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Examination of the perception of sweet- and bitter-like taste qualities in sucralose preferring and avoiding rats



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HIGHLIGHTS

• Sucralose avoiding rats detect an aversive taste quality in sucralose.

• Sucralose preferring rats do not treat sucralose as a unitary sweet stimulus.

· Sucralose preferring rats consume more sweet milk diet than sucralose avoiding rats.

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ABSTRACT

Sucralose avoiding rats detect a bitter-like taste quality in concentrations of sucralose that are strongly preferred over water by sucralose preferring rats. Here, we investigated whether sucralose preferrers (SP) also detect a bitter-like quality in sucralose that may be masked by an increased perception of sucralose's sweet-like quality. A microstructural analysis of sucralose intake revealed that, at concentrations they avoided in preference tests, sucralose avoiders (SA) consumed smaller and fewer bouts of sucralose than SP. Interestingly, the concentration-dependent increase in sucralose preference in SP was not associated with larger bouts or increased lick rate, two measures that are expected to increase with increasing perceived sweetness. This suggests that SP can detect an aversive quality in sucralose, but this perception of a presumably bitter-like quality may be masked by increased salience of a sweet-like quality that sustains high levels of intake in SP. Further evidence for increased sweet-taste perception in SP, relative to SA, was obtained in a second study in which SP consumed more of a palatable sweet-milk diet than SA. These are the first data to suggest that SP are not blind to the bitter-like quality in sucralose, and that there may be differences in sweet-taste perception between SP and SA.

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1. Introduction

Although the role of variable taste perception in guiding diet choice has interested researchers for decades, it has proven difficult to study. Attempts to link genetic variation in human bitter-taste perception to feeding behavior and body mass index have produced mixed results [1–5]. While some studies were unable to link taste sensitivity to measures of food preference [6,7], others strongly suggested that variation in the perception of taste quality may contribute to phenotypic variation in dietary preferences [8,9]. These equivocal findings may be related to a number of factors, including a lack of uniformity in assessing taste sensitivity, heavy reliance on self-report measures of caloric intake, and the difficulty in controlling for cognitive factors, such as dietary restraint, which can modulate diet choice and caloric intake [10].

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To address the relationship between taste perception and diet choice and to avoid these potentially confounding variables, our lab and others have begun to investigate how natural variation in the taste preferences of laboratory rats may affect food intake and dietary preferences [11–14]. These studies have shown that rats display a considerable variation in their intake and acceptance of the artificial sweetener sucralose in a 24-h two-bottle preference testing paradigm, with ~70% of rats displaying either a modest preference or indifference for low concentrations (<0.025 g/L) of sucralose over water but strongly avoiding sucralose at higher concentrations (sucralose avoiders, SA). The remaining ~30% of rats display a strong preference for sucralose across a wide concentration range (sucralose preference, SP) [12].

This non-overlapping variation in the acceptance of sucralose appears to be consistent with psychophysical studies in humans and rodents indicating that the sweet-like taste quality of many artificial sweeteners, including sucralose, is offset in some individuals by the perception of an aversive taste quality [15] that appears to be mediated by the activation of bitter taste receptors (T2Rs) and/or the transient receptor potential vanilloid-1 (TRPV1) receptor [16]. For instance, the

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variable acceptance of saccharin in humans is associated with allelic variation in *Tas2R31* [17]. These data, together with SA's strong avoidance of sucralose solutions >0.25 g/L (as opposed to indifference), even in brief-access paradigms, suggested to us that SA detect an aversive taste quality in sucralose that SP either do not detect or perhaps do not respond to.

As an initial step toward uncovering the aversive nature of sucralose, and to determine if taste was sufficient to distinguish SA from SP, we used an adaptation of the two-alternative, forced-choice psychophysical paradigm [18]. This paradigm allowed us to determine that the perceived taste quality of sucralose differs between SP and SA. Briefly, animals were trained to report (via an operant response in a gustometer) whether the taste of a given concentration of sucralose generalized to a prototypical sweet-like stimulus (sucrose) or a prototypical bitterlike stimulus (quinine). While SP reported a sweet-like taste quality at all concentrations of sucralose that were treated as different than water (i.e., assumed to be above threshold within this paradigm), SA were more likely to generalize the taste of these same concentrations of sucralose to guinine [19]. These data provide clear evidence that SA detect a bitter-like taste quality in normally avoided sucralose concentrations. SP also licked more to sucralose than SA in a brief-access paradigm at these same concentrations [19]. Taken together, these findings confirm that differences in sensory (taste-guided) processing are sufficient to explain the differential acceptance of sucralose in SP and SA. They also confirm that SA detect an aversive taste quality in sucralose, but do not address whether or not SP are "taste-blind" to this component. This is because animals were forced to choose if the solutions being presented in the gustometer were either sucrose-like or quinine-like. Thus, in the case of a mixture, animals would be expected to choose the taste quality that is more salient to them. Indeed, when the same animals were offered test solutions containing varying mixtures of sucrose and quinine, they reported a sweet-like quality in solutions containing low, suprathreshold concentrations of quinine, and did not report the presence of a bitter-like quality until quinine was sufficiently concentrated and presumably the more salient taste quality within the test solution [19]. Thus, while SP reported that the salient taste quality of sucralose was sweetlike, we cannot infer that "sweet" was the sole quality detected by SP or that SP were unable to perceive a bitter-like taste quality in the sucralose solutions. Rather, it merely suggests that SP's perception of "bitter" did not surpass the salience of "sweet".

