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Reinforcer-specificity of appetitive and consummatory behavior of rats after Pavlovian conditioning with food reinforcers

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Abstract

We examined the reinforcer-specificity of Pavlovian conditioning in the control of appetitive and consummatory behaviors in Pavlovian-toinstrumental transfer, cue-potentiated eating, and devaluation procedures. Rats received pairings of one conditioned stimulus with sucrose and another conditioned stimulus with maltodextrin. In Experiment 1, rats were also trained to earn sucrose for one instrumental response and maltodextrin for another. In a transfer test, the Pavlovian cues enhanced the rate of instrumental responding more when the food reinforcer predicted by the instrumental response and the Pavlovian cue were consistent than when they were inconsistent, but both cues enhanced both responses. In Experiment 2, sated rats' consumption of each food was potentiated in the presence of a cue for that food, but not in the presence of a cue for the other food. In Experiment 3, one food was devalued by pairing it with lithium chloride, prior to testing food consumption and food-cup directed behaviors. The food cues selectively controlled food-cup related behaviors, regardless of the presence of the devalued or nondevalued foods in the food cup. Together, these results are consistent with the view that conditioned cues modulate appetitive and consummatory behaviors with increasing levels of specificity. The closer an action comes to ingestion, the more it is controlled by sensory properties conveyed by learned cues. These data are discussed in the context of allostatic regulation of food foraging and intake. © 2007 Elsevier Inc. All rights reserved.

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1. Introduction

Overeating has become a problem of epidemic proportions. Thus, understanding the events that trigger appetitive and consummatory behaviors is of utmost importance. Considerable scientific attention has been focused on roles of food availability, meal size, energy homeostasis and pharmacological variables in determining feeding. The importance of learning and memory is often overlooked. The experiments reported here examined the effects of learned signals for foods on various aspects of appetitive and consummatory behavior. Progress in understanding the impact of learning on food-procuring and consuming behaviors should contribute to understanding the impact of environmental cues and food availability on eating habits.

Consideration of roles for learning in feeding behavior is consistent with the notion of *allostasis* [1], which has

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increasingly supplemented traditional homeostatic views of feeding behavior. From this perspective, relative stability of body weight is the product of mechanisms that predict future demands rather than merely adjust to physiologically determined setpoints. Ingestive behavior may be described as allostatic not only because animals forage and eat before their energy stores are depleted, but also because those behaviors are determined by information about the future availability or scarcity of food as well as by the animal's current deprivation state. When a future shortage of food is predicted, an animal acts upon that prediction, although its actual state may not have gone below a determined homeostatic setpoint or threshold. Thus, allostatic mechanisms are readily adaptable to constantly changing environmental challenges and demands.

Allostatic systems may deal with current or future scarcities of resources. For example, induction of a sodium deficit enhances long-term salt palatability beyond the moment of restoration of normal sodium levels [2,3]. From an allostatic standpoint, this form of sensory and/or hedonic stimulation of appetite is highly adaptive. Although the exquisite relation of sodium deficits and salt palatability may be unique, studies of acquired flavor preferences and aversions show that animals can alter their evaluations of foods that are enriched or deficient in particular nutrients. These learned changes in evaluation or preference may come under the control of a variety of cues, such as other sensory properties of those foods, or environmental cues associated with those foods during periods of nutrient scarcity. Furthermore, these cues might later guide procurement and eating of those foods and hence prevent depletion of that nutrient in the face of future scarcity. Thus, an important question addressed in the present experiments is the extent to which the influence of learned signals for foods on appetitive and consummatory behaviors is specific to the particular foods being sought or consumed.

The development of specific hungers and preferences might be especially advantageous if they were accompanied by the acquisition of corresponding food-specific foraging behaviors. For example, if a cue correlated with carbohydrate in a period of food scarcity especially enhances consumption of carbohydrateladen foods, it would be advantageous if it also enhanced foraging behaviors that secure possession of those particular foods. Experiments 1 and 2 were designed to examine the influence of learned cues for specific foods on both the consumption of those foods and on operant "foraging" for them, in the same rats. In Experiment 1 we addressed the question of the specificity of learned cues' effects on foraging behaviors in the context of Pavlovian-to-instrumental transfer (PIT), in which cues previously paired with the delivery of specific foods were presented while rats were performing instrumental leverpress responses that earned the same or different foods.

