adapted cSNC protocol. Specifically, the orofacial responses to a sucrose solution infused into the oral cavity were measured. It was observed that animals exposed to reward devaluation, from a 32% to a 4% sucrose solution, showed a decrease in the duration of appetitive responses (tongue protrusions, mouth movements, paw licks) as compared with subjects which only experienced the low concentration of sucrose. The results are consistent with the hypothesis that incentive devaluation in a cSNC not only results in reduced intake, but also in a reduction in the hedonic value or palatability of the devalued reward.

1. Introduction

Affective responses to reward loss or the reduction in the perceived incentive value constitutes one of the most characteristic evolutionary advances in mammals. They are an important motivational source for behavioral adaptation to environmental changes, orientation of behavior and searching for lost reinforcement (Papini, 2003). These responses require not only prior learning of the physical aspects of rewarding stimuli (e.g., intensity and magnitude) but also learning of their motivational aspects and emotional states associated with reward loss (Papini, 2002, 2006). An extensive body of evidence shows that the incentive devaluation has negative affective consequences that lead to an aversive emotional, cognitive and behavioral state called frustration (Amsel, 1958, 1992). There are several experimental protocols used as animal models for evaluating frustration responses, including Successive Negative Contrast (SNC) (Flaherty, 1996). In its consummatory version (cSNC) in rodents, the animals are exposed to the unexpected

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devaluation of a preferred reward (e.g., 32% sucrose solution) to one of lower hedonic value (e.g., 4%). The negative contrast effect is observed in an abrupt and transient reduced intake compared to animals which only experience the low concentration of sucrose (e.g., Cuenya et al., 2015; Cuenya, Fosacheca, Mustaca, & Kamenetzky, 2012; Papini, Galatzer-Levy, & Papini, 2014).

Different studies in rodents have shown that frustration state is closely related to the responses of fear and anxiety. For example, the incentive devaluation in a cSNC is accompanied by stress-related neuroendocrine responses such as increased release of corticosterone (Mitchell & Flaherty, 1998; Pecoraro, de Jong, & Dallman, 2009); the size of cSNC is diminished by the previous administration of benzodiazepines (e.g., Flaherty & Rowan, 1989; Mustaca, Bentosela, & Papini, 2000) and ethanol (Kamenetzky, Mustaca, & Papini, 2008); lesions in the corticomedial and central amygdala eliminate the negative contrast effect (Becker, Jarvis, Wagner, & Flaherty, 1984); and its size is reduced both by intra-amygdala infusion of diazepam (Liao & Chuang, 2003) and by inactivation of the centromedial amygdala (Kawasaki, Glueck, Annicchiarico, & Papini, 2015).

The response to incentive devaluation not only generates an aversive emotional state but also motivational changes around the devalued stimuli. The effect of cSNC is observed in rats even when the animals are trained under movement restriction at maximum, evidencing that the consumption decrease is not a mere by-product of searching behavior of the lost reward, but implies an active rejection of devalued reward (Lopez Seal, Cuenya, Suárez, & Mustaca, 2013). Motivational changes have also been reported around stimuli predicting frustration events, since rats learn to escape from cues previously associated with reward reduction (Daly, 1974). In this direction, Gray and McNaughton (2000) proposed a motivational equivalence between fear and frustration, according to which there would be a partial overlap between the responses generated by reward loss and punishment.

However, motivation is not a unitary construct. It has different subsystems that contribute to regulate searching and consummatory behavior (Castro & Berridge, 2014). Two of these motivational components are ‘liking’ (hedonic impact) and ‘wanting’ (incentive salience). Liking essentially consists of the hedonic or affective impact of a reward, the brain reaction underlying the sensory pleasure produced by the presence of a reinforcer (e.g., a sweet taste). Wanting constitutes the incentive motivation, that without involving sensorial pleasure, configures the incentive salience and has a fundamental role in predicting pleasurable situations and behavioral orientation to recover the reinforcement. These components have different neuronal substrates and mechanisms. Dopaminergic circuits are predominant in wanting, while opioid, cannabinoids and gabaergic circuits are prevalent in liking (Berridge & Kringelbach, 2015; Peciña, Smith, & Berridge, 2006).

In a cSNC protocol both components coexist, since the registration of the consumption response is determined by consummatory and preparatory behaviors (Konorski, 1967). However, there are appropriate experimental protocols to evaluate motivational subsystems in a differentiated way. The hedonic impact of taste stimuli can be reliably assessed by examining the animal’s orofacial reactions –stereotyped oral motor and somatic consummatory responses elicited by the fluid in the taste reactivity (TR) test (Grill & Norgren, 1978). In this test, rats are infused with a flavored solution via a cannula implanted in their oral cavity, and the orofacial taste reactivity responses are analyzed. These responses can be classified as appetitive reactions such as mouth movements, tongue protrusions, and paw licks (elicited, for example, by pleasant sweet tastes), or aversive (i.e., rejection reactions) such as gaping, chin rubbing, and paw treading (elicited, for example, by unpleasant sour or bitter tastes). Thus the assessment of TR behaviors provides information about why voluntary consumption has changed rather than merely assessing the size of the behavior modification (Berridge, 2000; Parker, 1998).

During the last decades, the theoretical discussions about the mechanisms involved in the cSNC were strongly focused on the weight attributed to the associative, cognitive and emotional components in this phenomenon (Amsel, 1992; Flaherty, 1996), but its hedonic consequences were neglected, leaving open the critical question of whether incentive devaluation results in the reduction of the hedonic value of the expected reward. There are few previous works in the literature that have investigated the hedonic shifts underlying an unexpected incentive devaluation (e.g., Grigson, Spector, & Norgren, 1993; Suárez, Mustaca, Pautassi, & Kamenetzky, 2013). If the negative contrast effect implies a decrease in the hedonic properties of reward, it is expected that the frustration response will be accompanied by a reduction in the orofacial indicators associated with appetitive solutions. In order to evaluate this hypothesis, an experiment was performed in which the animals were trained in an adapted cSNC protocol that analyzed the orofacial responses associated with the presentation of palatable solutions. Specifically, while the animals were exposed to reward devaluation, from a 32% to a 4% sweetened solution, we measured the orofacial taste reactivity responses associated with appetitive stimuli (mouth movements, tongue protrusions, paw licks). A decrease in these responses is expected in comparison to a control condition in which the animals were trained throughout the experiment to consume the less preferred reward.

2. Method

2.1. Subjects

Thirty male Wistar rats, approximately 90 days old and with a mean weight of 343 g (range: 315–393 g) at the start of the experiment, served as subjects. Upon arrival, they were housed individually in standard plastic cages (28 × 28 × 16 cm) in a colony room maintained on a 12-h light/dark cycle (lights on at 08:00) and at an ambient temperature of 21 °C. All experimental manipulations took place during the light phase of the cycle. Throughout the experiment, the rats were maintained on a food-deprivation schedule as described below. All behavioral procedures were conducted in accordance with guidelines of the European Council Directive (2010/63/UE) and Spanish regulation RD53/2013 regarding the care and use of laboratory animals.