THE INTERPLAY BETWEEN DIET, TASTE, AND HUMAN HEALTH

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Taste is a biological gate-keeping mechanism, which encourages the consumption or rejection of foods based on their sensory properties. Repeated consumption of palatable, high calorie foods contributes to obesity, one of the most pressing health concerns of our time. Recent reports suggest that taste is weakened in overweight or obese people, although it is unknown whether this dysfunction in the taste system is linked with compensatory eating behaviors to attain satisfactory reward. In a repeated measure study, we showed that those with weakened gustatory signals desired more intensely tasting and higher calorie stimuli. Building upon previous research, we demonstrated longitudinally that a modest weight gain over 8 months associated with decreases in sweet and salty tastes, primarily observed in males of a college-aged population. In the same study, we also found that changes in the consumption of umami-rich foods selectively correlated with umami taste perception. Aiming to clarify this relationship, we conducted a randomized controlled study to show that adaptive changes may occur in the taste system with prolonged exposure to the umami-rich stimuli, monosodium glutamate (MSG). After one month of exposure to MSG, females decreased in their sensitivity to umami taste, while both sexes experienced a lessened appetite for savory foods. Seeking to determine how taste may be connected to emotional eating, a large cross-sectional study evaluated the effect of day-to-day emotional variation on taste function and food liking after college hockey games. Analysis revealed that negative emotions correlated with diminished sweet and enhanced sour perception, and also affected hedonic responses to food. Taken together, our results suggest that weight gain, diet, and emotions can

independently influence the taste system, while effect often varies by sex. We supply evidence that decrements in taste may impact food preferences and eating behavior, potentially encouraging the consumption of higher calorie foods. With this in mind, our research provides support that taste and taste dysfunction should be considered in the complex multicomponent etiology of obesity and other diet-related diseases.

BIOGRAPHICAL SKETCH

Corinna A. Noel graduated with a Bachelor of Science in Mathematics from Saint Joseph's University in 2013. Throughout her undergraduate career, Corinna looked to combine her quantitative skills with her interest in food and public health, and found ways to integrate the two through research. With encouragement and funding from the John P. McNulty Scholars Program for Excellence in Science and Mathematics, Corinna designed and implemented an independent research project as a summer fellow in 2011. Co-mentored by Dr. Deborah Lurie and Dr. Richard George, she investigated the effect of calorie postings on menus on subsequent food choices. The following year, Corinna participated in the Cornell University Summer Scholar Program in the Department of Food Science. Working with Dr. Olga Padilla-Zakour, Corinna modeled the effect of different processing conditions on accumulated lethality in thermally processed foods. After graduation, Corinna returned to Cornell University to pursue a Ph.D., using her quantitative background to conduct research in taste psychophysics, aiming to understand how the taste system is linked with food preferences, diet, and obesity. During her time at Cornell, she studied epidemiology and applied epidemiological techniques to her own research. Corinna plans to pursue a research career in health analytics and epidemiology, investigating the impact of environmental or behavioral exposures on human health outcomes.

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LIST OF ABBREVIATIONS

ANOVA	Analysis of variance
AUC	Area under the curve
BMI	Body mass index
CI	Confidence interval
g	Grams
GMP	Guanosine monophosphate
GS	Gymnema sylvestre
gLMS	General labeled magnitude scale
IMP	Inosine monophosphate
kg	Kilograms
LSM	Least square mean
m	Meter
mm	Millimeter
mM	Millimole
MSG	Monosodium glutamate
OLS	Ordinarily least square
SAS	Statistical analysis system
SD	Standard deviation
SEM	Standard error of the mean
VAS	Visual analog scale

INTRODUCTION

Obesity affects over one third of the U.S. population (1), and is one of the most pressing health concerns of our time. Estimates show that approximately 300,000 deaths can be attributed to obesity-related complications annually (2), and that these disorders account for approximately 21% of U.S. health care spending (3).

Many researchers have investigated which factors are important in the development and persistence of obesity. A common view is that insufficient energy balance, or excess food intake, is linked with obesity (4). Indeed, higher caloric intakes are associated with higher body mass index in adults (5). It has been hypothesized that differences in food preferences, reward, and satiation contribute to this insufficient energy balance (4). Importantly, previous research has suggested that preference, reward, and satiation are linked to the taste system (6–8). If this is true, we argue that it important to study the external influences upon the taste system and clarify how variation in taste may influence responses to and appetite for certain foods. Understanding which biological and environmental factors affect taste and subsequent eating behavior may lead to interventions designed to assist people to make better food choices, and help to elucidate the taste system's role in the complex multicomponent etiology of obesity and other diet-related diseases.

Taste is a biological gate-keeping mechanism, which encourages the consumption or rejection of foods based on their sensory properties. Perception of the basic tastes of sweet, salty, umami, sour, and bitter as well as the oral sensation of fat, play a vital role in determining food acceptance, preference, and choice (9). The appetitive tastes of sweet, salt, fat, and umami are hypothesized to encourage consumption of essential nutrients which include sources of carbohydrates, mineral salts, dietary lipids, and protein (10). The aversive tastes of bitter and

sour have been suggested to inhibit the consumption of harmful substances, such as spoiled and poisonous foods.

We consume food not just for nutrition, but also for the positive central reward it offers. Psychophysicists have noted for many years that appetitive tastes, such as sweet, follow a psychophysical function resembling an inverted U. Hedonic response increases with stimulus intensity, before reaching a plateau, and decreases when the stimulus becomes unpleasantly strong (11). It is hypothesized that a diminished taste response may stimulate overconsumption, since taste is hardwired to dopaminergic reward centers in the brain (7). Therefore, those with a weakened taste response may desire and ultimately consume more intensely tasting foods, as a means to compensate for lowered taste input. Higher consumption in weak tasters presumably allows them to attain a reward equivalent to those with stronger taste function (7). These foods would likely also be higher in calories, since both sweet and the taste for fat signify caloric content in their common forms (12).

Studies have demonstrated that multiple environmental and biological factors correlate with variation in human taste function, including genetics (13), sex (14–16), age (13,14,17), body mass index (15,16,18–22), acute stress and emotions (23–25), input from other senses (26), tobacco and alcohol intake (14), and the consumption of certain foods (19,20,22,27,28). This highlights the inherent environmental plasticity of the taste system, and prompts us to further investigate how the sense of taste and subsequent responses to foods may be linked with obesity.

Since the sense of taste is a key determinant of foods consumed (9), it has been hypothesized to play an important role in weight gain and the onset of obesity (5,29,13). A number of sources suggest that overweight or obese people have a weakened sense of taste when compared to healthy weight counterparts, particularly for the appetitive tastes (19–22,18). Studies have demonstrated a blunted reward system in rodents with obesity (30), and lower activity in reward

centers of the brain of humans that are obese (31,32). Lessened responses in the taste system may influence appetite and foods preferences, and moreover, could be linked to unhealthy eating habits.

The work highlighted in this dissertation begins to unravel the complex relation between diet, taste, and human health, primarily related to food choice and obesity. Specifically, our research seeks to understand the links between taste and weight gain, diet, and emotions, as depicted in **Diagram 1**. Throughout our work, we also make connections to food preference, liking, satiation, and appetite. We will return to this schematic to illustrate our findings and highlight the interplay between factors.

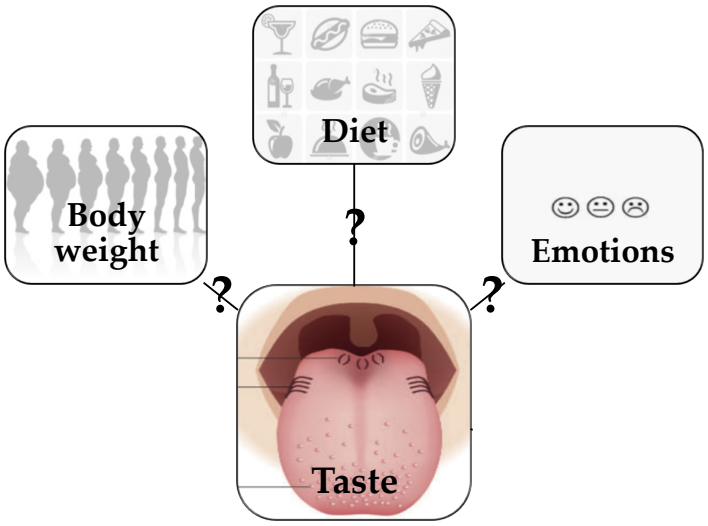

Diagram 1
Research aims: Understanding the relationship between taste and human health

We start by providing evidence that variation in taste is linked with alterations in food preferences. Generally, taste researchers assume that a weakened taste response associates with an increased desire for higher calorie foods to compensate for a weakened central reward, however this hypothesis has not been explicitly tested. **Chapter 1** reports a study where we pharmacologically impaired the sweet taste response of participants over multiple sessions. Our

study was the first to directly test and demonstrate that a lessened gustatory signal is linked with gravitation towards more intensely tasting sweet stimuli.

Following Chapter 1, we move to describe external influences on taste, starting by examining the effect of weight gain on the gustatory system. Human and animal studies report a blunted sense of taste in people who are overweight or obese, with heightened sensitivity also reported following weight loss. However, it is unknown if taste changes concurrently with, or in response to weight gain. **Chapter 2** highlights research where we evaluated the association of weight gain with within-person taste changes over time using a sample of first year college students, while adjusting for potentially confounding dietary habits and changes in alcohol consumption. We found that college-aged males decreased in perceived sweet and salty taste with weight gain, while females experienced no decrement in taste with similar increases in weight. A secondary outcome of this study revealed a negative association between the consumption of meat and other umami-rich foods and perceived umami taste intensity.

Supporting the latter finding, experimental studies provide evidence that increased consumption of sweet, salt, or fat associates with a diminished perceived taste intensity and shifted preferences for the respective stimuli. To date, no studies have examined habituation to umami taste with repeated consumption of umami-rich stimuli in humans, as was suggested by our work in Chapter 2. **Chapter 3** details a randomized controlled study designed to investigate the influence of repeated exposure to umami taste on umami taste perception, hedonics, and satiety. Subjects in the treatment group supplemented their diet for 4 weeks with a broth containing the umami-rich stimulus monosodium glutamate (MSG), while subjects in the control group consumed a sodium-matched broth without MSG. Relative to the control, increased dietary exposure to MSG for 4 weeks diminished umami taste (selectively in females) and decreased the desire for and intake of savory foods at an ad-libitum meal. This shows that repeated dietary exposure to umami taste could have implications for taste, food preferences, and appetite.

Certain emotional states correlate with increased consumption of palatable foods with high hedonic value, potentially providing positive gratification and comfort (33). However, repeated consumption of these energy-dense foods disrupts our energy balance and increases the likelihood of obesity, substantiating the need to clarify how affective state can impact our health. There is limited research exploring the impact of emotional manipulations on basic taste perception and hedonic responses under real-life conditions. **Chapter 4** presents a study designed to determine how emotions arising from the outcome of college hockey games, an environment shown to adequately induce both positive and negative emotions, influenced the perceived taste intensity and rated liking of real foods. We showed that emotional manipulations, in the form of pleasantly or unpleasantly perceived real-life events, correlate with the perceived intensity of sweet and sour tastes, potentially driving hedonics for less acceptable foods in emotional eating.

Finally with **Concluding Remarks**, we return to the conceptual diagram and summarize this research. We consider how our work contributes to our understanding of taste in obesity and provide recommendations for future research in this area.

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CHAPTER 1

PARTICIPANTS WITH PHARMACOLOGICALLY IMPAIRED TASTE FUNCTION DESIRE MORE INTENSE, HIGHER CALORIE STIMULI[1]

Introduction

Reports highlight a weaker sense of taste in people with obesity (1–3), and that losing weight enhances taste responses (4,5). We consume food not just for nutrition, but also for the positive central reward it offers, with emotions possibly linked to taste (6). Psychophysicists have noted for many years that appetitive tastes, like sweet, follow a psychophysical function resembling an inverted U. Hedonic responses increase with stimulus intensity, before reaching a plateau, and decrease when the stimulus becomes unpleasantly strong (7). Studies have demonstrated a blunted reward system in rodents with obesity (8), and a lower activity in reward centers of the brains of humans that are obese (9,10). Therefore, a common assumption is that a person with a weakened sense of taste may desire, and habitually consume, more intensely tasting foods. These foods would presumably also be higher in calories, since both sweet and the taste for fat signify caloric content in their common forms (11). Thus, a depleted taste response in those with obesity may influence diet, and moreover, could represent a form of eating disorder, driving unhealthy eating habits. However, research to support the assumption that decreased gustatory input correlates with an increased desire for more intensely tasting foods remains absent.

Gymnema sylvestre (*GS*) is a plant native to South Asia, known for its ability to temporarily suppress sweet tastes (12). Studies suggest this suppression is attributed to a glycoside known as gymnemic acid, which binds to lingual sweet receptors (13), reducing the perceived sweetness of a stimulus. When rats were given *GS*, their neural response to sweet taste was significantly

[1] A manuscript detailing this study will be published in October 2017 in the journal Appetite, titled "Participants with pharmacologically impaired taste function seek out more intense, higher calorie stimuli," authored by Corinna A. Noel, Meaghan Sugrue, and Robin Dando.

reduced compared to rats consuming the same foods without *GS* treatment (14). A relatively low concentration of *GS* is needed to reduce sweet tastes in both rats (14) and humans (12) , with studies suggesting that concentrated solutions of *GS* can suppress more than 75% of the pre-treatment perceived sweetness of a stimulus (15). *GS* selectively suppresses sweet intensity perception for a prolonged period, making it an intriguing tool to study how a diminished taste response influences a participant's reaction to foods. In a study by Riskey and colleagues, participants were treated with a series of diluted *GS* solutions ranging from 0.03 to 0.50 g/l and reported sweet taste intensity of sucrose solutions at three concentrations. Not surprisingly, with increasing *GS* concentration, the sweetness from sucrose was reported as less intense, reducing suprathreshold sweet intensity ratings between 61% and 68% (16). The group reported only minimal recovery after 20 minutes, highlighting *GS*'s suitability in a sensory study to selectively diminish sweet taste response.

In this study, we pharmacologically impaired the sweet taste response of participants over multiple sessions. Subjects subsequently completed a series of sensory tests probing the hypothesis that a depleted taste response correlates with a gravitation towards higher calorie stimuli. This hypothesis supports the notion that taste function may have consequences to the ongoing obesity epidemic.

Methods

All aspects of this study were reviewed and approved by the Cornell University Institutional Review Board. Healthy, non-smoking participants reporting a normal sense of taste and smell, without seasonal allergies, and not pregnant or breastfeeding, were recruited with postings on campus. 51 participants completed all phases of the study, which required attendance at four testing sessions on separate days. The sessions corresponded to three treatment conditions where rinsing with a tea-like beverage made with *Gymnema sylvestre* (*GS*) solutions of varying concentrations diminished sweet taste perception, and one control condition where rinsing with

an equally bitter control herbal tea maintained sweet taste function. The order that the subjects completed the sessions was randomized.

Participants abstained from eating and drinking 30 minutes prior to testing. Each testing session took place at approximately the same time of day, and took 30 minutes to complete. The sessions followed the same schedule: training in scale usage, pre-treatment taste assessment, *GS* or control treatment, post-treatment taste assessment, and finally sensory and hedonic measures of real foods. Upon completion of all four sessions, anthropometric measurements and demographic information were collected, and participants were compensated.

Experimental conditions

Gymnema sylvestre (*GS*) was used to experimentally diminish sweet taste perception, with increasing concentrations of *GS* hypothesized to result in greater reduction in perceived sweet taste (16). Dried and powdered *GS* leaves (Source Naturals, Scotts Valley, CA) were dissolved in deionized water at the following concentrations: 0.0 g/L for the control condition, 1.2 g/L for the lowest *GS* concentration treatment condition (*GS* 1), 3.6 g/L for the medium concentration *GS* treatment condition (*GS* 2), and 10.8 g/L for the highest concentration *GS* treatment condition (*GS* 3). In order to match the bitterness of the solutions containing *GS*, the control solution consisted of a strong herbal tea (judged as equally bitter in pilot testing), which has also been used as a control solution in previous studies using *GS* to temporarily reduce sweet taste perception (16,17). All solutions were presented at room temperature, identified by a random three-digit code in small opaque cups with lids. Participants were instructed to rinse their mouth with the tea solutions for 60 seconds and then expectorate. This procedure was sufficient in pilot testing to inhibit taste response for 40-60 minutes.