Recent work from our lab provides clear evidence that the differences in taste perception between the groups are not unique to sucralose and that the differences in taste perception between SA and SP drive differences in their intakes of other binary mixtures such as saccharin and sucrose-base solutions adulterated with increasing concentrations of quinine [20]. However, to date our work has not addressed the degree to which these divergent phenotypes are mediated by perceptual differences in sweet and/or bitter taste.

It is essential to understand the nature of the perceptual differences between these animals as such information is prerequisite to identifying mechanisms that may be driving the differences in the taste-guided behavior and therefore allowing comparisons to variation in other populations. One possibility is that SA are sensitive to a bitter quality in sucralose that SP are less sensitive to, or, perhaps, insensitive to. This would suggest that the underlying mechanism driving the phenotypic split may lie in bitter-taste signaling pathways, possibly at the receptor level, as is seen in human variation in the ability to taste 6-n-propylthiouracil (PROP) [21-23]. Some studies have shown that PROP tasters are more sensitive than PROP non-tasters to certain sweet and bitter foods, the bitter-like taste quality of saccharin, the creaminess of fats, and stimuli that cause oral burn [8,24-27]. Another possibility is that SP are more sensitive to the sweet-like quality of sucralose than SA, and this increased perception of sweet taste may overshadow the perception of any bitter-like quality in sucralose. This would suggest the underlying mechanism driving the phenotypic difference is in the sweet-taste signaling pathways, as seen in mouse variation for sucrose avidity. A polymorphism in the gene encoding the T1R3 subunit of the sweet taste receptor in mice has been shown to contribute to between-strain variation in avidity for sucrose [13,28]. At present, the degree to which either (or both) of these mechanisms mediates the phenotypic variation in SP and SA remains unclear.

As an initial step toward evaluating the taste-related perceptual differences in SP and SA, we conducted a microstructural analysis of sucralose drinking during a series of 24-h, 2-bottle preference tests used to categorize rats as SP or SA. Previous research has shown that the number and size of drinking bouts, and the rate of licking, can be used to make inferences regarding the palatability of a taste stimulus. For example, a microstructural analysis of saccharin drinking revealed decreases in bout size and the rate of licking as a function of increasing concentration, reflecting decreased palatability as the perception of a bitter-like quality increased [29]. A similar analysis of sucrose drinking revealed increases in bout size and the rate of licking as a function of increasing concentration, reflecting increased perception of sweetness [29]. Thus, this microstructural analysis was chosen for its ability to assess sensitivity to both bitter- and sweet-like taste qualities in increasing concentrations of sucralose with a greater resolution than has been employed in other intake tests conducted to date [12,20]. To better understand the functional consequences of the differences in taste perception in SP and SA, we conducted a second experiment to determine whether a heightened perception of "sweet" taste would promote greater intake of a palatable, sweetened-milk diet in SP, relative to SA.

2. Methods

2.1. Experiment 1a: microstructural analysis of sucralose preference trials

2.1.1. Animals and housing

Male Long-Evans rats (n = 24, Charles River Breeding Laboratory, Raleigh, NC), weighing 200–250 g at study onset, were individually housed in custom-designed Plexiglass cages. Food compartments at the front of the cages were equipped with infrared light-emitting diodes and photo detectors, which were used to monitor feeding bouts. The back of the cages held two drip-resistant bottles that were equipped with contact lickometers, which recorded individual licks and were used to monitor the size and duration of drinking bouts. Rats were allowed ad libitum access to Purina 5001 and tap water in addition to the test solutions. The colony room was maintained at 20 ± 2 °C with a 12:12 h light/dark cycle. All animal procedures were approved by the Florida State University Animal Care and Use Committee.

2.1.2. Experimental design

All rats were categorized as SP or SA via a series of 24-h two-bottle preference tests [12]. Rats were given water and increasing concentrations of sucralose (0.0001, 0.001, 0.01, 0.25, 0.5, 1.0, and 2.0 g/L) for two days per concentration with bottle position alternated daily. Rats with a side preference were excluded from the study (n = 4). Sucralose solutions were prepared by dissolving various concentrations of sucralose (Tate & Lyle) in tap water. Rats were categorized as SP if they displayed a preference (consumed > 50% of daily fluid as sucralose) at the two highest concentrations; the remaining rats were categorized as SA. Because SA are more than twice as common as SP in the population [12], the data from all SP and an equal number of SA (selected for having the lowest preference scores at 2 g/L sucralose) were analyzed (n = 8 per group).

Microstructure of licking was recorded throughout the process of categorizing rats as SP or SA. Drinking bouts of each test solution (i.e., water and sucralose) were defined by a minimum of 10 licks of the sipper tube of interest. Although two bottles were presented to the rat, a drinking bout was defined by licking activity at a single bottle and was not considered cumulative between the bottles. Drinking bouts were considered terminated when no licks were recorded for >5 min on the bottle of interest. Rats regularly switched between bottles within

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