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Estrogen increases the taste threshold for sucrose in rats

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Abstract

Anecdotal and empirical evidence suggests that females' preferences for sweet foods are affected by hormonal fluctuations across the reproductive cycle. In rats, the preference for sweet foods may involve estrogen-mediated changes in response to the taste of sweets. Our recent work showed that ovariectomized female rats lick less to dilute sucrose solutions when given estrogen than when given the oil vehicle. These findings suggest that estrogen decreases the preference for less concentrated sucrose solutions; however, an alternative explanation is that estrogen interferes with the ability to detect dilute sucrose solutions. To distinguish between these possibilities, we conditioned a taste aversion to 0.2 M sucrose in ovariectomized rats by pairing it with injection of LiCl and then examined the generalization of that taste aversion to 0.075 and 0.025 M sucrose solutions during estrogen or oil treatment. Oil-treated rats generalized the LiCl-induced aversion conditioned to 0.2 M sucrose to both 0.075 and 0.025 M sucrose. Estrogen-treated rats generalized the LiCl-induced taste aversion to 0.075 M sucrose but not to 0.025 M sucrose. Moreover, two weeks later, when estrogen had cleared the system, both groups generalized the aversion to both 0.075 and 0.025 M sucrose. These results show that estrogen affects the ability to discriminate dilute sucrose from water and suggest that estrogen may have short-term effects on the detection threshold for sucrose taste in rats.

Keywords: Gustation; Sweet taste; Conditioned taste aversion; Reproductive hormones

1. Introduction

Anecdotal and empirical evidence in humans suggest that there are sex differences in food preferences and that reproductive hormones may be important in these differences. For example, preferences for a variety of foods, including sweets, differ between males and females, and sweet preferences change across the menstrual cycle and during pregnancy [9,22,14]. Sex differences in food intake also have been reported in animal models, including rat [15,25,28], and reproductive hormones appear to be important in these differences as well. Feeding fluctuates across the estrus cycle in rats, with lowest levels of food intake associated with high levels of estrogen [15,25]. Moreover, ovariectomized rats consume more food than do intact female rats, and this effect is reversed by estrogen replacement [13,15,28]. However, tests evaluating the consumption of standard laboratory chow provide little information about differences in taste responses, as laboratory chow is not particularly palatable. In the real world, foods are more varied—and likely better tasting.

Are there sex differences in taste responses to palatable foods by laboratory rats? And, if so, does estrogen play a role in those differences? Little work has examined sex differences in taste preferences in animal models. Some studies have attempted to address the issue using long-term tests [17,28]; however, estrogen influences metabolism and gastro-intestinal function [1,3], making these results difficult to interpret. Another study examined the issue more directly using taste reactivity procedures [4] and found that estrogen does not affect taste reactivity measures to sweet tastes. However, this study used only one highly concentrated sucrose solution, and relied upon the characterization of responses during intraoral infusion of solutions, rather than during choice tests.

Our recent study [5] used a range of sucrose concentrations in short-term tests of behavioral taste responses and showed that estrogen affects licking by female rats to dilute, but not to concentrated, sucrose solutions. Specifically,

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when rats were ovariectomized (OVX) and then treated with estrogen, the rate of licking to dilute, 0.025 M sucrose was comparable to the rate of licking to water, whereas OVX rats that were treated with the oil vehicle licked at greater rates to 0.025 M sucrose than to water. These results may be explained by two possibilities. First, dilute sucrose may be less palatable or less rewarding than concentrated sucrose when OVX rats are treated with estrogen. In other words, estrogen may decrease the preference for dilute sucrose. Alternatively, OVX rats that are treated with estrogen may have an elevated detection threshold for sucrose that affects the ability to detect dilute sucrose solutions. The goal of this experiment was to examine the basis for estrogen-mediated sex differences in behavioral responses to sweet tastes in rats by determining whether estrogen affects the detection of dilute sucrose solutions.