Taste intensity scale training and evaluation

Electronic questionnaires on iPads (Apple Inc, Cupertino, CA) captured taste intensity ratings before and after treatment using the sensory software Compusense Cloud (Compusense, Guelph, Canada). Participants received instructions on using the generalized Labeled Magnitude Scale (gLMS) (18,19), rating a series of broadly varying auditory and visual, real and imagined sensations. Ratings ranged from 'no sensation' to 'strongest imaginable sensation of any kind'. The scale values were log-transformed: no sensation (0.0), barely detectable (0.14), weak (0.76), moderate (1.21), strong (1.52), very strong (1.70), and strongest imaginable sensation of any kind (1.98). Whole mouth taste intensity ratings were captured using a sip and spit procedure. Sucrose (sweet) was dissolved in deionized water and presented in a series of three ascending concentrations: 81.0, 243.0 and 729.0 mM/L, denoted as 'low', 'medium', and 'high', with one series presented before treatment and one after. All samples were served in uniform clear plastic cups at room temperature, identified by randomly assigned three-digit codes. Participants rinsed their mouth between each sample and a self-advancing timer ensured that participants were not able to progress through the electronic test without ample rest time, to curtail adaptation, fatigue, and any carry-over effects.

Quantification of optimal sweetness

Following post-treatment sweet taste assessment, participants performed an ad-libitum mixing task (20), titrating a beverage to their optimal level of sweetness. Participants were given a flavored beverage and two additional solutions: one solution of the same flavor labeled 'more sweet', containing a highly sweetened solution (250.0 g/L sucrose), and one flavored solution labeled 'less sweet', containing an unsweetened solution (0.0 g/L sucrose). Participants were instructed to continuously taste and adjust their beverage by adding as much or as little of each of the solutions, until the beverage reached their 'optimal level of sweetness'. This task was completed twice, starting once with an unsweetened beverage (0.0 g/L sucrose), and the other time starting with a highly sweetened beverage (250.0 g/L sucrose), to avoid context effects (21).

The final dissolved sugar content was quantified with a refractometer, and the two replicates were averaged as a measure of optimal sweetness (g/L).

Real food evaluation, demographic, and anthropometric measures

After the ad-lib mixing task, participants were presented with a variety of sweet beverages and foods (diet Coca-Cola, regular Coca-Cola, a sugar cookie) to determine how altered sweet taste perception influenced hedonic ratings of select real foods. Liking was captured on the hedonic gLMS (22), with scale descriptors ranging from 'strongest imaginable dislike of any kind' (-100), 'neutral' (0), to 'strongest imaginable like of any kind (100). Desired sweetness of the cookie was captured on a continuous 'Just About Right' visual analog scale (VAS), with scale descriptors ranging from 'not nearly sweet enough' (-100), 'just about right' (0), to 'much too sweet' (100). Satiety was assessed before treatment and after, and subjective ratings were made on a 100-point VAS scale for two appetite sensations: satiation ('How satiated are you?'; 0=Not at all, 100=Extremely) and desire to eat more ('How strong is your desire to eat more?'; 0=Extremely low, 100=Extremely high). At the final testing session, a questionnaire collected information on sex, age, race, and sweet food consumption habits. Body height and weight were measured using standard procedures and equipment (23). BMI was calculated with the formula: BMI=[weight (kg)/height (m^2)].

Data analysis

Repeated measure analyses of variance (ANOVA) assessed the effect of treatment as a categorical variable (control, *GS* 1, *GS* 2, *GS* 3) on sweet taste intensity perception, optimal level of sweetness in the beverage, perceived sweetness and hedonic responses to real foods, and subjective appetite sensations. Intensity perception was tested in one model, including a factor of concentration (low, medium, high) and time (pre-treatment, post-treatment); slice effects of relevant interactions are presented. For all analyses, mean and 95% confidence intervals (95%

CI) are given for each treatment condition, and statistical differences between levels are adjusted for multiple comparisons using the Tukey-Kramer method.

Bivariate analyses suggested a linear relationship between perceived sweet intensity post-treatment at the high concentration and taste outcomes, and thus linear mixed models with a random subject factor were fit to quantify the effect of varying sweet taste perception on optimal sweetness, perceived sweetness and liking of real foods, and satiety measures. With this, we were directly able to assess the association between perceived sweet taste (as opposed to experimental condition of *GS* treatment) and the outcome. Each model adjusted for the potentially confounding variables of sex, age, ethnicity, typical sweet food consumption, and BMI if inclusion of the covariate appreciably altered the regression coefficient for post-treatment sweet taste perception. Variables that were not confounders, but with p-values less than 0.10, were considered to represent an alternate causal pathway to the outcome and were adjusted in the model to reduce unexplained variability in the outcome. Including the interaction terms of 'sex' and 'typical sweet food consumption' with 'perceived sweet taste' assessed effect modification on the taste outcomes; p-value threshold for assessing effect modification was set at $p<0.10$. Any covariate or interaction meeting the inclusion criteria was included in the final model. Since the independent variable of perceived sweet taste intensity is log transformed, effect estimates and 95% CI are back-transformed for ease of interpretation for all regression models, and presented along with the value of the test statistic, degrees of freedom, and corresponding p-value. The analysis was conducted using SAS version 9.4 (SAS Institute Inc., Cary, NC). The threshold for statistically significance was $p<0.05$. Additional emphasis is put on effect estimation and confidence intervals to provide information on the clinical significance of results.

Results

Study population

51 participants completed for all 4 testing sessions, consisting of 82% women, primarily Caucasian (51%) and Asian (33%). Participants had an average BMI of 22.8 kg/m^2 (range 17.2 to 31.3) with an average age of 21.3 years (range 18 to 33), reporting a range of habits regarding consumption of sweet foods (**Table 1.1**).

Table 1.1
Baseline characteristics of study population. Values represent mean ± SD or count (percentage of category) at final testing session. N=51.

	Mean ± SD *or* count (%)
Age (years)	21.3 ± 3.2
BMI (kg/m^2)	22.8 ± 3.5
Sex	
Men	9 (17.7%)
Women	42 (82.3%)
Race/Ethnicity	
Caucasian	26 (51.0%)
Asian/Pacific Islander	17 (33.3%)
Other	8 (15.7%)
Habitual sweets consumption	
Less frequent	15 (29.4%)
Moderate	22 (43.1%)
More frequent	14 (27.5%)

Perceived sweet taste intensity for the three sucrose solutions (low, medium and high) tested prior to *GS* treatment did not vary between the 4 sessions (slice effect of treatment: $F(3,1150)=0.13$, p=0.94 for low; $F(3,1150)=0.20$, p=0.90 for medium; $F(3,1150)=0.70$, p=0.55 for high, **Figure 1.1A**) nor did it vary for the area under the curve (AUC), an overall measure of sweet taste ($F(3,350)=0.20$, p=0.90 for AUC, **Figure 1.1B**). Subjective appetite ratings assessing satiety did not differ prior to each treatment condition (main effect treatment: $F(3,150)=0.09$, p=0.97 for 'satiation'; $F(3,150)=0.80$, p=0.50 for 'desire to eat more'). Scale usage also did not vary across conditions for participants (main effect treatment: $F(3,150)=0.34$, p=0.80 for scale rating of 'loudest sound you've ever heard'), collectively confirming that any

effect of treatment on outcomes was not due to panelist differences in usage of the gLMS between sessions.

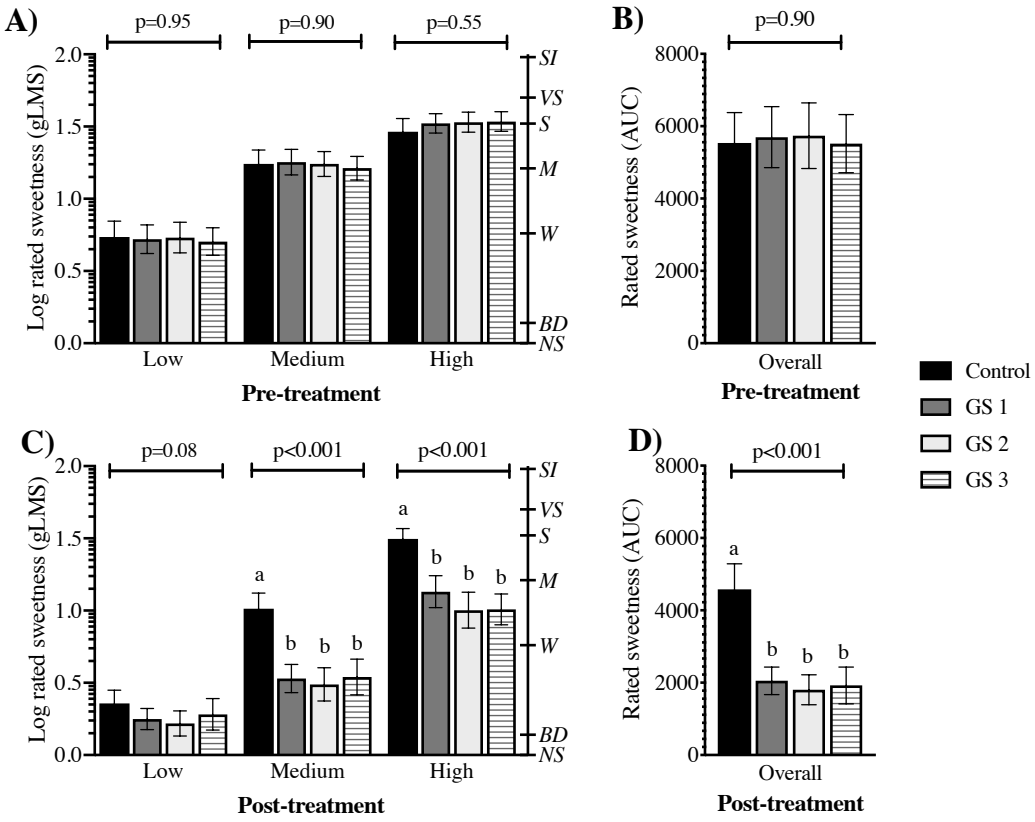

Figure 1.1
Experimentally reduced sweet taste perception before and after treatment with increasing concentrations of *Gymnema sylvestre* (*GS*). Bars represent mean and 95% confidence interval of sweet taste intensity perception measured on the general Labeled Magnitude Scale (gLMS) for low, medium, and high concentrations of sucrose before treatment (Figure 1.1A), and after treatment (Figure 1.1C), as well as area under the curve (AUC) as a measure of overall sweetness perception before treatment (Figure 1.1B) and after treatment with *GS* (Figure 1.1D) at the following levels: control (0.0 g/L), *GS* 1 (1.2 g/L), *GS* 2 (3.6 g/L), *GS* 3 (10.8 g/L). Right axes of Figure 1.1A and Figure 1.1C show scale descriptors of gLMS as follows: NS, no sensation; BD, barely detectable, W, weak; M, moderate; S, strong; VS, very strong; SI, strongest imaginable sensation of any kind. p-value specifies statistical significance of slice effect of treatment condition for the concentration in a repeated measure analysis of variance. a / b Lower case letters within each concentration depict means that are statistically different from each other at $p<0.05$ with post-hoc Tukey-Kramer adjustment; conditions that share a letter within a concentration are not significantly different from each other. N=51.

Diminished sweet taste perception with GS treatment

The perceived sweet intensity of sucrose solutions was diminished following *GS* treatment compared with the control, allowing us to conclude that the experimentally induced impairment

of sweet taste perception was successful (**Figure 1.1C** and **Figure 1.1D**). This reduction in sweet taste was seen primarily across the higher concentrations (slice effect treatment: $F(3,1150)=2.27$, $p=0.08$ for low; $F(3,1150)=39.43$, $p<0.001$ for medium; $F(3,1150)=34.64$, $p<0.001$ for high, Figure 1.1C), and also in an AUC measure of overall sweetness ($F(3,350)=28.89$, $p<0.001$, Figure 1.1D). We focus on the high concentration of sucrose, where participants rated the stimuli around the scale descriptor of 'strong' for the control condition, dropping to between 'weak' and 'moderate' following *GS* treatments. These differences in sweet taste represent a statistically significant reduction in perceived sweet intensity compared to the control condition (Figure 1.1C, **Table 1.2**). There is a trend of greater reduction in sweet taste with increased concentrations of *GS*, although with adjustment for multiple comparisons, the threshold for statistical significance was not reached.

Table 1.2
Effect of increasing concentrations of *Gymnema sylvestre* (*GS*) on taste and hedonic outcomes. Values represent mean and 95% confidence interval of outcomes following treatment of *GS* as follows: control (0.0 g/L), *GS* 1 (1.2 g/L), *GS* 2 (3.6 g/L), *GS* 3 (10.8 g/L). Sweet taste intensity quantified on general Labeled Magnitude Scale (gLMS) and integrated across concentrations with area-under-the-curve (AUC), optimal sucrose content with refractometer and presented as g/L, desired relative sweetness on visual analog scale (VAS), and liking on hedonic gLMS. a / b / c Lower case letters within each row depict means that are statistically different from one another at $p<0.05$ with post-hoc Tukey-Kramer adjustment; conditions that share or lack a letter are not significantly different from each other. N=51.

	Control Estimate (95% CI)	**GS 1** Estimate (95% CI)	**GS 2** Estimate (95% CI)	**GS 3** Estimate (95% CI)
Sweet taste intensity (gLMS)				
Low	0.4 (0.3, 0.4)	0.2 (0.2,0.3)	0.2 (0.1,0.3)	0.3 (0.2,0.4)
Medium	1.0 (0.9,1.1)[a]	0.5 (0.4,0.6)[b]	0.5 (0.4,0.6)[b]	0.5 (0.4,0.7)[b]
High	1.5 (1.4,1.6)[a]	1.1 (1.0,1.2)[b]	1.0 (0.9,1.1)[b]	1.0 (0.9,1.1)[b]
AUC	4579 (3872,5286)[a]	2053 (1672,2433)[b]	1805 (1389,2220)[b]	1924 (1414,2434)[b]
Optimal sucrose (g/L)	105.7 (99,112)[a]	134.8 (127,143)[b]	146.4 (136,157)[bc]	148.1 (139,157)[c]
Desired sweet (VAS)	-2.2 (-8.9 4.4)[a]	-20.5 (-30.0,-11.0)[b]	-32.7 (-41.7,-23.7)[c]	-37.4 (-47.9,-27.0)[c]
Liking (hedonic gLMS)				
Regular	13.4 (5.4, 21.4)[a]	9.9 (2.0,17.7)[ab]	2.0 (-6.9,10.9)[bc]	1.2 (-7.3,9.7)[c]
Diet soda	4.4 (-3.0,11.8)	-0.6 (-7.5,6.4)	-4.3 (-12.0,3.5)	-3.2 (-10.6,4.2)
Cookie	24.2 (17.7,30.8)[a]	13.8 (7.9,19.8)[b]	10.0 (3.3,16.6)[b]	7.1 (0.1,14.1)[b]

Reduced sweet intensity perception increases desired sucrose content

Treatment of *GS* influenced the panel's optimal level of sweetness from the sweetened beverage (main effect treatment: $F(3,150)=32.70$, $p<0.001$, **Figure 1.2**). The lowest optimal level of sucrose was observed in the control condition at 105.7 g/L [99.3, 112.1], followed by the *GS* 1 condition at 134.8 g/L [126.7, 142.9], *GS* 2 condition at 146.4 g/L [135.9, 156.9], and finally the highest level of optimal sweetness with the *GS* 3 condition at 148.1 g/L [139.2, 157.0].

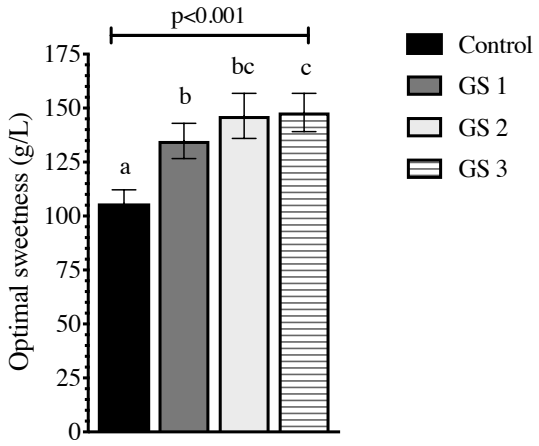

Figure 1.2
Increase in optimal level of sucrose following treatment with increasing concentrations of *Gymnema sylvestre* (*GS*). Bars represent mean and 95% confidence interval of optimal sucrose content in a beverage following treatment corresponding to levels of *GS* as follows: control (0.0 g/L), *GS* 1 (1.2 g/L), *GS* 2 (3.6 g/L), *GS* 3 (10.8 g/L). p-value specifies statistical significance of main effect of treatment in a repeated measure analysis of variance. a / b / c Lower case letters means that are statistically different from each other at $p<0.05$ with post-hoc Tukey-Kramer adjustment. N=51.