In Experiment 2 we examined whether cues paired with specific reinforcers while rats were food-deprived selectively enhanced consumption when the rats were food-sated. A number of studies have shown that learned visual or auditory cues that originally signaled food while animals were food-deprived can potentiate eating later, when those animals are food-sated [4-6]. However, in those experiments, animals were trained and tested with only one type of food. Thus, it is of considerable interest to determine whether cues associated with particular foods in periods of food scarcity may act selectively to enhance consumption of those same foods later in times of dietary repletion.

Finally, it is useful for animals to modify their behavior in response to food-related cues if subsequent experience alters the desirability of the foods signaled by those cues. For example, the induction of illness after consuming a particular food not only reduces consumption of that food but also reduces the likelihood that cues for that food will elicit approach to the source of that food [7]. In Experiment 3, we examined both food-source approach and food-consumption behaviors in the presence of food cues, after establishing an aversion to the taste of one of a pair of foods.

2. Experiment 1

Experiment 1 was designed to measure the sensory-specific effects of superimposing Pavlovian conditioned stimuli (CSs)

on instrumental behavior. This Pavlovian-to-instrumental transfer (PIT) procedure is commonly used to evaluate the motivational effects of Pavlovian stimuli on ongoing goaldirected behavior. Specifically, we examined the effects of a CS that predicted one food (e.g., sucrose) on instrumental responding that was trained with that same food as the reinforcer, and on instrumental responding that was trained with a different food (e.g., maltodextrin).

2.1. Method

2.1.1. Subjects

The subjects were 16 male naive Long–Evans strain rats (Charles River Laboratories, Raleigh, NC, USA) which weighed between 300–350 g when they arrived in the laboratory vivarium. They had free access to lab chow (2018 Rodent Diet, Harlan Teklad Laboratory, Madison, WI, USA) for a week before their food was restricted to maintain them at 85% of their *ad libitum* weights. The rats were caged individually in a colony room illuminated from 6:00am to 6:00pm. The research was approved by the Johns Hopkins University Animal Care and Use committee.

2.1.2. Apparatus

We used eight training chambers $(22.9 \times 20.3 \times 20.3 \text{ cm})$ with aluminum front and back walls and clear acrylic side walls and top. An infrared activity monitor (Coulbourn Instruments, Allentown, PA, USA) and a panel of infrared lights used to illuminate the chamber for video recording were placed on the top of each chamber. An illuminated clear acrylic food cup, with a capacity of about 1.7 ml, was placed behind a square hole in the center the front wall. A photocell beam in the food cup was used to detect head entries and time spent in the cup. An aluminum lever $(2.0 \times 2.0 \text{ cm})$ was mounted on each side of the food cup, centered between the cup and the side walls; throughout the Pavlovian training sessions, they were covered with aluminum boxes $(3.0 \times 2.0 \times 3.0 \text{ cm})$. A speaker which was used to present auditory cues was placed on the back wall of a double-walled sound-resistant shell which enclosed each experimental chamber. A television camera was placed 18 cm above the speaker to record the rat's behavior, and a second camera was placed under the transparent food cup, to record consummatory responses. Images from each camera were digitized, and were recorded and displayed in real time on video monitors, each of which showed 4 chambers or food cups. Video data are not presented in this article.

2.1.3. Pavlovian conditioning

Rats first received four 64-minute sessions designed to train them to approach the food cup and consume each of the 2 food unconditioned stimuli (USs). Each of these sessions included 16 0.1-ml deliveries of either 4% sucrose (2 sessions) or 4% maltodextrin solution (2 sessions), which served as the 2 USs. Each food was administered in a 4% (w/v) solution because pilot data from our laboratory indicated that at this concentration Long–Evans rats consume equal amounts of these foods. Solutions were delivered by infusion pumps located outside the Download English Version:

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