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Contextual control of flavor neophobia

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HIGHLIGHTS

- Neophobia habituation interacts with context novelty/familiarity.
- Dopamine levels affect to the neophobia habituation by context familiarity interaction.
- Exploring a context without aversive consequences generates a safe memory trace of such context.
- A context safe memory trace increases consumption of any flavor presented in its presence.

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ABSTRACT

The role of context in the retrieval of learned information has been widely analyzed in the associative learning domain. However, evidence about the effect of context on flavor memory retrieval is more limited. We have carried out four experiments with rats testing for possible interactions between neophobia habituation and the context in which flavors are presented, by manipulating prior experience with contexts. Our results point to the relevance of context familiarity for the establishment and recovery of a safe taste memory trace. More specifically, the use of the animals' home cages as experimental context favored neophobia habituation (Experiments 1A and 2), reduced dopamine levels induced by administration of the dopamine D1-like receptor antagonist SCH-23390 disrupted neophobia habituation when tested in presence of a new context (Experiment 1B), and testing in the animal's home cage increases the amount of flavor consumed, even when such flavor had a previous history of aversive conditioning (Experiment 3). We propose that exploring context without aversive consequences generates a safe memory trace of such context that becomes in the basis of increased flavor consumption.

1. Introduction

Any alteration in environmental conditions induces different responses that can change in intensity, duration or functionality depending on the stimulus characteristics and the novelty produced by its presentation or withdrawal. Thus, for instance, a new light or sound of medium intensity generates a set of orienting responses that allows to the animal to explore and process the stimulus more accurately. When the stimulus is presented repeatedly without consequence, the orienting responses gradually decline as the stimulus loses its novelty [1].

A particularly interesting case is that related to the responses that follow the tasting of a new flavor, because in this situation the potential value of the stimulus for the animal's survival is very high [2,3]. As described by Bermudez-Rattoni [4] animal survival depends, among other factors, on their capacity to differentiate those foods that are edible from those that have toxic components. Animals are highly adaptive in that when they come into contact with a new flavor there appears to be an unconditioned response of rejection that results in minimum consumption of the substance with that flavor, which is known as neophobia [5]. When a period of time has elapsed since the flavored item was consumed, and as the flavor memory trace is consolidated as a "safe" stimulus (that is, a stimulus without aversive consequences), consumption progressively increases, a phenomenon termed habituation of neophobia [6]. Conversely, if flavor consumption is followed by any kind of negative consequence an aversive conditioning develops [7] that is behaviorally expressed in a sharp reduction of flavor ingestion. Therefore, as a function of the consequences that follow flavor ingestion, a flavor memory trace will be established that is either safe, favoring an increase in consumption of the flavor in future encounters, or aversive, which will result in a reduction or even the complete rejection of flavor consumption [4,8].

This proposal is compatible with the learned safety theory [9,10], but contrasts with other general interpretations of the habituation process that propose mechanisms either associative or non-associative. Thus, from a non-associative perspective, the Dual-Process Theory proposed by Groves and Thompson [11] suggests that repeated presentations of a stimulus induce two independent processes in the central nervous

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system that interact to produce a response. The first process takes place in the stimulus–response pathway and is responsible for the progressive reduction of the response. The second process acts in the state system and gives rise to an increase in response intensity due to sensitization.

An alternative theory of habituation, which has great influence in the analysis of the processes underlying habituation mechanisms, was proposed by Wagner [12,13]. From his perspective, habituation depends on the association established between the stimulus and the context in which it appears. More specifically, Wagner proposes that, after repeated presentations of the stimulus, the contextual cues will activate a representation of the stimulus in short term memory which will prevent processing of the actual event, resulting in the reduction of the response to the stimulus that characterizes the habituation process.

All the theories mentioned recognize, in a more or less explicit way, the role of context in the habituation process. However, while for Wagner [12,13] the context is considered an essential element in the associative process that produces habituation, for the Dual-Process Theory of habituation [11], on the other hand, context would have merely the status of a stimulus that is also subjected to habituation after repeated presentations. For the specific case of neophobia habituation, the learned safety theory [9,10] implies that the context acquires properties as a modulator of the flavor significance by means of its capacity to recover the association between the flavor and the absence of consequences. In fact, there is some evidence showing contextual modulation of neophobia habituation. Thus, a context change, but only if the context is new, induces neophobia recovery [14,6]. However, when the change involves a familiar context, neophobia habituation remains intact [6].