Treatment with increasing *GS* concentrations correlated with both reductions in perceived sweet taste (Figure 1.1) and increases in a participant's optimal level of sugar in a beverage (Figure 1.2), suggesting a negative association of perceived sweet taste and optimal sugar concentration. A mixed linear model assessing the effect of perceived sweet taste post-treatment at the high concentration on optimal level of sugar in a sugar-sweetened beverage confirmed this (**Table 1.3**), adjusting for BMI. Every 1% reduction in perceived sweet taste intensity associated with a 0.40 g/L increase in optimal sucrose content (-0.40 [-0.51, -0.29], $F(1,50)=49.92$, $p<0.001$).

With the two-part analysis, our data show that increased concentrations of *GS* and a reduced peripheral sweet taste signal associated with a greater desire for more sucrose.

Table 1.3
Regression estimates of the effect of taste and hedonic outcomes with a 1% decrease in perceived sweet taste intensity. Values shown are transformed beta coefficients (95% CI), estimating unit increases (+) or decreases (-) in outcome with 1% increase in sweet taste. Optimal sucrose content quantified with refractometer and presented as g/L, desired relative sweetness on visual analog scale (VAS), and liking on hedonic general Labeled Magnitude Scale (gLMS). Stars indicate where the association of sweet taste on outcomes is statistically significant:***p<0.001; **p<0.01; *p<0.05. Uppercase letter subscripts indicate adjustment of estimate with the following covariates: $_{A}$ BMI; $_{B}$ age. N=51.

	Estimate (95% CI)	p
Optimal sucrose (g/L) $_{A}$	0.40 (-0.51, -0.29)	<0.001
Desired relative sweetness (VAS) $_{B}$	0.22 (0.12, 0.33)	<0.001
Liking (hedonic gLMS)		
Regular soda	0.12 (0.04, 0.19)	0.002
Diet soda	0.14 (0.04, 0.23)	0.005
Cookie $_{B}$	0.13 (0.06, 0.21)	0.013

Weakened sweet taste correlates with varying responses to real foods

Considering *GS* treatment diminishes perceived sweet intensity and increases the optimal level of sucrose a participant desires, it is not surprising that treatment with *GS* also influences reactions to real foods. When tasting a real sweet food (cookie), participants reported perceiving less sweetness under *GS* treatment (main effect treatment: $F(3,150)=21.46$, $p<0.001$, **Figure 1.3A**), but critically, also reported desiring more sweetness in the cookie (main effect treatment: $F(3,150)=26.6$, $p<0.001$, **Figure 1.3B**). Whereas mean ratings for the desired relative sweetness of the cookie converged around the 'Just about right' scale descriptor in the control condition, with greater *GS* treatment, they veered towards the 'Not nearly sweet enough' scale descriptor. Under treatment with higher concentrations of *GS*, there was a greater desire for more sugar (Figure 1.3B). A linear mixed model confirmed a positive association between sweet taste intensity perception and desired relative sweetness of the sample (Table 1.3). Every 1% reduction in perceived sweet intensity associated with a 0.22 unit decrease on the VAS scale

depicting desired relative sweetness, towards the scale descriptor of 'Not nearly sweet enough' (0.22 [0.12, 0.33], $F(1,50)=17.68$, $p<0.001$).

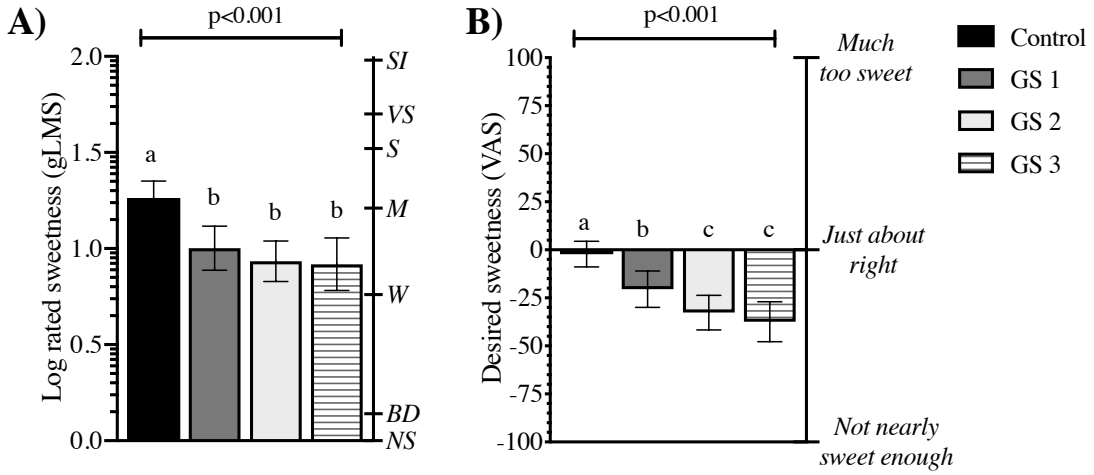

Figure 1.3
Intensity and desired relative sweetness of cookie following treatment with increasing concentrations of *Gymnema sylvestre* (*GS*). Bars represent mean and 95% confidence interval of sweet taste intensity perceived measured on the log-transformed general Labeled Magnitude scale (gLMS) (Figure 1.3A) and desired relative sweetness quantified on a visual analog scale (VAS) (Figure 1.3B) in a cookie following treatment of *GS* as follows: control (0.0 g/L), *GS* 1 (1.2 g/L), *GS* 2 (3.6 g/L), *GS* 3 (10.8 g/L). Right axis of Figure 1.3A show scale descriptors of gLMS as follows: NS, no sensation; BD, barely detectable, W, weak; M, moderate; S, strong; VS, very strong; SI, strongest imaginable sensation of any kind. p-value specifies statistical significance of main effect of treatment in a repeated measure analysis of variance. a / b / c Lower case letters within each figure depict means that are statistically different from each other at $p<0.05$ with post-hoc Tukey-Kramer adjustment. N=51.

Interestingly, foods sweetened by natural sugar differed in liking by treatment (**Figure 1.4**; main effect treatment: $F(3,150)=7.67$, $p<0.001$ for regular soda; $F(3,150)=13.05$, $p<0.001$ for cookie), but this trend was not as clear for foods sweetened by non-nutritive sweeteners ($F(3,150)=2.50$, $p=0.06$ for diet soda), at least in the statistical models where experimental condition was treated as a categorical variable. In general, sugar-sweetened foods was rated favorable under control conditions, with ratings subsequently falling towards the scale descriptor of 'Neither like nor dislike' with increased *GS* treatment (Figure 1.4). A similar negative trend was observed for foods sweetened by non-nutritive sweeteners, although the diet soda was rated fairly neutral on the gLMS in the control condition, nearing the scale descriptor of 'Neither like nor dislike' (4.4 [-3.1,11.8] on the hedonic gLMS).

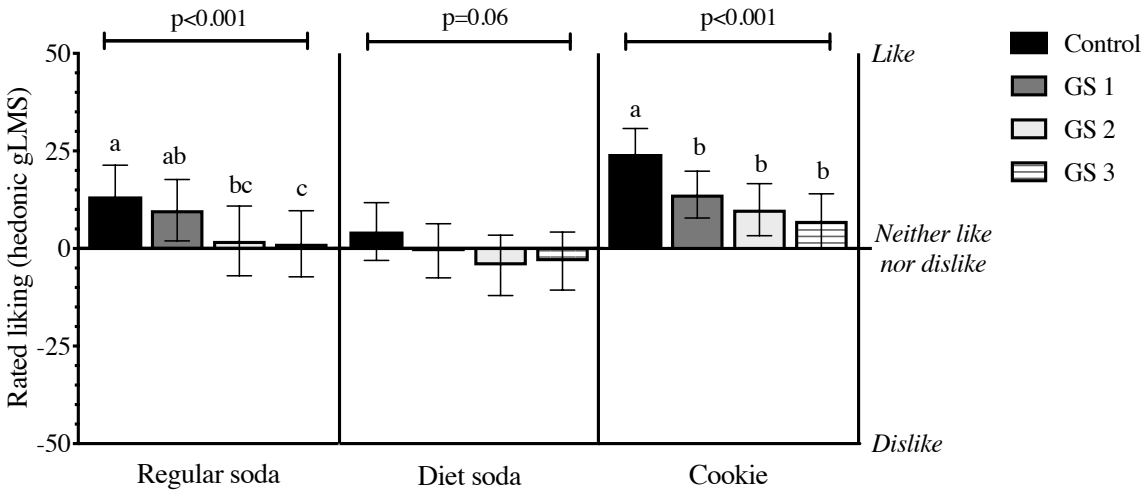

Figure 1.4
Liking of real foods following treatment with increasing concentrations of *Gymnema sylvestre* (*GS*). Bars represent mean and 95% confidence interval of rating on hedonic gLMS of real food stimuli following treatment with *GS* as follows: control (0.0 g/L), *GS* 1 (1.2 g/L), *GS* 2 (3.6 g/L), *GS* 3 (10.8 g/L). p-value specifies statistical significance of main effect of treatment in a repeated measure analysis. a / b / c Lower case letters within each stimuli depict means that are statistically different from each other at $p<0.05$ with post-hoc Tukey-Kramer adjustment. N=51.

We used linear regression to quantify the effect of perceived sweet taste intensity (as opposed to the experimental condition of *GS* treatment) on liking and observed a positive correlation of similar magnitude between sweet taste and liking of all foods tested, including those sweetened with non-nutritive sweeteners (Table 1.3). Specifically, a 1% reduction in sweet taste intensity associated with a 0.12 unit decrease in liking for regular soda (0.12 [0.04, 0.19], $F(1,50)=11.0$, $p=0.002$), a 0.14 unit decrease in liking for diet soda (0.14 [0.04, 0.23], $F(1,50)=8.30$, $p=0.005$), and a 0.13 unit decrease in liking for the cookie (0.13 [0.06, 0.21], $F(1,50)=14.87$, $p<0.001$) on the hedonic gLMS.

Although sweet taste perception influenced hedonic responses to foods, subjective appetite ratings did not change (main effect treatment: $F(3,150)=0.97$, $p=0.41$ for satiation and $F(3,150)=1.19$, $p=0.31$ for desire to eat more).

BMI and age influence desired sucrose content and hedonics

There was a positive trend between BMI and optimal sweetness, where every unit increase in BMI correlated with a 1.69 g/L increase in optimal sweetness (1.69 [-0.12, 3.50]), although the association did not reach threshold for statistical significance ($F(1,102)=3.42$, $p=0.07$). Desired sweetness and liking of the cookie were influenced by age, as every year older associated with a 2.81 unit decrease on the desired sweetness VAS scale, towards the scale descriptor of 'Not nearly sweet enough' (-2.81 [-5.15, -0.47], $F(1,102)=5.70$, $p=0.02$), and a 2.2 unit decrease on the hedonic gLMS, towards 'Strongest imaginable dislike of any kind' (-2.20 [-3.92, -0.48], $F(1,102)=6.46$, $p=0.01$).

Discussion

Taste is often identified as the primary driver of food choices (24), superseding cost, convenience, and nutritional value. It has been suggested that we partially rely on reinforcement from central reward, arising from our sense of taste, to regulate our caloric intake (25). Considering weakened taste function is reported in obese states (1,2,26,27), we speculate that people who are overweight or obese may desire more intensely tasting stimuli, and therefore may be vulnerable to overconsumption in order to compensate for a diminished reward system. Our data suggest a positive trend between body weight and preferred concentration of sweet; every unit increase in BMI associated with a 1.69 g/L increase in optimal sweetness. Although this association misses the threshold for statistical significance ($p=0.07$), it should be noted that this study was not powered to detect differences in sweet preferences with varying body weights. Nonetheless, this relationship supports previous assumptions and is a trend that warrants noting.

The central hypothesis of this report is that a weakened sense of taste associates with an increase in the preferred amount of sugar in a solution, shifting preferences towards stimuli that are more intensely tasting (and usually higher calorie). Our results show that those with experimentally reduced gustatory input for sweet taste gravitate towards sweeter stimuli, judge moderately sweet

stimuli to be less pleasant, and desire these moderately sweet stimuli to be sweeter. Overall we see that with a lessened gustatory input, participants desire more intensely tasting stimuli, at least for sweet taste.

Our model predicts that every 1% reduction in sweetness intensity perceived associates with a 0.40 g/L increase in the optimal level of sucrose desired. Using this estimate and extrapolating to a clinically significant threshold of a 20% decrement in sweet taste (3), we speculate that a 20% reduction in perceived sweet taste intensity associates with an 8.0 g/L increase in optimal sucrose content. If one were to translate this observed effect into a 16-ounce (0.47 L) beverage of typical sweetness for a soda, we reason that a participant with a 20% reduction in sweet taste would desire about 1 teaspoon (3.8 g) extra sucrose in a beverage to reach his or her optimal level of sweetness compared to someone with unaltered gustatory response. Since the USDA estimates that the average American consumes between 150 to 170 pounds of sugars in one year, a person with a 20% reduction in gustatory input may desire up to an extra 12 pounds of sugar each year to compensate for this reduced input. We acknowledge that this is a much-simplified view, but assuming that this increased desire for sweet translates to changes in intake of sugar, consuming an additional 12 pounds of sugar is enough to gain 5 pounds per year, holding all other factors constant. Despite numerous simplifications in logic here, we suggest that taste deficiency should be considered an eating disorder of concern, giving it relevance in the national conversation on obesity. This also highlights the taste bud as a possible locus for therapeutic intervention, if such interventions could adequately reach the taste bud (28).

While liking for naturally sweetened foods is consistently decreased in both analyses assessing treatment condition and varying sweet taste, a weaker effect is observed by condition for the liking of foods with non-nutritive sweeteners. We hypothesize that a lower initial liking of diet soda in the control condition (4.4 [-3.1,11.8] on hedonic gLMS) may have limited downward movement on the scale, resulting in a seemingly attenuated effect of treatment with *GS*.

However, it should be noted that linear regression revealed a definitive positive association between perceived sweet intensity and liking for diet soda, in line with the direction and magnitude of effects observed for foods sweetened with natural sugars. Thus, liking of these select sweet foods appears to decrease with decrements in sweet taste.

One inherent limitation to our approach is that we are not weakening the taste system in its entirety, since *GS* treatment primarily influences sweet taste function. Sour, bitter, and salty tastes are not affected by *GS* treatment (little research exists on *GS* and umami), although suprathreshold intensity ratings of a wide range of sweet stimuli, including artificial sweeteners, are diminished following *GS* treatment (15,16,29). The effect of *GS* in taste mixtures was highlighted in a study conducted by Gent et al. (30) where participants who consumed a tastant mixture, such as sucrose-NaCl, experienced the non-sweet taste as primary. In another study conducted by Schroeder and Flannery-Schroeder (13), participants perceived sour much more strongly in a sweet-sour hard candy, bitter much higher in the artificial sweetener aspartame, and bitter and salty much higher in a nutty chocolate candy following *GS* treatment. It would be valuable to replicate our experiment with a treatment that systematically impairs all basic tastes, however to our knowledge, there is no well-controlled method to achieve this. Despite the action of *GS* on the sweet receptor, there are a minority of reports that *GS* also has some influence on other tastes (31), which is plausible since we do not experience tastes in isolation.

Several groups have investigated a link between taste function and hedonics or food choice. Lundgren et al (32) reported little association between a taste discrimination measure and hedonic response to sucrose in experiments that spanned 5 labs and 4 continents. Alternatively, our study assessed relatively large differences in suprathreshold taste intensity and hedonic responses to real foods. Several groups detail the genetic link between sensitivity to aversive tastants detected by the Tas2R38 receptor and food preference in adults (33) and children (34), highlighting a link between taste perception and subsequent liking. Bertino et al (35)

demonstrated an increase in the rated salty intensity of a solid food and also a decrease in the preferred level of salt after a low sodium diet, again showing that taste function and hedonics appear to be connected. In an observational study, De Jong et al (36) found that elderly participants (mean age of 79 years) perceived sweet foods as less intense than the young (mean age of 22 years), and also preferred higher calorie stimuli. However, the study lacked a behavioral assessment of desired sweetness, and so we are reluctant to make any inferences here relating taste and eating behavior. Building on this foundation, our study is the first to manipulate taste function in a healthy population to show that decreased gustatory signaling associates with desire for less-healthy food, in a well-controlled, repeated-measure design. We propose that if taste response does indeed weaken in obese states, as researchers have suggested, the taste system could represent an important nexus in the generation of obesity.

Conclusion

Diminished taste response has been linked to subjects that are overweight or obese. Taste researchers generally assume that a weakened taste response associates with increased desire for higher calorie foods to compensate for the weakened central food reward. Our study is the first to directly test and show that a lessened gustatory signal is linked with a gravitation towards more intensely tasting sweet stimuli. With this, we argue that taste and taste dysfunction should be considered in the establishment of obesity.

