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Research report



Associative and occasion-setting properties of contextual cues in flavor–nutrient learning in rats [☆]

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ABSTRACT

This article studied the role of contextual cues, present at the time flavor conditioning occurs, on intake behavior in rats. In three experiments animals were given flavor–sucrose pairings in one distinctive context (Context A) whereas the flavor was presented unreinforced in an alternative context (Context B). Experiments 1 and 2 used a simple Pavlovian discrimination procedure (A: X+, B: X–) and tested consumption of flavor X in each context. Consumption of the flavor was higher in Context A than in Context B. In Experiment 2 rats were given a treatment (exposure to water in the context) designed to extinguish associations between the context and the reinforcer. This procedure did not affect the ability of the context to control intake of flavor X. Experiment 3 used a biconditional discrimination procedure (A: X+, Y–; B: X–, Y+; where X and Y were different flavors) in which no single context or flavor predicted reinforcement. The rats learned this discrimination, consuming more of each flavor in the context in which it had previously been reinforced. The results are interpreted in terms both of the effects of direct associations between context and events presented in them, and in terms of the modulatory or occasion-setting properties of the context.

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Introduction

Eating behavior is, in part, the consequence of learned responses to food cues. Consumption of a given substance depends on its look, smell, and, importantly, on its flavor (an emergent property based on taste, oral somatosensory, and retronasal olfactory cues; see Stevenson, 2009). Flavor cues are susceptible to the effects of conditioning, can form associations with the reinforcing properties of foods, and thus influence intake when the flavor is encountered subsequently. It is well established that pairing a neutral flavor with a food substance such as sucrose will increase subsequent acceptance of that flavor (i.e., willingness to consume it), and produce a preference for it in a choice test (see, e.g., Capaldi, Campbell, Sheffer, & Bradford, 1987; Fedorchak & Bolles, 1987; Harris, Gorrissen, Bailey, & Westbrook, 2000; Mehiel & Bolles, 1984). Although the reinforcing power of the sucrose in this procedure appears to derive both from its palatable taste and also from its nutritive post-ingestive consequences, we will refer to the phenomenon simply as flavor–nutrient learning.

Conditioning is not confined to the cues provided by discrete cues, such as flavors, directly associated with food. Contextual cues (by which is meant the set of varied properties, e.g., spatial, olfactory, auditory, identifying a particular place) that are present when food is consumed may also enter into associations, and serve not only to locate and identify food (e.g., Maes & Vossen, 1993; Shishimi & Nakajima, 2007), but also to determine food preference and intake. For instance, it has been shown that contexts can serve as conditioned cues that potentiate eating in rats, and this cueenhanced eating can be relatively specific to the food used during training (Petrovich, Ross, Gallagher, & Holland, 2007; but see Boggiano, Dorsey, Thomas, and Murdaugh (2009) for evidence of a generic increase in food consumption). Again, Albertella, Harris, and Boakes (2008) have shown that, during conditioning of flavor preferences, the training context may acquire value as a signal for food and affect the expression of the preference. In general, learning processes may play an important role in determining how contexts affect food intake and contextual influences should be considered as environmental risk factors for obesity and for poor dietary habits (see, e.g., Jansen, 2010) from which individuals may need the kind of protection that falls under the mission of public health (e.g., Cohen & Babey, 2012).

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The mechanisms by which contextual learning might come to influence food intake remain to be determined. One possibility is to attribute it to the formation of simple associations between the context and the (palatable) food, in the manner described by Petrovich et al. (2007) and Boggiano et al. (2009). Another possibility is that the context acts not as a simple conditioned stimulus (CS), but as an occasion setter (e.g., Holland, 1992); that is, the context in which food is consumed might come, independently of its own direct association with the food unconditioned stimulus (US), to signal that a particular flavor CS, which is otherwise without consequence, will be followed or accompanied by the US. It should be noted that these possibilities (i.e., direct association and conditional control) are not mutually exclusive alternatives. It has been shown that a discrete stimulus can serve both as a CS and as an occasion setter at the same time (e.g., Holland, 1992; Urcelay & Miller, 2010), and it has been argued (Bouton, 2010) that the same will apply for contextual cues.

