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US-preexposure effects in flavor-preference and flavor-aversion learning with nonnutritive USs

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ABSTRACT

In two experiments, rats received exposure to either a saccharin or quinine solution followed by conditioning with a solution of almond as the conditioned stimulus (CS) and either saccharin or quinine as the unconditioned stimulus (US). In Experiment 1, rats received preexposure and conditioning using saccharin as the US; in Experiment 2 quinine was the US. In both cases the magnitude of the conditioning effect (an enhanced preference for the CS in Experiment 1; a reduced preference in Experiment 2) was reduced by preexposure to the US. The results provided confirmation of the occurrence of the US-preexposure effect in the flavor-preference procedure and demonstrate that the effect can be obtained with nonnutritive USs that lack significant post-oral consequences. The implications of these results for theories of the US-preexposure effect are discussed.

1. Introduction

Prior exposure to the event to be used as the unconditioned stimulus (the US) in classical conditioning can retard subsequent learning (the US-preexposure effect). The effect is particularly well established for the case of nausea-induced flavor-aversion learning (Hall, 2009; Riley and Simpson, 2001). Rats given a series of injections of a nausea-inducing substance such as lithium chloride (LiCl) show retarded acquisition of the aversion to a novel flavor when this flavor is paired with LiCl in a conditioning procedure (and the same is true of a range of other substances normally capable of supporting aversion learning; Riley and Simpson, 2001). The effect is not confined to aversive learning—for example, Gil et al. (2011) have shown that preexposure to sucrose will reduce the effectiveness of sucrose to function as a reinforcer in establishing a preference for a previously neutral flavor.

The US-preexposure effect is of special interest, as it seems to imply the existence of a learning process that modifies the effectiveness of this stimulus and thus modulates the operation of standard associative mechanisms. Randich and Lolordo (1979), in their review of the effect, acknowledged this possibility by including habituation of the US as a possible mechanism. They also pointed out that a standard associative process (blocking) could be responsible—that cues present during preexposure (such as those supplied by the experimental context) could become associated with the US and that their presence during conditioning could block the acquisition of associative strength by the event designated by the experimenter as the conditioned stimulus (the CS). There is evidence that this latter mechanism operates in the flavor aversion learning procedure (although the cues critical for blocking are not those supplied by the environmental context, but those associated with the process of giving an injection; De Brugada et al., 2004). There is little evidence to support the notion that habituation to the US plays a role (see De Brugada et al., 2005).

In order to investigate the US-preexposure effect in a procedure in which initial presentations of the US would not be accompanied by salient cues, Gil et al. (2011) turned to flavor-preference conditioning. In this procedure pairing of a neutral flavor with a valued substance such as sucrose, will establish a preference for that flavor, an outcome that we will assume to depend on the formation of an association between the flavor as a CS and some aspect of the sucrose US. Preexposure to the US can easily be arranged simply by giving access to a sucrose solution; rats will consume

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this readily, thus eliminating the injection-related cues involved in aversion conditioning. Using this procedure, Gil et al. showed that the size of the conditioned preference was reduced by preexposure to sucrose (see also Harris et al., 2004) They also showed that this US-preexposure effect was fully evident when the environmental context used for conditioning was different from that used for preexposure, thus ruling out the possibility that this effect might depend on blocking by associative strength acquired by contextual cues during the preexposure phase. They tentatively concluded that the effect obtained in their experiments was the consequence of a habituation process that reduced the effectiveness of sucrose as a reinforcer.

Although the results reported by Gil et al. (2011) are not to be explained in terms of blocking by contextual (or injection-related) cues, another possible source of blocking, when sucrose is the US needs to be considered. This arises from the fact that sucrose has both sensory (a sweet taste) and post-consumption (nutritive) properties, and that both of these may play a role in flavor-preference learning (e.g., Sclafani and Ackroff, 1994; Sclafani et al., 1993). In terms of an associative analysis, pairing a flavor with sucrose will establish both flavor-taste and flavor-nutrient associations (e.g., Harris et al., 2000) and normally both will contribute to the preference seen on test. The situation may be different, however, if preexposure to sucrose is given. Prior exposure would allow the subject to experience the novel taste of sucrose followed by its nutritional effects and thus a taste-nutrient association could be formed in rats given US preexposure. Such an association could block the formation of a flavor-nutrient association during conditioning trials. The flavor-sweet taste association would still be formed, but the preexisting association between taste and nutrition would prevent the flavor-nutrient association from acquiring strength. The reduced preference in preexposed subjects would thus reflect that it was generated only by the flavor-taste association, with no contribution from flavor-nutrient learning.