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CHAPTER 2

COLLEGE-AGED MALES EXPERIENCE ATTENUATED SWEET AND SALTY TASTE WITH MODEST WEIGHT GAIN [2]

Introduction

Obesity affects over one third of the U.S. population, and is one of the most pressing health concerns of our time. Obesity is dependent on diet, with higher caloric intake associating with a higher body mass index in adults (1). Given that the sense of taste is a key determinant of food choice (2), taste has been hypothesized to play an important role in weight gain, and the onset of obesity (1,3,4). A number of sources suggest that those who are overweight or obese have a weakened sense of taste compared to healthy weight counterparts, particularly for the appetitive tastes (5–9). A diminished taste response may stimulate overconsumption, since taste is hardwired to dopaminergic reward centers in the brain (10). Thus, a weakened taste response may drive over-consumption as a means to compensate for lowered taste input (10,11). Higher consumption in weak tasters presumably allows them to attain a reward that is equivalent to those with stronger taste function.

Cross-sectional studies indicate that sweet (5,6), umami (7), fat (8,9), salt (5), sour and bitter (12) perception may be weaker in participants with a higher BMI, with some reports also suggesting that associations vary with sex (12,13). Evidence is inconsistent, with studies reporting no association (14) or an inverse relationship (15) between taste and BMI. With drastic weight loss, a weak taste response may also be strengthened (16–18), suggesting the taste system may be somewhat plastic. Research shows that sugar (6,19) and fat (6,20) preference or intake positively correlates with BMI. However, the relationship between dietary intake of umami-rich

[2] A manuscript detailing this study was published ahead of print in August 2017 in the Journal of Nutrition, titled "College-Aged Males Experience Attenuated Sweet and Salty Taste with Modest Weight Gain," authored by Corinna A. Noel, Patricia A Cassano, and Robin Dando.

stimuli and BMI is less clearly defined. Recent reports show that obese women prefer higher concentrations of monosodium glutamate (MSG) (7), and suggest that MSG intake associates with increased risk of being overweight in an Asian population (21), although the latter relationship is not consistently supported (22). Meanwhile, evidence suggests that habitual consumption of salty (23), sweet (5), and fatty (8) foods correlates with a weaker taste response, or preference for higher concentrations in the respective tastes. These findings suggest a complex and uncertain relationship between BMI, dietary intake, and the perception of taste.

Research in mice suggests that chronic inflammation as a result of weight gain attenuates the regenerative capacity of taste cells (24), decreasing the abundance of taste buds. These findings proffer a mechanism for the decreased taste response observed in various human sensory studies of subjects with obesity. However, the causality of this relationship remains unclear; whether becoming obese weakens taste, or whether being born with a weak sense of taste makes one more susceptible to becoming obese. Since a blinded, randomized controlled study design to address this research question is not feasible in a free-living human population, we designed a longitudinal, observational study evaluating concurrent weight and taste change, assessing the plasticity of the taste system with a moderate gain in weight. Although many studies have investigated a weight—taste association using a cross-sectional approach (5–8,12), only a few studies have investigated this relationship longitudinally, with each focusing on the association of extensive weight *loss* with changes in taste, often after bariatric surgery in clinically obese patients (16–18). One epidemiologic study examined the association of baseline taste and subsequent 5-year weight gain, but did not assess changes in taste over the time period (25).

To evaluate the association of weight gain and concurrent taste changes over time, a sample of first year college students was recruited. The first year of college is a period in which weight gain is common, primarily due to changes in dietary habits, including alcohol consumption (26,27). This study aims to investigate the effect of weight gain on within-person taste change in

a free-living population, using a longitudinal design, while adjusting for potentially confounding changes dietary habits and alcohol consumption. We hypothesized that an increase in weight would associate with a decrease in suprathreshold taste intensity perception. A secondary aim was to explore how any changes in diet during this period independently influenced taste in this sample population.

Methods

All aspects of this study were reviewed and approved by the Cornell University Institutional Review Board. 118 first year students were recruited at the start of the fall semester to complete the first testing session, with follow-up sessions after 3 months (end of first semester) and 8 months (end of first academic year). Increasing monetary compensation at subsequent sessions incentivized continued participation, and minimized panel attrition. To curtail bias, participants were not informed of the full hypothesis of the study; participants were informed that the investigators were monitoring the taste and dietary habits of a group of freshmen.

Participants were asked to abstain from eating and drinking 30 minutes prior to each testing session. Testing sessions took about 40 minutes to complete and were conducted in the Human Metabolic Research Unit at Cornell University. Session followed the same schedule: anthropometric measurements, demographic and dietary questionnaires, and training in scale usage for taste testing, followed by taste evaluations. Based on the time of day that the participant completed the baseline session, individuals were instructed to sign up for follow-up sessions around the same time to minimize time-of-day effects.

Anthropometric measurements

Body height and weight were measured using standard procedures and equipment (28). BMI was calculated with the formula: BMI=[weight (kg)/height (m^2)].

Demographic and dietary intake questionnaire

Electronic questionnaires were administered on iPads to collect data on participant age, sex, race, weekly alcohol and cigarette consumption, and exercise habits. In order to assess patterns of dietary intake, participants completed the NHANES Dietary Screener Questionnaire, which provided an estimated daily intake of fruits and vegetables, dairy products, added sugars, and meat (29).

Taste intensity scale training and taste evaluation

Sensory evaluation instructions and rating scales were presented on iPads using the sensory software Compusense Cloud (Compusense, Guelph, Canada). Before the taste evaluation task, participants received detailed instructions on using the general Labeled Magnitude Scale (gLMS) (30), and rated a series of broadly varying auditory and visual, real and imagined sensations using the gLMS. Ratings ranged from 'no sensation' to 'strongest imaginable sensation of any kind' and the scale values were log-transformed: no sensation (=0.0), barely detectable (=0.14), weak (=0.76), moderate (=1.21), strong (=1.52), very strong (=1.70), and strongest imaginable sensation of any kind (=1.98). Participants were considered to have mastered the scale if they ranked the last set of remembered visual practice sensations in the correct order (31).

Whole-mouth taste intensity ratings were captured on the gLMS using a sip and spit procedure. Sucrose (sweet), sodium chloride (salty), citric acid (sour), monosodium glutamate (umami), and quinine (bitter) were dissolved in deionized water and each was presented in a series of three concentrations, denoted as 'low', 'medium', and 'high': sucrose concentrations were 27.0, 81.0,

and 243.0 mM/L; sodium chloride were 33.3, 100.0, and 300.0 mM/L; citric acid were 1.0, 3.0, and 9.0 mM/L; monosodium glutamate were 3.0, 9.0, and 27.0 mM/L; quinine were 0.056, 0.168, and 0.498 mM/L. Solutions were served in pseudo-random blocked order, with the bitter solutions always presented last. All samples were served in uniform clear plastic cups at room temperature, identified by randomly assigned three-digit codes. Participants were directed to rinse their mouth between each sample, and a self-advancing timer ensured that participants were not able to progress too rapidly through the electronic test without ample rest time, to curtail adaptation, fatigue, and carry-over effect.

Data Analysis

Participants with incomplete data for the baseline to 8-month analysis (n=23, 19.5%) were excluded. Chi-square, Fisher's Exact, and t-tests were used to assess dropouts. Participants who did not return for the last session did not have different responses or characteristics compared to those who completed all sessions (BMI p=0.34, race/ethnicity p=0.56, sex p=0.17, age p=0.96). Because cigarette smoking is known to influence taste perception (14,32), participants who self-identified as smokers (n=2) at any point during the study were excluded from the final analysis. T-tests and paired t-tests assessed differences between sexes at baseline, and change from baseline of participant characteristics.

Ordinary least squares (OLS) regression models assessed the association of weight change with sweet, umami, salty, sour, and bitter taste intensity change, adjusting for scale usage, baseline taste rating, sex, race, and potentially confounding dietary changes. The outcome variable (relative taste intensity change) was computed by taking the difference in log taste intensity rating across two time periods (baseline to 3 months, baseline to 8 months). Relative taste intensity change on the log scale was back-transformed for presentation, and can be interpreted as the percentage increase or decrease in taste intensity perception from baseline. Changes in percent weight and dietary intake were calculated across the 3-month and 8-month time periods.

For each taste, relative taste change was assessed at three concentrations to yield concentration-dependent models and by area-under-the-curve (AUC) to integrate across all studied concentrations to compute a measure of overall taste sensitivity for each taste (23,33).

A model selection process was predetermined to maintain consistency in selecting the models for each basic taste. To control for scale usage, the change in rating (from baseline to 8 months on study) of the remembered sensation 'the brightness of the sun on a sunny day' was included as a covariate (31). Changes in dietary intake (including alcohol) were considered confounding variables if including them in the model appreciably altered the regression coefficient for weight change. Dietary intake variables that were not confounding variables, but with p-values less than 0.10, were considered to represent an alternate causal pathway to the outcome and were adjusted in the model to reduce unexplained variability in the outcome. Sex and race were assessed as effect modifiers by including the interaction terms 'sex x weight change' and 'race x weight change' in the model; a p-value threshold of 0.10 was used to assess effect modification. Variables that fit these criteria for any concentration were included in the final model for the basic taste to control for their influence on the outcome. In addition, all models adjusted for baseline taste, race, and sex. Cook's distances and residual analysis assessed potential influential data points. Results focus on the eight-month change models, given negligible effects observed in the three-month models. Analysis was conducted using SAS version 9.4 (SAS Institute Inc., Cary, NC). Unless otherwise specified, the threshold for statistically significance was $p<0.05$.

Results

Study population

93 young adults with an average age of 18 years completed the final testing session, comprising 63 females and 30 males, and primarily identifying as Caucasian and Asian/Asian Pacific Islander (**Table 2.1**). Participants were generally of a healthy body weight, with an average BMI of 21.9 kg/m^2.

Table 2.1
Baseline characteristics of study population. Values shown are mean ± SD or count (%) of participants at baseline. Conversion from kilograms (kg) to pounds (lbs) is as follows: lbs=2.2 x kg. N=93 total; 30 male, 63 female.

	Male Mean ± SD	**Female** Mean ± SD
Age (years)	18.0 ± 0.6	17.8 ± 0.4
Race/Ethnicity		
Caucasian	13 (43.3%)	20 (31.7%)
Asian/Pacific Islander	12 (40.0%)	32 (50.8%)
Other	5 (16.7%)	11 (17.5%)
Anthropometric measurements		
Height (cm)	176.8 ± 6.0	163.5 ± 6.7
Weight (kg)	68.5 ± 8.3	58.5 ± 10.0
BMI (kg/m^2)	21.9 ± 2.2	21.9 ± 3.5
Estimated dietary intakes		
Fruit/vegetables (cups/day)	3.5 ± 1.4	2.9 ± 1.1
Added sugars (tsp/day)	17.6 ± 7.0	12.5 ± 4.0
Dairy (cups/day)	2.9 ± 1.6	1.5 ± 0.7
Meat (times/day)	0.9 ± 0.6	0.7 ± 0.6
Alcohol (drinks/week)	3.8 ± 4.9	1.8 ± 3.1
Cigarette consumption		
None	30 (100.0%)	63 (100.0%)
Exercise (hours/week)	3.3 ± 2.4	2.6 ± 2.3

Taste intensity perception at baseline

Perceived taste intensity at baseline for the three concentrations of each basic taste ranged from the gLMS scale descriptor of weak to the descriptor of very strong (**Figure 2.1**), limiting floor and/or ceiling scale effects. Within each taste, the perceived intensity progressively increased with increasing concentration, verifying that participants ably distinguished increasing concentrations, and rated them appropriately in a dose-dependent fashion. Overall (AUC) perceived taste intensities of sweet, salty, sour, and bitter at baseline did not differ substantially by sex. Females rated most tastes marginally stronger than males, as follows: sweet 5.8%

(p=0.59), salty 2.7% (p=0.74), sour 12.5% (p=0.22), and bitter 5.9% (p=0.52). The exception was umami, where females consistently rated umami as about 32.6% less intense compared to males (p=0.009) (Figure 2.1).

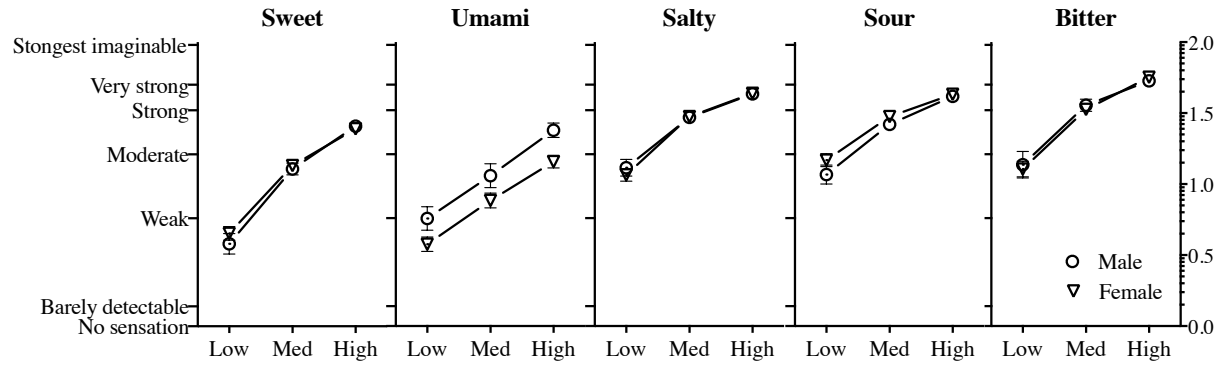

Figure 2.1
Perceived taste intensity at baseline. Data points are log mean and standard error (SE) of rating on the general Labeled Magnitude Scale (gLMS) of basic taste intensity for the three (low, medium, high) concentrations at baseline, stratified by basic taste and sex. Left y-axis scale shows gLMS scale descriptors, while right y-axis shows log gLMS values; n = 93 total; 30 male, 63 female.

Population weight gain across freshman year

As predicted, the majority of participants gained weight over the academic year, evident in both body weight and BMI. Panelists gained an average 3.1% body weight (4.1 lbs) in the first 3 months and 3.9% body weight (5.1 lbs) over the 8-month academic year. Across the sample, the change in percent body weight ranged from -5.7% to +13.8% (-8.8 to 19.8 lbs). Males gained an average 2.6% in body weight (4.0 lbs) over 8 months, while females gained an average 4.5% (5.6 lbs) (**Table 2.2**). Approximately 75% of the sample gained weight over the 8-month period (defined as weight change > 0.5 kg) while 10% of the sample lost weight (< 0.5 kg), and 15% remained relatively stable (within ± 0.5 kg). Participants who gained weight gained an average of 5.5% of their body weight (7.2 lbs), while those who lost weight lost an average of 3.0% (4.3 lbs). Over 8-months, participants reported negligible changes in exercise habits and did not significantly change height between time points (average change: exercise - 0.3 hours, p=0.16; height + 0.1 cm, p=0.11).

Table 2.2
Change in participant characteristics from baseline to 8-month follow-up. Values shown are mean change (95% CI), where positive values denote an increase from baseline; Conversion from kilograms (kg) to pounds (lbs): lbs=2.2 x kg; * Bolded values indicate statistically significantly increase or decrease from baseline at $p<0.05$ for that group. N=93 total; 30 male, 63 female.

	Male Mean (95% CI)	**Female** Mean (95% CI)
Change in anthropometric measurements		
Height (cm)	0.1 (-0.1, 0.3)	0.1 (-0.1, 0.3)
Weight (kg)	**1.8 (0.9, 2.8)***	**2.5 (1.9, 3.1)**
BMI (kg/m^2)	**0.6 (0.3, 0.9)**	**0.9 (0.7, 1.2)**
Percent weight (%)	**2.6 (1.3, 4.0)**	**4.5 (3.5, 5.6)**
Change in estimated dietary intakes		
Fruit and vegetables (cups/day)	**-0.5 (-0.9, -0.1)**	**-0.3 (-0.6, -0.1)**
Added sugars (teaspoons/day)	-1.9 (-4.2, 0.4)	**-1.7 (-2.6, -0.7)**
Dairy (cups/day)	**-0.7 (-1.3, -0.2)**	**-0.4 (-0.6, -0.3)**
Meat (times/day)	-0.2 (-0.4, 0.0)	**-0.3 (-0.4, -0.1)**
Alcohol (drinks/week)	-0.2 (-1.5, 1.2)	0.9 (-0.1, 2.0)
Change in exercise (hour/week)	-0.3 (-1.0, 0.5)	-0.3 (-0.9, 0.2)

Reduction in perceived intensity of salty stimuli across the study period

Perceived intensity for all tastes fluctuated somewhat in the 8-month period (**Figure 2.2**). However, participants consistently rated salty solutions as less intense compared to baseline. Adjusted estimates show that males experienced a 23.4% ($p=0.032$) and females a 28.9% ($p<0.001$) decrease in salty suprathreshold taste intensity ratings over the study period.