From a physiological perspective, the involvement of the dopaminergic system in appetitive learning [15] and in the role of context as a learning modulator [16] makes it a possible neurochemical candidate for the development the mentioned context-dependent safe flavor memory trace based in an association between the taste and the absence of aversive consequences. More specifically, previous studies have shown modulation of dopaminergic transmission as a function of the motivational valence and novelty of the stimuli [17]. In particular, it has been observed an increase in dopamine release in the nucleus accumbens (NAc) shell in response to appetitive but not aversive unfamiliar stimuli. It also has been demonstrated the role of dopamine in studies of context modulation of conditioning through a circuit which involves indirect projections from the ventral subiculum to the NAc [16].

The general purpose of the experiments that follow is to evaluate the role played by context familiarity on the development and the recovery of the safe memory trace of the flavor. To this end, we conducted four experiments using contexts that were new or the home cages, to evaluate a possible interaction between neophobia habituation and context novelty or familiarity (Experiment 1A), to evaluate whether dopamine levels differentially affect to the interaction between neophobia habituation and context familiarity (Experiment 1B), to check the role of novelty/familiarity by introducing in the experimental design a previously familiarized context in addition to the home and new environments (Experiment 2), and to analyze whether the intensity of a conditioned response after a taste aversion episode changes as a function of the test context degree of novelty (Experiment 3).

2. Experiments 1A and 1B

These experiments evaluated possible differences in the process of neophobia habituation as a function of the context (home cages vs. new experimental context) in which flavor is consumed (Experiment 1A) and the effect of dopamine D1-like receptor antagonist administration during saccharin habituation in the presence of the home cage vs. a new experimental context (Experiment 1B).

The available experimental evidence on contextual modulation of neophobia habituation shows that a context change, but only if the context is new, induces neophobia recovery [14,6]. A particularly interesting situation occurs when the experimental context involves the animals' home cages [3,18]. As far as we know, there are not any evaluation of neophobia habituation or recovery of neophobia using the home cages as an experimental context, but there are some experiments analyzing latent inhibition that have reported particular effects when using home cages as an experimental context as opposed to new or familiar contexts. Thus, it has been reported that when using a conditioned taste aversion for reproducing the latent inhibition effect, the animals' home cages seem to have properties that make it easier to establish a safe memory trace of the flavor when it is not followed by relevant consequences [19,20].

Regarding the role of different neurotransmitters in flavor processing, dopamine could be playing a relevant role in the development of the hypothetical flavor safe memory trace [21]. For instance, it has been observed an increase in dopaminergic activity when the animal is exposed to a sweet flavor in the NAc, and a decrease when the flavor had been previously associated with gastric malaise [22]. These results have lead to the proposal that dopamine is not implied in the processing of the sweet flavor per se, but in the positive/affective reinforcement value [23,24]. The proposal that flavor presentation without aversive consequences generates a safe memory trace could be related in some extent with the mentioned rewarding value of the flavor. In fact, the relevance of the dopaminergic system, and more specifically of the D1 receptors, on the establishment of flavor preferences has been already demonstrated [25].

Regarding the context, there are also empirical results demonstrating the role of mesolimbic dopaminergic system in place preferences learning [26]. However, and attending to the modulatory role proposed for the context in the development of the flavor safe memory trace, we propose that it could be mediated in the same way observed with classical or instrumental conditioning paradigms. More specifically, contextual modulation of latent inhibition or extinction seems to be dependent of dopaminergic projections from the hippocampus to the NAc [27], and the activation of such circuit is linked to context novelty because when there is no context change such circuit is not activated [16]. From this perspective, the development of the saccharin safe memory trace would imply higher dopaminergic activity when the habituation context is novel than when it is familiar.

In Experiments 1A and 1B, the animals were allowed to drink a saccharin solution four consecutive days, for 5 min each day, in their home cages or in a new experimental context. In Experiment 1A we expected that the home cage would offer an additional source of safety that favored the development of the memory trace as safe, and, as a result, that consumption in home cages will be greater than in the new experimental context. In Experiment 1B we expect that the diminished dopaminergic activity in the group injected with the D1-like receptor antagonist (SCH-23390) would reduce the flavor habituation rate in the group exposed to the new context.

2.1. Method

2.1.1. Subjects

The subjects were 45 male Wistar rats (16 in Experiment 1A and 29 in Experiment 1B, n = 7/8) with weights ranging from 320 to 460 g. The animals in these and the following experiments remained undisturbed in their home cages for a minimum of three weeks before the start of the experimental treatments. Each animal was individually housed in 40 × 20 × 24 cm Plexiglas cages with wood shavings as bedding, and maintained on a regular 12:12-h light/dark cycle. The vivarium was illuminated by four 100 W bulbs. All