Previous work investigating these issues has provided evidence that the context can acquire an occasion-setting function in flavor-nutrient learning, at least under some circumstances of training. Occasion setting was demonstrated by Dwyer and Quirk (2008), who used a biconditional discrimination design involving two flavors and two contexts. During training flavor X was paired with a US (e.g., fructose or maltodextrin) in context A, whereas flavor Y was not; in context B, Y was paired with the US and X was not. The rats successfully learned the discrimination, showing contextdependent preferences on test (i.e., preferring X over Y in A, and Y over X in B). As the design ensured that the direct association with the US would be the same for both contexts, this outcome may be attributed to the acquisition of occasion-setting powers by the contexts. Campbell, Capaldi, Sheffer, and Bradford (1988) used a similar biconditional design, but a procedure in which the presence of a given flavor signaled what consequence would follow. Thus in context A, X signaled that sucrose would shortly become available whereas Y signaled that quinine would be available; the assignments were reversed in context B. Campbell et al. recorded the latency to approach the bottle containing the consequence, taking a short latency to indicate expectancy of a positive outcome (sucrose). This behavior exhibited conditional control with the rats showing short latencies after presentation of flavor X in context A, but after flavor Y in context B. Interestingly, however, conditioned preference, as assessed by a two-bottle choice test between flavors X and Y, did not show a context-specific effect.

Consuming food in a particular place may provide the opportunity for different types of learning to occur: flavor-nutrient learning, context conditioning, and contextual occasion setting. The experiments to be reported here investigate the relation among these forms of learning. There is little evidence directly addressing the question of whether the association of a context with a nutrientpaired itself with a flavor-will make that context capable of influencing preference for (or degree of acceptance of) the flavor. Thus, in the first experiment to be reported here, we sought to demonstrate that a context in which flavor-sucrose conditioning has occurred can acquire the power to enhance consumption of the flavor when presented subsequently unreinforced. We made use of a discrimination procedure in which rats were allowed to drink a compound solution made of flavor X and sucrose (X+) in one context (context A) whereas the solution was presented unreinforced (X-) in another context (context B). When this discrimination had been acquired we tested consumption of flavor X in both contexts and demonstrated, to anticipate, that it was greater in context A than in context B. In Experiment 2 we used an extinction manipulation to investigate the extent to which this effect was determined by direct associations (excitatory for context A and inhibitory for context B) between contextual cues and the US used in training. The possibility that occasion-setting may also contribute to the effects seen with the contexts, flavors, and motivational conditions used in the present experiments was tested in Experiment 3, which employed the biconditional discrimination procedure.

Experiment 1

In Experiment 1 rats received flavor–sucrose pairings in context A (A: X+) whereas the flavor was presented unreinforced in context B (B: X–). The contexts differed in their visual, auditory, and tactile properties. Because flavor preferences based on a nutrient appear to be enhanced by food deprivation (Fedorchak & Bolles, 1987; see also Balleine, Espinet, & González, 2005; Harris et al., 2000; Yiin, Ackroff, & Sclafani, 2005), food was removed from the home cages before the test sessions. Afterwards, rats had the opportunity of consuming flavor X (unreinforced) in each of the two contexts to test for contextual control over consumption of the trained flavor.

Methods

Subjects

The subjects were 16 experimentally naive male Wistar rats with a mean weight of 283 g at the start of the experiment (range 269–293 g). They were housed in individual home cages and kept in a large colony room located in the laboratory of the University of Granada under a 12-h light/12-h dark schedule (lights coming on at 0800 h). The rats were water deprived, as detailed below, but had continuous access to food throughout the experiment, with the exceptions mentioned below. The home cages measured 50 cm long \times 26 cm wide \times 14.5 cm high; the walls and floors were made of translucent plastic, and the roof of wire mesh that held food and a water bottle (when available); a layer of wood shavings covered the floor. Training sessions took place twice a day at approximately 0900 h and 1500 h.

Apparatus

Two sets of cages, each distinct from the home cage, served as the experimental contexts. The first set of cages (Type 1) was located in a separate room dimly lit by a single 40-W red bulb positioned in a corner close to the cages. This room contained a speaker supplying constant background white noise with an intensity of 70-75 dB measured close to the cages. The cage walls and floor were made of opaque grey plastic and the roofs were made of wire mesh, containing a hole through which a drinking spout could be inserted. The cages were 32 cm long \times 22 cm wide \times 12 cm high. The floor was covered with commercially obtained cat litter. The cages in the second set (Type 2) were 20.5 cm $long \times 20.5$ cm wide \times 23 cm high, and were located in a separate brightly lit room. The floors and walls of these cages were made of white wood, and the wire mesh roofs included a section through which a drinking spout could be inserted. The floor was covered with a clean piece of white paper.

Fluids using during training and tests were administered in an inverted 50-ml plastic tube with a rubber stopper fitted with a stainless steel ball-bearing tipped spout. Fresh solutions were made daily with tap water and administered at room temperature. Consumption was measured by weighing the tubes before and after fluid presentation to the nearest 0.1 g. The US was a 10% (w/v) sucrose solution. The target flavor X was a 2% (v/v) almond solution (SuperCook, Leeds, UK).

Procedure

Water bottles were removed from the home cages 24 h before the start of the experiment. Rats were given 3 days to accommodate to water deprivation, with access to water restricted to two periods of 30 min (morning and afternoon sessions). The next Download English Version:

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