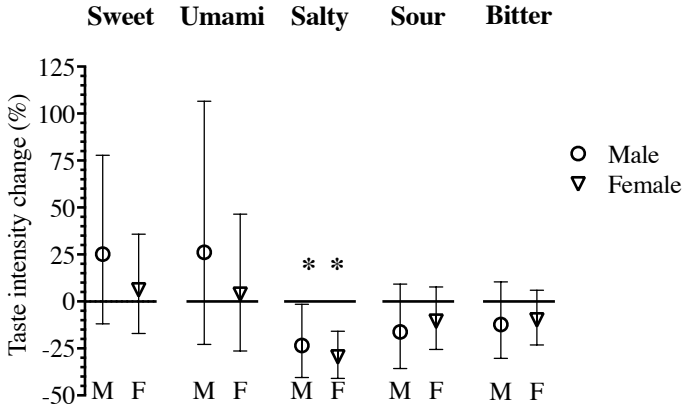

Figure 2.2
Changes in perceived taste intensity over eight months. Data points show the estimated average change in relative taste intensity (using AUC, incorporating all concentrations tested) over 8 months, and associated 95% CI, stratified by sex and adjusted for scale usage, baseline taste intensity rating, and race. Horizontal line at y = 0 indicates no change from baseline. * Indicates significant change from baseline at $p<0.05$. All models are based on n = 93 total; 30 male (M), 63 female (F).

Changes in dietary patterns associate with variation in taste

Alcohol consumption habits did not notably influence sweet, umami, sour or bitter taste perception, although one additional alcoholic drink per week correlated with a 4.6% increase in salty taste intensity ratings at low concentrations (95% CI 1.2, 8.0; p=0.008). There were a wide variety of changes in alcohol consumption relative to baseline, ranging from -11.0 to +20.0 drinks/week, with a mean change of +0.6 drinks/week. Interestingly, eating meat (red and processed) one *less* time per day associated with a 39.1% increase (95% CI -56.3, -15.0; p=0.004) in perceived umami intensity at the lowest concentration, but did not influence other tastes. This estimate should be interpreted with some caution however, since we did not see a large change in meat-eating habits over the academic year (mean -0.2 times/day; range -2.2 to 0.8). In order to further explore this negative association of umami-rich food intake and perceived umami intensity, other umami-rich foods groups were assessed. A similar relationship was observed between the umami-rich food group of tomato-based foods (salsa, tomato sauce, pizza) and umami taste (estimate -36.7%; 95% CI -59.2, -1.9; p=0.04). In all of the analyses, there was no evidence that the association of diet with taste differed by sex (p-interaction diet x sex: alcohol p=0.16; meat p=0.76; tomato-based p=0.87).

Attenuation of sweet and salty taste with weight gain in males

In males, a 1% increase in body weight was associated with an 11.0% decrease (95% CI -18.9, -2.3; p=0.015) in overall perceived sweet intensity and a 7.5% decrease (-13.1, -1.5; p=0.015) in perceived salty intensity at the lowest concentration after 8 months (**Table 2.3**). This negative association was evident across all concentrations tested, for both sweet and salty tastes. Further analyses showed that the negative associations in males were evident both in males who gained

weight as well as males who lost weight, who perceived sweet and salty tastes as more intense after weight loss. No notable trends were observed in the 3-month models (**Table 2.4**).

Table 2.3
Regression estimates of the percentage change in perceived taste intensity with 1% increase in body weight over 8-months. Values shown are transformed beta coefficients (95% CI) and associated p-values, adjusted for baseline rating, ethnicity, and influential change in dietary intake variables, stratified by sex for each concentration and an overall area under the curve (AUC) measure; * Bolded values indicate groups where the association of weight gain on taste is statistically significant at $p<0.05$. N=93 total; 30 male, 63 female.

	Male		**Female**	
	Estimate (95% CI)	p	Estimate (95% CI)	p
Sweet				
Low	**-8.1 (-14.7, -0.9)***	**0.03**	1.9 (-2.6, 6.6)	0.40
Medium	**-6.3 (-11.0, -1.4)**	**0.01**	2.2 (-0.9, 5.4)	0.17
High	-3.8 (-7.7, 0.3)	0.07	0.7 (-1.7, 3.3)	0.55
AUC	**-11.0 (-18.9, -2.3)**	**0.02**	3.9 (-1.7, 9.9)	0.17
Umami				
Low	-2.7 (-9.7, 4.9)	0.48	2.1 (-2.3, 6.8)	0.35
Medium	-5.3 (-12.3, 2.4)	0.17	2.3 (-2.4, 7.2)	0.34
High	-3.9 (-9.3, 1.8)	0.17	3.0 (-0.5, 6.7)	0.09
AUC	-10.5 (-21.7, 2.3)	0.10	8.2 (-0.1, 17.3)	0.05
Salty				
Low	**-7.5 (-13.1, -1.5)**	**0.02**	2.0 (-1.7, 5.9)	0.29
Medium	-2.6 (-6.1, 1.1)	0.16	-1.2 (-3.4, 1.0)	0.27
High	-2.0 (-4.8, 0.8)	0.16	0.4 (-1.3, 2.1)	0.68
AUC	-5.8 (-11.9, 0.8)	0.08	-0.6 (-4.5, 3.5)	0.78
Sour				
Low	0.5 (-5.5, 6.8)	0.87	**6.5 (2.6, 10.5)**	**< 0.01**
Medium	-0.2 (-3.9, 3.6)	0.90	1.7 (-0.5, 4.1)	0.14
High	-1.3 (-4.3, 1.8)	0.42	0.7 (-1.2, 2.6)	0.47
AUC	-2.1 (-8.9, 5.2)	0.55	3.4 (-1.0, 7.9)	0.13
Bitter				
Low	1.6 (-2.3, 5.7)	0.42	1.6 (-2.3, 5.7)	0.42
Medium	-0.8 (-2.6, 1.1)	0.43	-0.8 (-2.6, 1.1)	0.43
High	-1.5 (-3.1, 0.2)	0.08	-1.5 (-3.1, 0.2)	0.08
AUC	0.9 (-2.3, 4.1)	0.60	0.9 (-2.3, 4.1)	0.60

Table 2.4
Regression estimates of the percentage change in perceived taste intensity with 1% increase in body weight over 3 months. Values shown are transformed beta coefficients (95% CI) and associated p-values, adjusted for baseline rating, ethnicity, and influential change in dietary intake variables, stratified by sex for each concentration and an overall area under the curve (AUC) measure; * Bolded values indicate groups where the association of weight gain on taste is statistically significant at $p<0.05$. N=87 total; 28 male, 59 female; Sample sizes are different for 3-month and 8-months models because n=6 subjects did not complete for mid-year session.

	Male		**Female**	
	Estimate (95% CI)	p	Estimate (95% CI)	p
Sweet				
Low	-0.7 (-10.7, 10.5)	0.90	-4.2 (-10.2, 2.2)	0.19
Medium	-3.0 (-10.7, 5.3)	0.46	0.2 (-4.7, 5.4)	0.93
High	3.0 (-2.9, 9.3)	0.32	-0.2 (-3., 3.5)	0.93
AUC	2.3 (-11.3, 18.2)	0.74	0.1 (-8.3, 9.3)	0.98
Umami				
Low	1.9 (-9.2, 14.4)	0.74	-3.3 (-9.7, 3.6)	0.34
Medium	1.2 (-8.8, 12.4)	0.82	0.9 (-5.4, 7.6)	0.78
High	1.6 (-6.4, 10.3)	0.70	3.6 (-1.5, 9.0)	0.17
AUC	2.2 (-15.3, 23.4)	0.82	4.7 (-6.6, 17.4)	0.42
Salty				
Low	0.5 (-8.3, 10.2)	0.91	-2.8 (-8.0, 2.7)	0.31
Medium	1.8 (-2.9, 6.6)	0.46	1.0 (-1.8, 3.8)	0.49
High	2.8 (-2.8, 8.6)	0.33	0.4 (-2.9, 3.8)	0.82
AUC	4.2 (-5.4, 14.8)	0.40	1.4 (-4.4, 7.4)	0.64
Sour				
Low	-7.0 (-15.7, 2.7)	0.15	1.7 (-4.3, 8.1)	0.58
Medium	1.1 (-3.8, 6.2)	0.66	2.5 (-0.5, 5.6)	0.11
High	1.9 (-2.5, 6.5)	0.40	1.8 (-0.9, 4.5)	0.19
AUC	3.7 (-6.5, 14.9)	0.49	4.7 (-1.7, 11.5)	0.15
Bitter				
Low	-1.0 (-5.3, 3.6)	0.67	-1.0 (-5.3, 3.6)	0.67
Medium	-0.1 (-3.3, 3.1)	0.93	-0.1 (-3.3, 3.1)	0.93
High	1.1 (-1.1, 3.4)	0.33	1.1 (-1.1, 3.4)	0.33
AUC	3.0 (-2.1, 8.4)	0.25	3.0 (-2.1, 8.4)	0.25

While weight gain in males was negatively associated with perceived sweet taste intensity, males on average perceived sweet to be sweeter over the 8-month period (Figure 2.2). Therefore, an absolute decrease in taste compared to baseline (rating at 8-months < rating at baseline) was evident only when weight gain exceeded 4.2% of baseline body weight (**Figure 2.3).**

Meanwhile, the decrease in salty intensity perception experienced by males on average over 8-months was further amplified by a greater weight gain. A negative trend was noted for other tastes (umami and sour), but findings were not statistically significant.

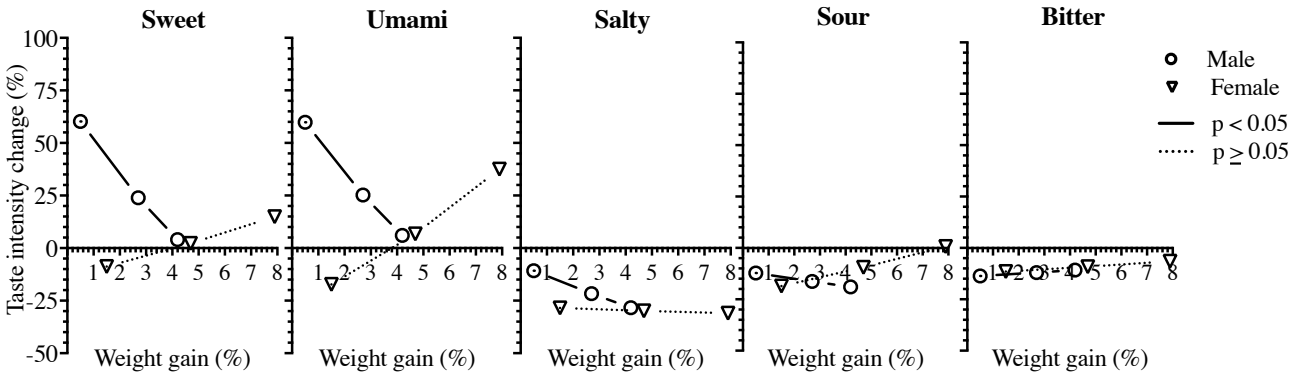

Figure 2.3
Effect of weight gain on change in perceived taste intensity over eight months. Slopes depict regression coefficient estimates of weight gain (%) on taste intensity change (%) over 8-months from baseline, derived from AUC OLS regression models; transformed beta coefficients and 95% CI are as follows: sweet male -11.0% (-18.9, -2.3), sweet female 3.9% (-1.7, 9.9), umami male -10.5% (-21.7, 2.3), umami female 8.2% (-0.1, 17.3), salty male -5.8% (-11.9, 0.8), salty female -0.6% (-4.5, 3.5), sour male -2.1% (-8.9, 5.2), sour female 3.4% (-1.0, 7.9), bitter male -0.9%(-2.3, 4.1), bitter female -0.9% (-2.3, 4.1). Statistical significance is represented by solid lines ($p<0.05$) and dotted lines ($p\geq0.05$). Effect estimates at the 25th (male: 0.5%, female: 1.5%), 50th (male: 2.7%, female: 4.7%), and 75th (male: 4.2%, female: 7.9%) percentile of percent body weight gain over 8 months for each sex are adjusted for scale usage, baseline taste intensity rating, race, and influential dietary change variables. All models are based on n = 93 total; 30 male, 63 female.

Minimal taste changes with weight gain in in females

In females, no significant effect was observed for sweet or salty taste. However, a 1% increase in body weight from baseline was associated with a 6.5% increase (95% CI 2.6, 10.5; p=0.007) in perceived sour intensity at the lowest concentration. Additional analyses reveal that females who gained weight primarily drove the positive association. In contrast, taste remained relatively unchanged in participants who lost weight. The 3-month models showed generally comparable trends, albeit of smaller magnitude (Table 2.4).

Although the association of weight gain with taste intensity change over 8 months did not reach the threshold for statistical significance for other tastes (Table 2.3), a positive trend was also evident for umami taste, which marginally missed the threshold for statistical significance with an increase of 8.2% relative to baseline (95% CI -0.1, 17.3; p=0.05).

Discussion

College students gain weight in the first year of college

Males in our study gained an average 2.6% in body weight over 8 months, while females gained an average 4.5% in body weight, consistent with findings in other settings (27). Since a change in weight without an accompanying change in height or exercise habits is accepted as a measure of change in adiposity (34), this suggests that the increase in weight observed in this study was primarily due to adiposity, as opposed to increased muscle mass or skeletal growth due to maturation.

Change in taste with variation in diet

We speculate that the decrease in salt taste over the academic year in both males and females was likely related to an increase in the consumption of salty foods. An increase in salty food intake could be driven by the shift away from home-prepared meals. Indeed, at the end of the academic year, 95% of first year students reported consuming the majority of their meals at the dining hall. Given that meals cooked outside of the home typically contain more sodium (35), and salty taste perception and preferences vary with salt intake (36,37), it is plausible that the decrease in salty taste over the study period could be linked with increased dietary sodium.

In contrast to a prior study (14), we found a positive association between a change in alcohol consumption and salty taste intensity, at least at the lowest NaCl concentration. While the previous study investigated an association between taste and alcohol intake with one intensely

salty stimulus in a cross-sectional design, the present study assessed varying intensities of salty stimuli in a longitudinal design.

To our knowledge, this is the first study to report a change in perceived umami taste intensity related to meat consumption. Decreases in the intake of meat and other umami-rich foods associated with enhanced umami intensity, in a manner similar to previous reports for sweet, fatty, and salty food consumption and their respective tastes (5,37,38). Umami taste is thought to be linked to protein consumption (39) and protein 'liking' (40). Meat is a main source of protein and umami in the American diet, suggesting that decreased stimulation of the umami taste system is correlated with heightened perceptual response to umami stimuli, potentially due to altered taste receptor expression (41).

Change in taste with modest weight gain

The variation in weight observed in this study is small in comparison with previous studies that investigated an association between weight and taste. For example, studies of weight loss after bariatric surgery examine around a 20% loss in body weight (18). In our sample, only 5.4% of participants became overweight (BMI≥25) and 2.2% became obese (BMI≥30) (42). However, the modest weight gain experienced in our study population associated with a change in taste intensity perception, differing by sex. Consistent with our results, cross-sectional research has shown that taste intensity perception varies both with body weight (5–7,12) and sex (12–14,43).

Males perceived sweet and salty tastes to be up to 11.0% less intense for sweet and 7.5% less intense for salty with every 1% increase in body weight, corroborating previous research (5,16–18). Our results suggest that gaining weight may attenuate perceived sweet and salty tastes, while losing weight may heighten taste perception in males. Meanwhile, females rated sour taste 6.5% more intense for every 1% increase in body weight, and experienced marginal increases in umami taste, driven mainly by those that gained weight. Though a recent study showed that

women with obesity have lower umami sensitivity than normal weight counterparts (7), another reported no change in umami perception before and after bariatric surgery in clinically obese patients (18). Sour taste was not assessed in these studies. In contrast with these previous studies, our participants started at a healthy weight and experienced only moderate weight gain, on average about 3.9% after 8 months, with only 2.2% of people becoming classified as obese (42).

Simplified analyses using stratified models by sex and examination of raw relative taste intensity averages showed similar effects. To ensure that results did not differ based on the weight change variable or type of model used, alternative models examining absolute weight change, absolute BMI change, and percent BMI change in place of percent body weight gain, and fixed effect models in place of OLS models, were also run. Results were further confirmed in these alternative models.