2. Methods

2.1. Animals and surgical procedures

Adult female Sprague–Dawley rats (Charles River) were individually housed in a temperature controlled colony room on a 12:12 dark:light cycle. Rats were bilaterally ovariectomized (OVX) under sodium pentobarbital anesthesia (Nembutal Sodium; Abbott Laboratories, North Chicago, IL; 50 mg/kg BW, ip) using a ventral approach. The abdominal muscles then were sutured, wound clips were applied to the skin, and rats were permitted to recover for seven days.

2.2. Behavioral testing

Rats then were placed on a schedule during which they had access to water for 30 min in the afternoon. During the morning, deionized water was given in graduate drinking tubes, and intakes were recorded after 10 min. Stable 10-min water intakes were established by 6 days. On the following day (Day 1), all rats were given 10-min access to 0.2 M sucrose in graduated drinking tubes. Intakes were recorded and immediately thereafter rats were injected with 0.15 M LiCl (3 mEq/kg BW, ip; $n=16$) or the 0.15 M NaCl vehicle (ISO; 20 ml/kg BW, ip; $n=16$). The conditioned taste aversion to 0.2 M sucrose was verified in 10-min, 2-bottle (0.2 M sucrose and water) tests conducted on Day 2. On Day 3, rats were given 10-min access to water. Two-bottle (sucrose and water), 10-min tests were conducted on subsequent days to evaluate the generalization of the taste aversion conditioned to 0.2 M sucrose to less concentrated sucrose solutions. Rats were given 0.025 M sucrose and water on Day 4, 0.075 M sucrose and water on Day 5, and 0.025 M sucrose and water on Day 6.

Rats were given ad libitum access to water from Day 7–17 before again restricting access to water as described. Ten-min morning water intakes were stable by Day 19. On Day 20, an additional 10-min, 2-bottle (0.075 M sucrose and water) test was conducted; on Day 21, a final 10-min, 2-bottle (0.025 M sucrose and water) test was conducted.

To minimize the possibility of effects attributable to position preference related to training and/or conditioning, we alternated the position of the drinking tubes so that for each rat, tubes containing sucrose solutions were equally likely to be in the 'conditioning' position or in the 'non-conditioning' position on any test day.

2.3. Hormone replacement

On Day 3 and Day 4, rats treated with LiCl were given sc injections of estradiol benzoate (EB; 10 μg/0.1 ml oil; Sigma, St. Louis, MO; $n=7$) or the oil vehicle (OIL; 0.1 ml; $n=9$). Rats treated with ISO also were given sc injections of EB ($n=8$) or OIL ($n=8$). This estrogen replacement schedule frequently is used in studies of ingestive behaviors by rats [12,13,15,18] and mimics the pattern of fluctuations of estrogen levels in the intact, cycling female rat [30]. Moreover, in a study using this schedule and dosage, Woolley and McEwen [30] also showed that plasma estrogen concentration decreases to levels present in non-cycling, OVX rats within ~nine days after the second injection. Thus, a second series of 2-bottle tests was conducted ~2 weeks after hormone replacement.

2.4. Statistical analysis

Preferences for sucrose solutions during 2-bottle tests were expressed as preference scores, calculated as [intake of sucrose (ml)/total intake (ml)]. Scores ≥ 0.6 indicate a preference for sucrose; scores ≤ 0.4 indicate an aversion to sucrose; scores between 0.4–0.6 indicate indifference to sucrose. During EB or OIL treatment, intake of 0.025 M sucrose and water and preference for 0.025 M sucrose were calculated by averaging the intakes and preference scores on Days 4 and 6 for each rat. Data are presented as group means ± S.E.M.

Statistical comparisons of the taste aversion conditioned to 0.2 M sucrose were made using two-factor (Drug × Hormone) analysis of variance (ANOVA; Statistica, StatSoft, Tulsa, OK). Comparisons of the generalization of the conditioned aversion to 0.075 and 0.025 M sucrose solutions were made using four-factor (Drug × Hormone × Concentration × Time) repeated-measures ANOVA. Pair-wise comparisons of statistically significant ($p<0.05$) main effects or interactions were evaluated using Student Newman–Keuls tests. Additional planned comparisons were made using Bonferroni corrections.

3. Results

3.1. Conditioned taste aversion

Rats that were injected with LiCl showed a robust conditioned taste aversion to 0.2 M sucrose, regardless of