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Flavor change and food deprivation are not critical for post-oral glucose appetition in mice

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HIGHLIGHTS

- Mice will lick a sweet flavor paired with intragastric (IG) water in 1-h tests.
- Shifting to a new flavor paired with IG glucose rapidly increases licking.
- Both food-restricted and ad lib mice increase licking and preference for the flavor.
- Mice show appetition even without a change in the flavor with the shift to glucose.

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ABSTRACT

When mice trained to consume a CS− flavored solution paired with intragastric (IG) water self-infusion are given a new CS+ flavor paired with IG glucose self-infusion, their intake is stimulated within minutes in the first CS+ test. They also display a preference for the CS+ over the CS− in two-bottle tests. These indicators of post-oral appetite stimulation (appetition) have been studied in food-restricted mice, with novel CS+ and CS− flavors. Two experiments tested whether deprivation and flavor novelty are needed for stimulation of intake. Exp. 1 compared food-restricted and ad libitum fed C57BL/6 mice trained for 1 h/day: 3 sessions with CS− flavor and IG water followed by 3 sessions with a novel CS+ flavor and IG 16% glucose. Ad libitum (AL) fed mice licked less overall, but like the food-restricted (FR) group they increased licking in the first session. In the choice test, FR mice displayed a significant CS+ preference (73%) whereas AL mice had a weaker preference (64%). In Exp. 2, food-restricted mice were trained with a flavor and IG water, and then the Same or a New flavor paired with IG 8% glucose. The glucose infusion rapidly stimulated intakes in the first and subsequent sessions and to the same degree in the two groups. Both groups also showed similar reductions in licking in extinction tests with IG water infusions. These data show that mice need not be explicitly food deprived or given a novel flavor cue to increase ongoing ingestion in response to post-oral glucose stimulation.

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1. Introduction

Food flavors have an intrinsic level of attractiveness that is modifiable by post-oral consequences of ingestion. This has long been known for negative events (e.g., an attractive sweet solution paired with LiCl-induced malaise is subsequently avoided) [21] and more recently has been amply demonstrated for positive post-oral events (e.g., an unattractive bitter solution paired with intragastric (IG) glucose infusion is subsequently preferred) [29].

While substantial progress has been made, our understanding of the post-oral flavor preference conditioning process is incomplete. Two studies demonstrated one-trial flavor conditioning with IG sugar infusions [2,16], but did not focus on the behavior during these acquisition sessions. A recent modification of the typical IG flavor conditioning procedure has provided a window on the earliest stage of learning. In this new method [38], food-restricted mice were trained to consume a flavored saccharin solution (the CS−) in daily 1-h sessions. Intake of this CS− solution was paired with IG self-infusion of water controlled by the animal's licking. After several daily CS−/water sessions, the mice were given a new flavored saccharin solution (the CS+) which was paired with IG glucose. Within minutes, intake was stimulated above the level observed with the CS−, showing that the mice rapidly detected the post-oral glucose. In the first session, CS+ intake was 44% greater than that of CS− sessions, and the mice increased their intakes further in subsequent sessions and displayed a preference for the CS+ over the CS− in a two-bottle choice test.

These behaviors are the defining features of appetition, the stimulation of appetite based on post-oral nutrient sensing. The rapid stimulation of licking when post-oral detection of the nutrient occurred in the first session, the conditioned response to the oral cue as demonstrated

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by early elevation of licking in the second session, and the subsequent preference for the nutrient-paired CS+ are hallmarks of positive post-oral effects. Analysis of the early stimulation of intake, which was not detected in studies that focused on other measures of flavor conditioning, will aid in the identification of the post-oral signals that stimulate intake and lead to conditioned preferences.

One goal of the present research was to evaluate the importance of nutritional status on post-oral sugar appetition in mice. In our prior studies food restriction was used to encourage CS intake in the daily 1-h sessions, and it could also render the animals more sensitive to the post-oral nutrient signals [3,4,30,38–40]. In an early study we observed that food-restricted and ad libitum fed rats displayed similar preferences for a CS+ flavor paired with IG infusions of a glucose polymer (maltodextrin) over a CS− flavor paired with IG water infusions [36]. This study, however, did not determine if deprivation state influenced the stimulation of intake by the glucose infusions because CS intakes were limited during the 30 min/day training sessions. In other studies in which ad libitum fed rats or mice were trained 24 h/day, IG infusions of glucose, sucrose, maltose, or maltodextrin stimulated CS+ intake during training and conditioned robust CS+ preferences [5,25–28]. These experiments were not designed to reveal post-oral sugar effects on initial training bouts, however. Other labs have reported differences in acquisition, expression, or both as a function of food restriction using oral conditioning procedures, which do not separate oral vs. post-oral nutrient effects [e.g., 6,12].

A second goal was to determine whether it is necessary to provide a change in flavor to signal the change in the infusion in order to observe a rapid stimulation of intake. In our standard procedure, IG glucose infusion is signaled by the presentation of a new flavor, the CS+. This flavor change may serve as a critical attention signal to the animals that facilitates their response to the IG glucose infusion. The dramatic increase in the early licking response to the CS+ solution in subsequent sessions indicates a conditioned response to the new flavor (i.e., conditioned appetition, which is the reverse of conditioned satiation [29]). It is possible that the increased licking observed in the initial CS+ session represents a rapidly conditioned response to the new flavor. Alternatively, the increase in first session licking may represent an unconditioned response to the IG glucose or may involve, in part, a glucose-conditioned change in the evaluation of the sweet taste of the flavored saccharin solution.