Physiological differences between males and females may account for the differing effect of weight gain on taste observed in our study. Sex influences taste perception regardless of weight (12,14,43,44), and sex differences have been previously recorded when studying taste and BMI associations (13,45). In line with previous literature, females consistently rated umami as less intense compared to males at baseline (13,43), although umami was not consistently assessed in previous studies revealing sex-dependent taste effects (12,14). A recent report showed BMI to be positively correlated with umami taste intensity in females but not males (13), corroborating the positive trend we observed between weight gain and umami taste selectively in females.

Literature suggests that hormones may influence the taste system (46–49). Alterations in sex hormones throughout the lifespan (44), pregnancy (47), and the menstrual cycle (48) have been suggested to contribute to variability in taste function. Several metabolic and sex-linked hormone receptors have been identified in the taste buds (see reviews 48,50), potentially

influencing taste signaling at the periphery. As a specific example, ghrelin differs with sex (50,51) and body weight (51,52), and is linked with taste response (53). Estrogen also influences ghrelin (54) and CCK (55) in rats, both of which have receptors in taste buds (53,56). Additionally, the first year of college is a stressful time of transition (57,58), and males in college experience stress differently than females (58). Reports suggest that negative emotions and stress may influence taste perception (43,59), possibly due to altering levels of serotonin and noradrenaline (60). While we speculate varying hormones and/or stress profiles may contribute to the variation we see here, we cannot assess their influence, since we had no measurement of either factor in our study population.

Even though a similar amount of weight was gained after 3 months, a weight gain—taste association was most apparent after 8 months, suggesting any change to the taste system may lag behind weight gain. Some research has suggested that it can take anywhere between 1.5 to 6 months for a patient's taste to change following bariatric surgery (16,18), thus a lag time of more than 3 months is plausible when examining only a moderate weight change.

Limitations, recommendations, and future study

Although our study population consisted of first year college students, which mitigated potentially confounding factors like eating environment, lifestyle, and age, the external validity of these results is limited to normal weight, non-smoking, college-aged adults. While we did not assess 'supertaster' status, which contributes to variation in taste response between those of varying body weights (6), our longitudinal design allowed each person to act as his/her own control, adjusting for baseline inherent differences in our models. Importantly, by surveying college freshmen, we were able to assess the effect of moderate weight gain on perceived taste intensity in a free-living environment, filling a gap in the scientific literature.

Replication of the study in a broader general population, with greater variation in weight change would be informative. While subjects did gain weight, few moved to a phenotype of true obesity in our study. It would be valuable to examine sex differences in the taste system with weight gain, while assessing hormonal and stress variation. Further research should clarify the relationship between diet and taste, especially in umami taste. Due to the lack of a clinical "gold standard" of assessing problematic or abnormal differences in tastes (31), we cannot draw conclusions on the perceptual significance of the change in taste intensity we observe, or its potential impact on food choice, which could also be addressed in future research.

Conclusion

As the first longitudinal study examining an association between weight gain and taste in humans, we found that a modest weight gain associates with changes in perceived taste intensity, differing by sex. College-aged males showed a decrease in perceived sweet and salty taste with weight gain, while females experienced no decrement in taste with similar increases in weight, even displaying a slight increase in sour taste. This suggests that males of this age may be more susceptible to taste loss with weight gain compared to females.

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CHAPTER 3

EXPOSURE TO MONOSODIUM GLUTAMATE DECREASES PERCEIVED UMAMI TASTE IN FEMALES AND APPETITE FOR SAVORY FOODS REGARDLESS OF SEX[3]

Introduction

Experimental and observational studies provide evidence that increased dietary consumption of sweet, salt, or fat associates with diminished perceived intensity of the stimulus, shifting preference to higher concentrations with prolonged exposure (1–3). Research suggests that adaptive changes occur within the sensory system with repeated exposure to stimuli, decreasing the sensory response and ultimately requiring more intense stimulation to elicit the same response (1,2,4,5). Specific to the taste system, supplementation of the diet with highly sweetened beverages for one month is linked with altered sweet taste and preference (3), while a low sugar diet increases perceived sweet intensity after three months (6). A high dietary salt increases preferred concentration of salt after three weeks (2), while a low salt diet increases the perceived salt intensity and decreases preferred concentrations of salt within two months (7). A high fat diet decreases fat sensitivity, while a low fat diet increases sensitivity after a four week treatment (1), possibly due to altered expression of the putative fat taste sensitive transporter CD36 (8).

While sweet, salt and fat have been comprehensively studied, umami is the least-characterized taste, despite being highly relevant to our diet, food preferences, and metabolic health. There is limited research on umami perception and its connection to diet (9), with epidemiological studies investigating taste often lacking an assessment of umami (10,11). The umami taste is thought to signal the ingestion and regulation of protein and amino acids (12–14), and may be linked to

[3] A manuscript detailing this study is in preparation to be submitted to American Journal of Clinical Nutrition, authored by Corinna A. Noel, Graham Finlayson, and Robin Dando.

body weight maintenance, obesity, and satiation (13–19). Frequently described as savory or meaty, umami taste is elicited strongly by the presence of glutamate or glutamic acid (20,21). Glutamate stimulates the umami-sensing G-protein coupled receptor heterodimer of T1R1 and T1R3 proteins (22) and possibly other receptors (23–25). Glutamates are naturally abundant in many foods (19,26), including breast milk, providing vital early life exposure to umami taste (27).

A common and powerful stimulus of umami taste in the human diet is monosodium glutamate (MSG), the sodium salt of glutamic acid. Taste sensitivity to MSG has been linked to increased liking of dietary protein (12), while liking for MSG is positively correlated with habitual protein intake when in a state of protein deprivation (28). High protein foods are naturally high in umami (29) and the body may not distinguish added MSG from dietary glutamates (20).

To our knowledge, no studies have examined habituation to umami taste with repeated consumption of umami-rich stimuli in humans. We tested the hypothesis that repeated consumption of umami-rich MSG in healthy adults would decrease perceived umami intensity and hinder the ability to discriminate low concentrations of umami, and further would alter hedonics, food preferences, and satiation. We present a randomized controlled study, where participants in the treatment group supplemented their diet for 4 weeks with a broth containing the umami-rich stimulus MSG, while participants in the control group consumed the same broth (sodium-matched), but without the added MSG.

Methods

All aspects of this study were approved by the Cornell University Institutional Review Board. The protocol is registered at clinicaltrials.gov (NCT03010930).

Design and participants

A parallel group, single blinded randomized controlled study design with 1:1 allocation examined habituation to umami taste. Based on the variation observed in taste after controlled dietary changes in Wise et al. (6) and research in our lab, a power calculation suggested that a sample size of 50 would detect a 30% difference in perceived taste intensity between groups at α=0.05 with a power of 1-β=0.80.

Potential participants were recruited by emailing prior study participants at the Cornell University Sensory Evaluation Center, and advertising with paper flyers around campus. A prescreening questionnaire assessed eligibility, excluding those that were hypertensive or on a low sodium diet, smokers, those allergic or sensitive to MSG, nuts, or dairy, classified as restrained eater (score > 12 on the dietary restraint subscale of Three Factor Eating Questionnaire (1,30)), vegan, frequent consumers of Asian foods, under the age of 18 years, over the age of 55 years, or outside of a healthy BMI range of 18.5-25.0 kg/m^2 (31) with self reported height and weight.

Participants completed a semi-quantitative food frequency questionnaire (Diet History Questionnaire, National Cancer Institute), which provided valid estimates of daily protein and glutamic acid intakes (32). We hypothesize that glutamate may act as a proxy for habitual consumption of umami stimuli, since dietary glutamates are a main source of umami taste in the diet (20), although this has not been confirmed. Based on the DHQ estimates, enrolled participants were stratified into groups via median split based on low and high daily glutamic acid consumption (median=12.1 g/day).

A stratified block randomization was employed with a random allocation sequence generation (Sealed Envelope, London, UK), balancing groups by sex (male, female) and habitual glutamic acid consumption (low, high) prior to the start of the intervention. As a single-blinded study,

participants were not aware which treatment arm they were in; randomly assigned numbers identified both participants and treatment groups.

Interventions

Participants consumed 8 ounces of low glutamate vegetable broth (Vegebase, Vogue Cuisine Foods) daily for four weeks. The treatment group's broth was supplemented with 3.8g MSG, equivalent to increasing the average US daily dietary glutamate consumption by 20% (33). The control group broth contained no added MSG, but was sodium-matched with sodium chloride to ensure both broths contained the same amount of sodium. Bench testing confirmed both broths were palatable, and that neither was out of the ordinary for the taste of traditional broths. Broths contained approximately 15 calories, making it a suitable vehicle to covertly increase stimulation of umami taste with added MSG in the treatment but not the control group, with minimal changes in caloric or macronutrient intake due to the intervention vehicle.

To ensure adherence, participants were required to pick up the prepared broth at a central location after lunch every weekday, and attendance was taken daily. Participants consumed broth remotely on weekends, and were provided prepackaged instant broth with instructions on preparation. Text message reminders and brief surveys to assess study adherence were sent on weekend days (TXT Signal, Inc., Gainesville, FL).

Testing session outline

All outcomes were evaluated at baseline and following the 4-week intervention. The two testing sessions were conducted at the Cornell Sensory Evaluation Facility, and took approximately 60-80 minutes to complete. Participants were directed to abstain from eating and drinking 3 hours prior to testing. No broth was consumed on the day of testing to minimize acute effects from MSG consumption. All sessions were conducted around lunchtime, curtailing any time of day

taste or appetite-related effects. Both the baseline and post-treatment testing sessions followed the same procedure (**Figure 3.1**).

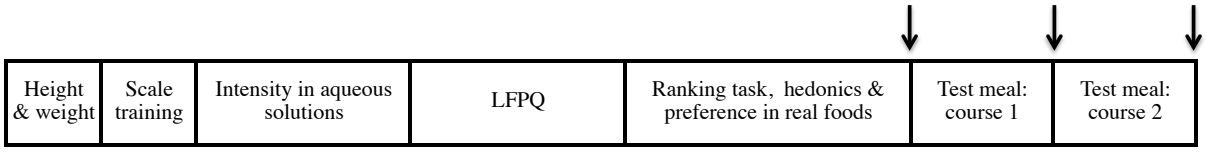

Figure 3.1
Testing session timeline. LPFQ: Leeds Food Preference Questionnaire. Arrow indicates appetite ratings.

Electronic questionnaires captured responses during testing sessions using RedJade sensory software (Tragon, San Franscisco, CA). All samples were served in uniform clear plastic cups at room temperature, identified by randomly assigned three-digit codes (34). Participants were directed to rinse their mouth with water between each sample. A self-advancing timer controlled progress of the test and minimized fatigue.

Taste measures: intensity and discrimination

Participants received training on using the generalized Labeled Magnitude Scale (gLMS, (35,36)), rating a series of broadly varying auditory and visual, real and imagined sensations. After correctly ranking the last set of remembered sensations (37), whole mouth suprathreshold taste intensity ratings for aqueous solutions were captured on the gLMS, with scale descriptors and values were as follows: no sensation (0.0), barely detectable (1.4), weak (6.0), moderate (17.0), strong (34.7), very strong (52.5), and strongest imaginable sensation of any kind (100.0). Aqueous taste stimuli were prepared in deionized water and were presented twice, separately, in a series of three ascending concentrations: sucrose for sweet taste at 27.0, 81.0, 243.0 mmol/L; sodium chloride (NaCl) for salty taste at 11.1, 33.3, 100.0 mmol/L; monosodium glutamate (MSG) for umami taste at 3.0, 9.0, 27.0 mmol/L. Duplicate gLMS ratings were averaged with a simple arithmetic mean. The solutions were served in pseudo-random blocked order, and employed a sip and spit procedure.

Participants ranked four sodium-matched solutions with varying MSG content (0.0, 3.0, 6.0, 9.0 mM/L) according to perceived umami intensity. A rank scoring system based on the methods of Steward et al. (1) assessed the ability to discriminate lower concentrations of MSG. Participants received a score out of 5 for this task, based on the order of the ranked solutions and number of inversions, with a higher score indicating greater agreement.

Test meal: satiation and satiety measures

An ad-libitum test meal was used to assess satiation and satiety, consisting of two separate courses (38). Pasta and sauce (spaghetti, Allegra; marinara sauce, Furmano's) was served first as the savory course, while ice cream (vanilla ice cream, Cornell Dairy) was served last as the sweet course. All participants were instructed to eat as much as they desired, and were prompted to indicate to if they wanted more of either course. All food left on the plates was weighed covertly following the experiment. Satiation was quantified by the amount of food eaten in the courses (39).

Subjective appetite ratings were assessed throughout the ad-libitum test meal: before the savory course, between courses, and immediately after the sweet course (Figure 1). Ratings were made on a 100-point visual analog scale (VAS) for six dimensions of appetite: hunger, fullness, satiety, prospective food consumption, desire for savory, and desire for sweet (40). Appetite sensations were also examined at each point in the meal and over the whole eating episode with an area under the curve (AUC) measure.

Liking, wanting, and preference measures

Participants were instructed to consume small samples of a variety of real foods (Parmesan cheese, Wegmans brand; unsalted dry roasted almonds; Sincerely Nuts; sundried tomato, California Sun Dry; strawberry jam, Wegmans; dill cucumber pickles, Wegmans). Hedonic ratings were captured on the hedonic gLMS (41), a bipolar scale with similar descriptors and

values to the gLMS, ranging from greatest imaginable disliking of any kind (-100.00), neutral (0.0), to greatest imaginable liking of any kind (100.00). Preference for MSG in a real food (no salt tomato juice, Red Gold) was assessed in a forced choice preference test between a sample with added MSG (0.5% w/v, see (42)) and a sodium-matched sample without MSG.

Liking and wanting for high protein foods was evaluated for four outcomes (explicit liking, explicit wanting, relative food preference, and implicit wanting) using the Leeds Food Preference Questionnaire (LFPQ) (43–45). The LFPQ is sensitive to month-long changes in diet (43) and has been associated with food choices and intake in a free-living environment (45). 16 foods of varying protein content (low or high) and taste (sweet or savory) were presented on a computerized program. For each outcome, mean scores for the low protein foods were subtracted from the high protein foods to provide a measure of the 'appeal' for high protein foods (46). A positive score indicates a greater appeal for high protein foods, and a negative score indicates a greater appeal for low protein foods.

Demographic questionnaires captured information on sex, age, and race/ethnicity. Body height (cm) and weight (kg) were measured with standard procedures and equipment (47). BMI was calculated with the formula: BMI=[weight (kg) / height^2 (m)].

Data analysis

General linear models assessed the effect of treatment on change (difference from baseline) in taste intensity, liking, wanting, satiation, and appetite sensations. The change outcomes can be interpreted as an increase (positive value) or decrease (negative) from baseline. Models assessing the effect of treatment group on change in taste intensity controlled for usage of the gLMS by including the remembered sensation 'the brightness of the sun on a sunny day' as a covariate (37). The outcomes for the LPFQ data (explicit wanting, explicit liking, relative food preference, implicit wanting) were assessed in separate models, each with a random subject

effect. Rank analysis of covariance analyzed the change from baseline in umami discrimination from the ranking task scores. Logistic regression evaluated the preference of MSG in a real food following the intervention. All analyses adjusted for baseline outcome, controlling for inherent group differences prior to the intervention.

Including the interaction term of 'sex x treatment group' assessed effect modification of sex on outcomes; the p-value threshold for assessing effect modification was set at $p<0.10$. If the p-value threshold was not reached, the interaction term was removed from the model and overall estimates of treatment are presented by combining sexes. Sensitivity analyses were conducted based on adherence to the testing protocol. Adherent was defined as consuming the broth > 90% of the time throughout the month-long testing period, and was assessed with an objective measure of attendance at weekday consumption sessions and confirmatory text response on weekends.

Data on figures represent mean ± SEM of outcomes, adjusted for baseline value and stratified by treatment group and sex, if it was determined to be an effect modifier. Main effects of treatment are presented with the test statistic, degrees of freedom, and associated p-value, and outcomes by treatment group are presented as model estimates of the outcome and 95% confidence intervals (95% CI). The analysis was conducted using SAS version 9.4 (SAS Institute Inc., Cary, NC). The threshold for statistically significance was $p<0.05$, with additional emphasis on effect estimation and confidence intervals to provide information on clinical significance of results.