The experiments to be reported here are intended to seek evidence for a US-preexposure effect using as the US a substance without major post-consumption consequences. With such a US, any change in the preference for a flavor paired with it will be the consequence solely of the formation of an association between the flavor and the taste of the US. In these circumstances, a US-preexposure effect could not be attributed to the blocking process just described. In Experiment 1 we used saccharin as the US; in Experiment 2 we used quinine (for which conditioning is evidenced by a reduction in the preference for the flavor associated with the US). In both experiments we used a solution of almond flavoring as the CS. This is likely to be detected primarily as an odor, but since it may also have some taste- (particularly at higher concentrations) we will refer to it as a flavor (acknowledging the possible presence of both taste and odor). Saccharin and quinine are taken to be tastes.

2. Experiment 1

In this experiment we gave rats exposure to presentations of a solution of saccharin prior to conditioning trials in which saccharin was presented in compound with almond. Preference for this flavor on test was compared with that shown by control subjects given conditioning but no preexposure. A lesser preference in the subjects given preexposure would be evidence of a US-preexposure effect. As the ability of saccharin to support the acquisition of a flavor preference depends critically on the exact conditions of training (e.g., Fanselow and Birk, 1982; Holman, 1975), we conducted a preliminary study, in which no US preexposure was given, in order to confirm that a conditioning effect could be obtained with our experimental parameters and procedures. In this we compared the preference generated by our pairing procedure, with that shown by rats given equivalent exposure to saccharin and almond, but on separate occasions. This study is reported as Experiment 1a; the effect of US preexposure as Experiment 1b. The experimental designs are summarized in Table 1.

Table 1
Experimental designs.

Experiment 1a		
Group	Conditioning	Test
SIM	4 A + Sacc	A vs. W
UNP	4 A/Sacc	

Experiment 1b			
Group	Preexposure	Conditioning	Test
PRE	8 Sacc	4 A + Sacc	A vs. W
CON	8 Water		

Experiment 2a		
Group	Conditioning	Test
SIM	4 A + Quin	A vs. W
UNP	4 A/Quin	

Experiment 2b			
Group	Preexposure	Conditioning	Test
PRE	8 Quin	4 A + Quin	A vs. W
CON	8 Water		

Note: Sacc: sodium saccharin solution; Quin: quinine sulphate solution; A: almond solution; W: water; SIM: paired presentations; UNP: unpaired presentations; PRE: preexposed: CON: nonpreexposed control.

2.1. Method

2.1.1. Subjects and apparatus

The subjects in Experiment 1a were 16 male hooded Lister rats (from Charles River Laboratories) with a mean free-feeding weight of 482 g (range: 473–492 g). They had previously served as subjects in an experiment using the conditioned suppression paradigm but were naïve to all aspects of the current stimuli and procedures. Experiment 1b used 16 male naïve Wistar rats (obtained from the University of Seville Laboratories) with a mean free-feeding weight of 285 g (range: 256–312 g). The rats were housed individually in home cages measuring $35 \times 22 \times 18$ cm, and made of translucent white plastic with wood shavings as bedding. They were maintained on a 12-h light/12-h dark cycle (lights on at 8:00 a.m.). All experimental procedures were conducted in the home cages. The stimuli used were, as the CS, a 1% (v/v) almond solution (almond flavoring supplied by Supercook, Leeds, UK), a 4 g/l sodium saccharin solution (US), and a compound of almond and saccharin made up so as to preserve these concentrations. All solutions were made with tap water and given to the animals in inverted 50-ml centrifuge tubes equipped with stainless steel, ball-bearing-tipped spouts in the home cages. Fluid consumption was measured by weighing the tubes before and after fluid presentations.

2.1.2. Procedure

To initiate a schedule of water deprivation, the standard water bottles were removed overnight; over the next two days, access to water was restricted to two 30-min sessions per day (starting at 11 a.m. and 4:30 p.m.). Fluids continued to be given at these times throughout the experiment. For Experiment 1a, the rats were assigned to two equal-sized groups. Over the next four days, the simultaneous group (SIM in the table) received a daily presentation of 10 ml of the compound solution in one of the