Experiment 1 compared two groups of mice, one maintained on ad libitum chow and the other on restricted rations. Using the appetition procedure, these mice were first trained with CS−/water sessions before a shift to a novel CS+ flavor paired with IG 16% glucose. Although unrestricted feeding was expected to reduce licking during the sessions, we predicted that ad libitum fed mice would also show stimulation of intake by IG glucose. However, whether the time course of the stimulated licking and the magnitude of the resulting CS+ preference would differ from that of the food-restricted mice was not certain. Experiment 2 also compared two groups, one with mice treated like the food-restricted group of Experiment 1 with differently flavored CS+ and CS− solutions and another group treated identically except that the flavor did not change from water-infusion to glucose-infusion sessions. If flavor change is crucial, then the latter group should show impaired stimulation of intake. These groups were given several extinction sessions with water infusions to test the persistence of conditioned increases in licking as a function of flavor novelty during acquisition.

2. Experiment 1: food deprivation state

The mice in our initial studies were tested food restricted, but restriction is not required to obtain glucose-conditioned flavor preferences. In several of our 24-h flavor conditioning studies with alternating-session CS+ and CS−, ad libitum-fed mice licked more for the CS+ than the CS−, on the first [25,26] or second [27,28] exposure to carbohydrate infusions. This demonstrates that IG nutrient conditioning is not mediated by signals related to recovery from an energy deficit. However, these instances of conditioned acceptance in 24-h sessions do not reveal when the detection of nutrient begins. Shorter sessions are more appropriate for such probes, as the behavior can be compared to a stable baseline intake paired with water infusion. We previously reported that IG maltodextrin infusions conditioned CS+ flavor preferences in both food restricted and ad lib fed rats with daily 30-min training [36]. However, to minimize differences in the training intakes of the food-restricted and unrestricted rats, CS intakes were limited to 7 ml/session. Experiment 1 determined if IG glucose self-infusions stimulated CS+ intakes in ad libitum fed as well as food-restricted mice given unlimited access to the CS solutions during daily 1-h sessions. To reduce intake differences between the two groups, the ad libitum mice were trained with sweeter CS solutions than were the food-restricted mice, a technique used to equate intakes in a prior study [26]. We predicted that IG glucose infusions would stimulate licking in ad lib fed mice, though we expected less pronounced stimulation of licking than that of food-restricted mice.

2.1. Methods

2.1.1. Subjects

Adult male C57BL/6J (B6) mice (10 week old) purchased from Jackson Laboratories (Bar Harbor, ME) were singly housed in plastic tub cages kept in a test room maintained at 22 °C with a 12:12-h light–dark cycle (lights on 0900 h). The mice were maintained on chow (LabDiet 5001; PMI Nutrition International, Brentwood, MO) prior to food restriction. During testing they were fed fixed-size chow pellets (0.5 or 1 g, Bio-Serv, Frenchtown, NJ), which allowed for precise adjustment of daily food rations. Rations were provided in the home cage 1 h after the end of the sessions. Experimental protocols were approved by the Institutional Animal Care and Use Committee at Brooklyn College and were performed in accordance with the National Institutes of Health Guidelines for the Care and Use of Laboratory Animals.

2.1.2. Surgery

Mice were fitted with IG catheters (0.84 mm OD × 0.36 mm ID, Micro-Renathane tubing, MRE-033, Braintree Scientific, Braintree, MA) while anesthetized with isoflurane (2%) inhalation as previously described [27]. About 12 days after surgery the mice were briefly (5 min) anesthetized with isoflurane, and tubing was attached to the gastric catheter and then passed through an infusion harness with a spring tether (CIH62, Instech Laboratories, Plymouth Meeting, PA). The tubing was then attached to an infusion swivel mounted on a counterbalanced lever (Instech Laboratories). The body weight of each mouse was measured before and after it was fitted with the infusion tether/swivel system; daily body weights were monitored by weighing the mouse with the attached infusion tether/swivel system. Each animal was then returned to a tub cage and the swivel counterbalanced lever was attached above the cage.

2.1.3. Apparatus

IG infusion tests were conducted in plastic infusion cages [26]. The sipper spouts were interfaced via electronic lickometers (Med Electronics, St. Albans, VT) to a computer, which operated a syringe pump (A-99; Razel Scientific, Stamford, CT) that infused liquid into the gastric catheters as the animals licked. The pump rate was nominally 0.5 ml/min, but the animal controlled the overall infusion rate and volume by its licking response. In particular, the computer accumulated licks during 3-s bins and activated the pump for 3 s when a criterion number of licks were recorded. The oral-to-infusion intake ratio was maintained at ~1:1 by adjusting the lick criterion for each mouse. Daily oral fluid intakes were measured to the nearest 0.1 g, and IG infusions were recorded to the nearest 0.5 ml.

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