Results

Participant flow and baseline characteristics

A prescreening questionnaire assessed the eligibility of 240 participants, excluding 132 participants that did not meet the eligibility criteria, and 42 who later declined participation, resulting in a randomization of 66 participants into control and treatment groups (**Figure 3.2**). 3

people were lost to follow-up in the control group, while 4 people dropped out of the study in the treatment group, all citing time constraints and inability to meet the daily attendance requirement of the study. Chi-squared, Fisher's exact, and t-tests revealed no significant differences in age, gender, dietary glutamate, race/ethnicity, or restrained eating score (all $p \geq 0.05$) between those that completed the intervention (n=59) and those that were lost to follow up (n=7), although those that dropped out had slightly lower BMI than those that remained in the study (mean: dropout 19.4 kg/m^2, complete 21.3 kg/m^2; effect of dropout group: $F(1, 62)=5.18$, $p=0.019$). One additional participant in the treatment group failed to follow directions at the testing session and was excluded from data analysis due to incomplete data.

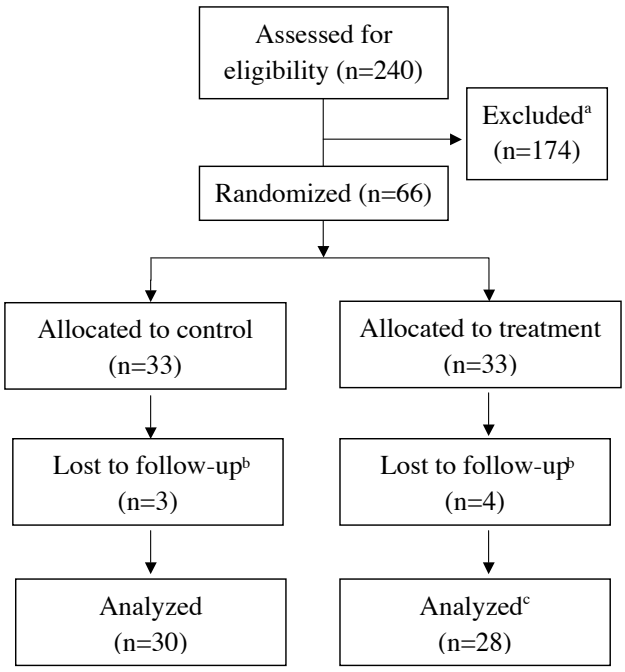

Figure 3.2
Flowchart summarizing participant recruitment, screening, randomization, and study completion. [a] Did not meet inclusion criteria (n=132); Declined to participate (n=42). [b] Cited time constraints and/or did not complete study requirements (i.e. missed multiple days of broth consumption). [c] Missing data due to failing to follow directions at testing session (n=1).

In total, data were analyzed from 58 participants, consisting of 30 in the control group and 28 in the treatment group. The study population overall represented a fairly healthy, normal weight

(21.8 ± 2.2 kg/m^2) group of young adults (22.7 ± 6.2 years), primarily female (72.4%) and Caucasian (62.1%) (**Table 3.1**).

Table 3.1
Baseline characteristics of treatment groups. N=58 total, 30 control group, 28 treatment group. Values represent mean ± SD or count (percentage of category) at baseline session; Other: African American, Hispanic, and mixed races; TFEQ: Three Factor Eating Questionnaire. Dietary glutamate and protein assessed with a month-long food frequency questionnaire (Diet History Questionnaire, National Cancer Institute). *Bolded values refers to statistical test of difference in means or proportions between treatment groups at $p<0.05$

	Control Mean ± SD	**Treatment** Mean ± SD
Age (years)	22.6 ± 4.7	22.9 ± 7.6
Sex		
Male	8 (26.7%)	8 (28.6%)
Female	22 (73.3%)	20 (71.4%)
Dietary glutamate (g/day)	13.5 ± 6.4	14.5 ± 9.7
Protein (g/day)	68.6 ± 33.1	75.1 ± 54.8
Race/Ethnicity		
Caucasian	19 (63.3%)	17 (60.7%)
Asian/Pacific Islander	10 (33.3%)	6 (21.4%)
Other	1 (3.3%)	5 (17.9%)
BMI (kg/m^2)	**21.3 ± 2.2***	**22.5 ± 2.2**
Restrained eating score (TFEQ)	6.9 ± 3.8	6.6 ± 2.9

There were no significant baseline differences in age, gender, dietary glutamate, protein intake, race/ethnicity, and restrained eating score between groups (all $p\geq0.05$). Regardless of treatment group, males tended to report a greater daily intake of protein (M: 88.4g ± 17.2; F: 65.4g ± 4.6) and dietary glutamate (M: 16.9g ± 3.1; F: 13.0g±0.9) than females, although not significantly (protein: $F(1,56)=3.20$, $p=0.08$; dietary glutamate: $F(1,56)=2.75$ $p=0.10$). While the BMI of the treatment group was marginally higher than the control group (control: 21.3 kg/m^2 ± 2.2; treatment: 22.5 kg/m^2 ± 2.2), both groups were within a within a normal BMI range (31). To assess any potential confounding influence, baseline BMI was included in the final models assessing the primary and secondary outcomes. Inclusion of BMI as a covariate did not appreciably alter the regression coefficients, and so it was excluded in our analyses.

Controlling for baseline differences, treatment groups did not gain weight differentially across the study period ($F(1,55)=0.21$, $p=0.65$), although males had greater gains in BMI than females (M: 0.37 kg/m^2 [0.1, 0.6]; F: -0.03 kg/m^2 [-0.2, 0.1]; $F(1,55)=8.29$, $p<0.01$). Throughout the study period, adherence for participants was high, as only 2 participants in each group (6.7% of control group; 7.1% of treatment group) failed to reach the threshold of greater than 90% adherence. Sensitivity analyses revealed that outcomes did not considerably differ based on adherence, and thus all results presented represent the entire sample of 58 participants.

Ratings of taste intensity

At baseline, umami, sweet, and salt taste intensity for the low, medium, and high concentrations were rated in a typically dose-dependent fashion, certifying correct use of the gLMS (**Table 3.2**). There was a non-significant trend for the treatment group to rate umami stimuli slightly lower than the control group in the baseline session (low P=0.26, medium P=0.06, high P=0.07). In our statistical models, we evaluated all effects as change from baseline, controlling for such differences. Regardless of treatment group, baseline variation in umami perception was not explained by sex, habitual glutamate consumption, or protein consumption (all $p\geq0.05$).

After consuming broth for 4 weeks, there was a marginal difference between treatment groups for the high concentration of umami (effect of treatment group: $F(1, 54)=3.16$, $p=0.08$), but not for sweet or salty tastes (**Figure 3.3**). Specifically, following the intervention, the treatment group rated the high concentration 5.6 units lower [95% CI: -10.3, -1.0] than the baseline rating of 25.8 ± 3.6, while the control negligibly changed relative to baseline (baseline: 34.4 ± 2.8; change: 0.2 [-4.3, 4.7]).

Table 3.2
Umami, sweet, and salty taste intensity ratings at low, medium, and high concentrations on the general Labeled Magnitude Scale (gLMS) before and after an intervention of daily consumption of broth (control group) or broth with MSG (treatment group) for 4 weeks. Baseline values represent mean and SE. Change from baseline values show mean estimate and 95% confidence interval (95% CI) of change in taste intensity rating, derived from general linear models; change values are adjusted for baseline taste rating and scale usage. P-value specifies statistical significance of main effect of treatment group in change from baseline models. Overall: N=58 total, 30 control, 28 treatment; Male: N=16 total, 8 control, 8 treatment; Female: N=42 total, 22 control, 8 treatment. [a]Males and females are stratified if statistical significance of 'sex x treatment group' interaction term $p<0.10$ [b]Overall effect of both sexes is presented if statistical significance of 'sex x treatment group' interaction term $p\geq0.10$ *Bolded values represent statistically significant difference between groups in change from baseline at $p<0.05$.

		Baseline		Change from baseline		
		Control Mean ± SE	**Treatment** Mean ± SE	**Control** Mean ± SE	**Treatment** Mean ± SE	p
Umami[a]						
Low	Male	14.2 ± 4.5	13.6 ± 2.6	-2.9 (-7.7, 1.9)	-0.9 (-5.7, 3.9)	0.56
	Female	12.7 ± 2.5	8.5 ± 2.1	-1.4 (-4.2, 1.5)	-3.9 (-7.0, -0.9)	0.23
Med	Male	22.8 ± 6.3	18.6 ± 2.2	-2.6 (-9.0, 3.8)	0.8 (-5.6, 7.2)	0.46
	Female	24.8 ± 3.4	16.1 ± 3.9	-2.6 (-6.5, 1.3)	-3.8 (-7.8, 0.3)	0.69
High	Male	30.8 ±5.1	24.4 ± 3.4	-2.9 (-11.3, 5.5)	1.2 (-7.2, 9.7)	0.49
	Female	35.7 ± 3.4	26.3 ± 4.9	**1.3 (-3.6, 6.5)***	**-8.4 (-13.8, -3.1)**	**0.01**
Sweet[a]						
Low	Male	4.2 ± 0.9	5.9 ± 1.6	0.7 (-4.0, 5.4)	2.2 (-2.5, 6.9)	0.66
	Female	6.3 ± 1.4	3.6 ±0.9	1.4 (-1.5, 4.3)	2.4 (-0.6, 5.4)	0.64
Med	Male	24.0 ± 6.6	20.7 ± 2.9	-9.0 (-16.5, -1.6)	-1.6 (-9.1, 5.8)	0.17
	Female	21.3 ± 2.5	15.3 ± 2.7	-0.2 (-4.6, 4.3)	-2.9 (-7.7, 1.9)	0.41
High	Male	44.6 ± 7.9	39.1 ±5.8	-10.6 (-20.5, -1.7)	0.4 (-8.2, 9.3)	0.09
	Female	40.5 ± 3.7	38.7 ± 4.5	1.4 (-3.9, 6.7)	-6.0 (-11.6, -0.5)	0.06
Salt[b]						
Low	Overall	3.1 ± 0.6	2.8 ± 0.5	0.2 (-1.0, 1.3)	0.5 (-0.6, 1.7)	0.64
Med	Overall	14.5 ± 1.7	19.0 ± 2.8	-3.0 (-5.8, -0.3)	-1.4 (-4.3, 1.4)	0.43
High	Overall	35.9 ± 2.9	38.7 ± 4.0	-2.7 (-7.1, 1.8)	-1.0 (-5.6, 3.6)	0.61

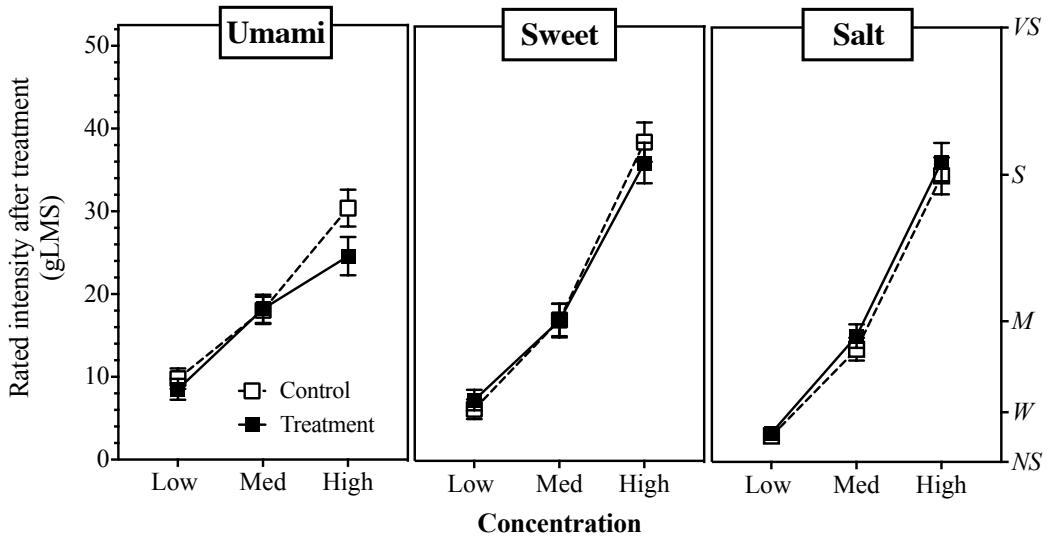

Figure 3.3
Umami, sweet, and salt taste intensity rating mean and SEM of solutions following daily consumption of broth (control group) or broth with MSG (treatment group) for 4 weeks, adjusted for baseline rating and scale usage on the general Labeled Magnitude Scale (gLMS). Left y-axis shows rating on gLMS, while right y-axis shows the corresponding scale descriptors on the gLMS: no sensation (NS) weak (W), moderate (M), strong (S), very strong (VS). N=58 total, 30 control, 28 treatment. P≥0.05 for main effect of treatment from general linear models in all tastes/concentrations.

Importantly, further analysis revealed that the effect of treatment group on change in rated umami intensity differed by sex (P-interaction=0.05). Females primarily drove the observed difference between the treatment groups (F(1, 52)=6.67, p=0.013), which was lacking in males (F(1, 52)=0.48, p=0.49) (**Figure 3.4).** Rating the highest concentration of umami to be 26.3 ± 4.9 gLMS units at baseline, females rated the stimulus 8.4 units lower on the gLMS (95% CI: [-13.8, -3.1]) following repeated daily exposure to MSG. Meanwhile, perceived umami intensity for females in the control group remained relatively stable (baseline mean ± SE: 35.7 ± 3.4; change: 1.3 [-3.9, 6.5]). This relationship was not observed in males (Table 3.2).

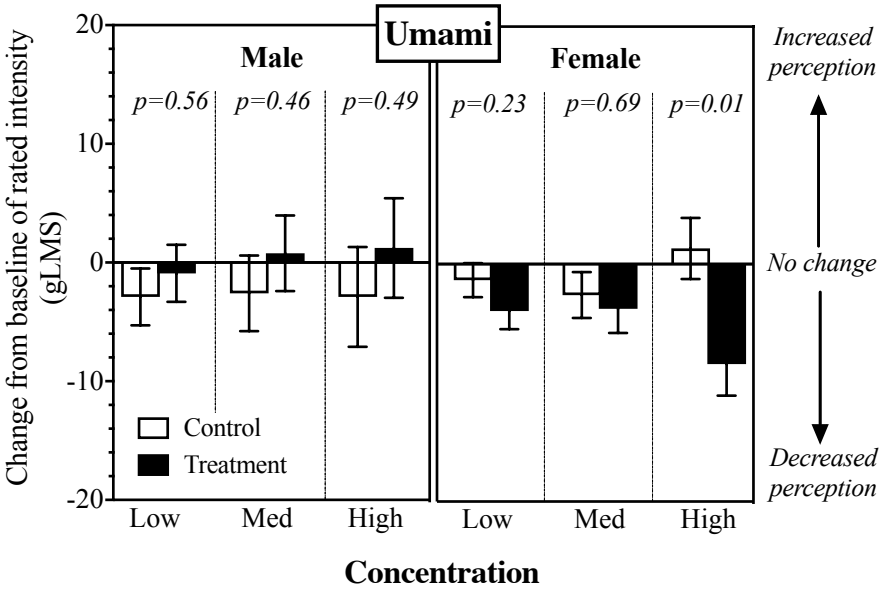

Figure 3.4
Effect modification by sex: change in umami taste intensity rating from baseline following daily consumption of broth (control group) or broth with MSG (treatment group) for 4 weeks. Taste evaluated on the general Labeled Magnitude Scale (gLMS). Values represent mean change and SEM, adjusted for baseline rating and scale usage and stratified by sex (interaction sex x treatment group: p=0.05). A positive value indicates an increase from baseline and a negative value indicates a decrease, depicted by right y-axis. P-values represent main effect of treatment from general linear models. Male: N=16 total, 8 control, 8 treatment; Female: N=42 total, 22 control, 8 treatment.

Interestingly, effect of the intervention on sweet taste intensity change was also modified by sex (P-interaction=0.015). Females in the treatment group tended to rate the high concentration of sucrose less sweet than at baseline (baseline: 38.7 ± 4.5; change: -6.0 [-11.6, 0.5]), while the control group did not appreciably change in their ratings (baseline: 40.5 ± 3.7; change: 1.4 [-3.9, 6.7]), although the difference between groups did not reach the threshold for statistical significance (effect of group: F(1, 54)=3.79, p=0.06). Again, this effect was not observed in males (Table 3.2).

As expected, salt taste did not differ with MSG supplementation relative to the control group (effect of group: F(1, 54)=0.27, p=0.61), although both groups tended to rate the higher salt stimuli lower on the gLMS following daily broth consumption (Table 3.2). The effect of group on salt taste did not differ by sex (P-interaction=0.98).

Umami ranking task

Both groups struggled to correctly rank umami solutions at baseline, with average scores of 2.9 ± 0.4 for the control group and 1.9 ± 0.4 for the treatment group. Although the treatment group appeared to lose the ability to correctly rank low concentrations of MSG by intensity (estimated change in rank: -2.2 [-8.4, 4.1]), rank analysis of covariance controlling for baseline rank revealed no change in umami discrimination by treatment group (effect of group: $F(1,55)=0.89$, $P=0.35$), with neither sex driving this effect (P-interaction=0.12).

Test meal intake and appetite ratings

At baseline, the amount of food eaten at the ad-libitum meal by the treatment group was similar to controls (463±43g versus 508±50g, p=0.50), as was the proportion of sweet and savory foods (savory: 0.75±0.03 versus 0.78±0.02; p=0.40). Following the intervention, there were group differences in the total amount eaten at the ad-libitum meal relative to baseline ($F(1,55)=4.51$, $p=0.04$), driven primarily by differences in the savory course ($F(1,55)=4.23$, $p=0.04$) (**Figure 3.5**). The control group increased in consumption of pasta and sauce relative to baseline (42g [-11, 96]), while the treatment group decreased intake (-36g [-91, 19]). This effect was also reflected in the total amount of food eaten. There were negligible changes in intake of the sweet ice cream course (**Table 3.3**). Sex did not modify these relationships (P-interaction≥0.10).

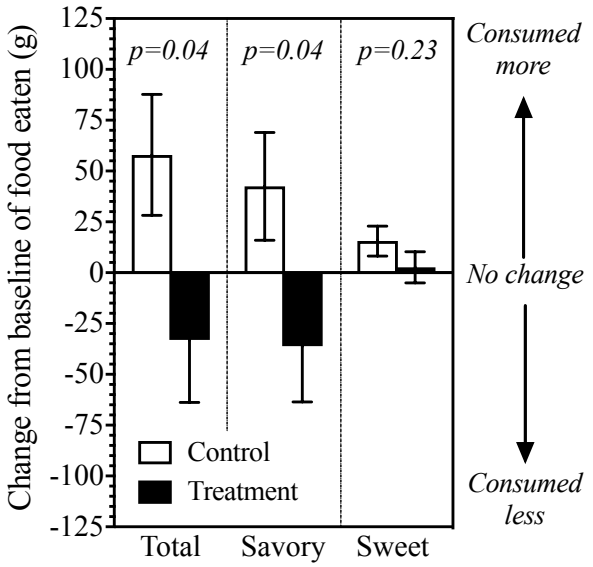

Figure 3.5
Change from baseline in total, savory, and sweet food consumed (g) at ad-libitum meal consisting of pasta (savory) and ice cream (sweet) following daily consumption of broth (control group) or broth with MSG (treatment group) for 4 weeks. Values represent mean change and SEM, adjusted for baseline amount of food eaten. A positive value indicates an increase in food eaten compared to the baseline session, and a negative value indicates a decrease, depicted by right y-axis. P-values represent main effect of treatment from general linear models. N=58 total, 30 control, 28 treatment.

Table 3.3
Amount of total, savory, and sweet food eaten (g) at ad-libitum lunchtime meal consisting of pasta (savory) and ice cream (sweet) following intervention of daily consumption of broth (control group) or broth with MSG (treatment group) for 4 weeks. Baseline values represent mean and SE. Change from baseline values show mean estimate and 95% confidence interval (95% CI) of change in amount of food eaten, derived from general linear models; change values are adjusted for baseline amount eaten. P-value specifies statistical significance of main effect of treatment group in change from baseline models. N=58 total, 30 control, 28 treatment. *Bolded values represent statistically significant difference between groups in change from baseline at $p<0.05$.

	Baseline		**Change from baseline**		
	Control Mean ± SE	**Treatment** Mean ± SE	**Control** Estimate (95%CI)	**Treatment** Estimate (95%CI)	p
Food eaten (g)					
Savory	365 ± 37	389 ± 42	**42 (-11, 96)***	**-36 (-91, 19)**	**0.04**
Sweet	98 ± 12	119 ± 15	16 (1, 30)	3 (-13, 18)	0.23
Total	463 ± 43	508 ± 50	**58 (-2, 117)**	**-33 (-95, 29)**	**0.04**

Subjective appetite sensations rated throughout the ad-libitum meal were similar by treatment group at baseline (**Table 3.4**). Following the intervention, the 'desire to eat something savory' rating differed between groups (**Figure 3.6**) prior to the start of the meal ($F(1,55)=3.50$, $P=0.07$) and following the savory course ($F(1,55)=4.64$, $P=0.04$), but not at the conclusion of the meal ($F(1,55)=0.29$, $P=0.59$). Desire for savory foods decreased relative to baseline in the treatment group (mid-meal at baseline: 27.9 ± 4.6; change: 7.7 [-13.7, -1.7]) but not in the control group (baseline: 29.7 ± 4.6; change: 1.2 [-4.5, 7.0]). This trend was also reflected in the area-under-the-curve (AUC) measures, even after adjusting for amount of food eaten at the meal. No other appetite sensations differed between treatment groups (Table 3.4).

Exploratory analysis revealed that there was no evidence to suggest that changes in savory food intake at the test meal were linked to changes in umami perception regardless of treatment group ($P\geq0.05$). However, analysis across the entire sample showed a positive association between change in umami perception at lower concentrations and rated desire to eat something savory, especially after the savory course (0.76 [0.27, 1.25]; $F(1,55)=9.81$, $P<0.01$). Changes in intake at the test meal were partially explained by changes in reported 'desire to eat something savory', as our data show an association between decreased ratings and decreased intake when controlling for baseline intake (2.29 [0.49, 4.08]; $F(1,55)=6.53$, $P=0.01$).

Table 3.4
Subjective appetite sensations throughout ad-libitum lunchtime meal (pre-meal, between sweet and savory course, post-meal) following an intervention of daily consumption of broth (control group) or broth with MSG (treatment group) for 4 weeks. Ratings made on 100-point visual analog scale (VAS) for six dimensions of appetite: hunger ('How hungry are you?'; 0=Not at all, 100=Extremely), fullness ('How full are you?'; 0=Not at all, 100=Extremely), satiety ('How satiated are you?'; 0=Not at all, 100=Extremely), prospective consumption ('How much do you think you could eat right now?': 0=Nothing at all, 100=A very large amount), desire for savory ('How strong is your desire to eat something savory?'; 0=Extremely low, 100=Extremely high), desire for sweet ('How strong is your desire to eat something sweet?'; 0=Extremely low, 100=Extremely high).Baseline values represent mean and SE. Change from baseline values show mean estimate and 95% confidence interval (95% CI) of change in amount of food eaten, derived from general linear models; change values are adjusted for baseline rating. P-value specifies statistical significance of main effect of treatment group in change from baseline models. N=58 total, 30 control, 28 treatment. *Bolded values represent statistically significant difference between groups in change from baseline at $p<0.05$.

	Baseline		**Change from baseline**		
	Control Mean ± SE	**Treatment** Mean ± SE	**Control** Estimate (95%CI)	**Treatment** Estimate (95%CI)	p
Hunger					
Pre	72.4 ± 3.3	71.0 ± 4.3	-1.9 (-8.6, 4.8)	-5.0 (-12.1, 1.8)	0.50
Mid	20.4 ± 3.2	21.6 ± 4.1	-0.1 (-6.3, 6.1)	0.2 (-6.2, 6.6)	0.94
Post	9.0 ± 2.2	6.1 ± 1.5	0.7 (-3.6, 5.0)	3.7 (-0.8, 8.3)	0.34
Fullness					
Pre	17.0 ± 3.9	18.0 ± 3.3	-1.5 (-6.7, 3.8)	0.5 (-4.9, 6.0)	0.59
Mid	69.8 ± 3.3	68.3 ± 3.7	0.3 (-6.5, 7.1)	0.2 (-6.8, 7.3)	0.99
Post	76.2 ± 4.5	79.1 ± 3.0	2.3 (-2.2, 6.9)	0.8 (-3.9, 5.6)	0.66
Satiety					
Pre	22.7 ± 4.3	30.8 ± 5.0	2.4 (-5.8, 10.6)	-0.4 (-8.8, 8.1)	0.64
Mid	71.8 ± 3.4	67.1 ± 3.9	-5.1 (-12.8, 2.7)	-3.8 (-11.8, 4.2)	0.82
Post	76.5 ±3.1	78.5 ± 4.1	1.1 (-6.6, 8.7)	-0.2 (-8.3, 7.9)	0.82
Prospective food					
Pre	65.1 ± 3.8	67.9 ± 3.9	-3.1 (-9.0, 2.8)	-7.9 (-14.0, -1.8)	0.26
Mid	32.6 ± 2.8	36.1 ± 3.5	-1.7 (-7.1, 3.7)	-2.8 (-8.4, 2.8)	0.78
Post	17.0 ± 3.1	13.8 ± 2.5	-3.1 (-6.6, 0.5)	0.1 (-3.7, 3.8)	0.23
Desire for sweet					
Pre	39.5 ± 5.1	51.6 ± 5.5	0.8 (-8.2, 9.7)	5.6 (-3.7, 14.9)	0.46
Mid	52.7 ± 4.7	54.3 ± 4.3	0.5 (-7.4, 8.4)	2.9 (-5.2, 11.1)	0.67
Post	12.7 ± 2.3	14.8 ± 3.5	-0.4 (-4.4, 3.5)	-3.4 (-7.5, 0.8)	0.32
Desire for savory					
Pre	72.1 ± 4.2	69.8 ± 4.2	0.7 (-6.1, 7.5)	-8.5 (-15.5, -1.4)	0.07
Mid	29.7 ± 4.6	27.9 ± 4.6	**1.2 (-4.5, 7.0)***	**-7.7 (-13.7, -1.7)**	**0.04**
Post	26.6 ± 4.9	14.0 ± 3.9	-0.6 (-7.2, 6.0)	-3.2 (-10.1, 3.7)	0.59

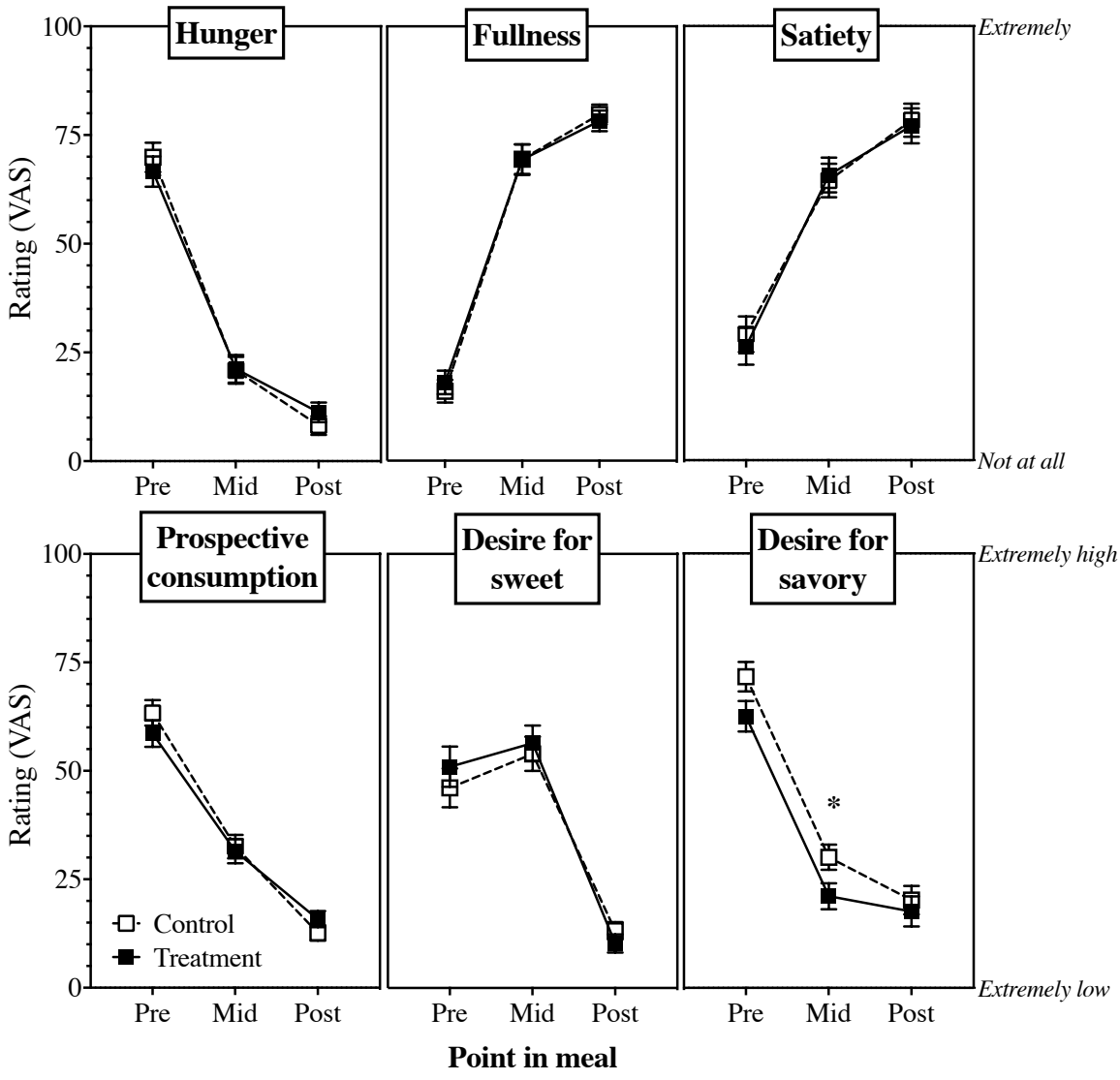

Figure 3.6
Subjective appetite sensations mean and SEM throughout ad-libitum meal (pre-meal, between sweet and savory course, post-meal) following daily consumption of broth (control group) or broth with MSG (treatment group) for 4 weeks, adjusted for rating made at baseline session. Ratings on 100-point visual analog scale (VAS) for six dimensions of appetite: hunger ('How hungry are you?'; 0=Not at all, 100=Extremely), fullness ('How full are you?'; 0=Not at all, 100=Extremely), satiety ('How satiated are you?'; 0=Not at all, 100=Extremely), prospective consumption ('How much do you think you could eat right now?': 0=Nothing at all, 100=A very large amount), desire for savory ('How strong is your desire to eat something savory?'; 0=Extremely low, 100=Extremely high), desire for sweet ('How strong is your desire to eat something sweet?'; 0=Extremely low, 100=Extremely high). Left y-axis shows rating on VAS, while right y-axis shows the corresponding scale descriptors on the VAS. *P-value<0.05 for main effect of treatment from general linear models. N=58 total, 30 control, 28 treatment.

Liking, wanting, and preferences

Appeal scores from the LPFQ at baseline revealed a generally greater liking and wanting for low protein relative to high protein foods in the control group (-9.1±2.9 for explicit liking, -8.7±3.1 for explicit wanting, -3.0±2.0 for relative food choice, -8.1±5.1 for implicit wanting), with limited inclination for high or low protein foods in the treatment group (-1.0±2.9 for explicit liking, -0.9±3.1 for explicit wanting, -0.1±2.0 for relative food choice, 0.6±5.1 for implicit wanting). After consuming broth for 4 weeks, there were marginal differences in the change in appeal scores between treatment groups when controlling for baseline scores, for both relative food choice ($F(1, 55)=3.37$, $p=0.07$) and implicit wanting ($F(1,55)=3.17$, $p=0.08$), but not for explicit liking ($F(1,55)=1.62$, $p=0.21$) or explicit wanting ($F(1,55)=0.17$, $p=0.68$) (**Figure 3.7**). In general, the treatment group tended to increase relative to baseline in the food choice and implicit wanting measures for high protein foods (food choice: 2.7 [0.3, 5.0], wanting: 9.2 [2.3, 16.0]), while the control group remained fairly stable relative to baseline (food choice: -0.3 [-2.6, 1.9], wanting: 0.7 [-6.0, 7.3]). Although the interaction for taste (sweet versus savory) and treatment group did not reach statistical significance ($P=0.12$ for food choice and $P=0.19$ for implicit wanting), it appears as if the appeal for sweet high protein foods was driving the difference between treatment groups for both outcomes. Mean scores from the raw data confirmed that the changes in implicit measures are primarily due to differences in sensory (i.e. sweet) as opposed to nutrient (i.e. protein) characteristics. No liking or wanting outcome differed by sex (P-interaction$\geq$0.10).

Further analysis revealed that regardless of treatment group, decreased umami intensity perception from baseline correlated with decreased implicit wanting for high protein foods, most evident at lower concentrations of umami stimuli (0.63 [0.05, 1.20]; $F(1,57)=4.71$, $P=0.03$). However, our data also show that change in appeal for high protein foods did not explain any differences in food intake for the test meal across the study population (all $P\geq0.05$).

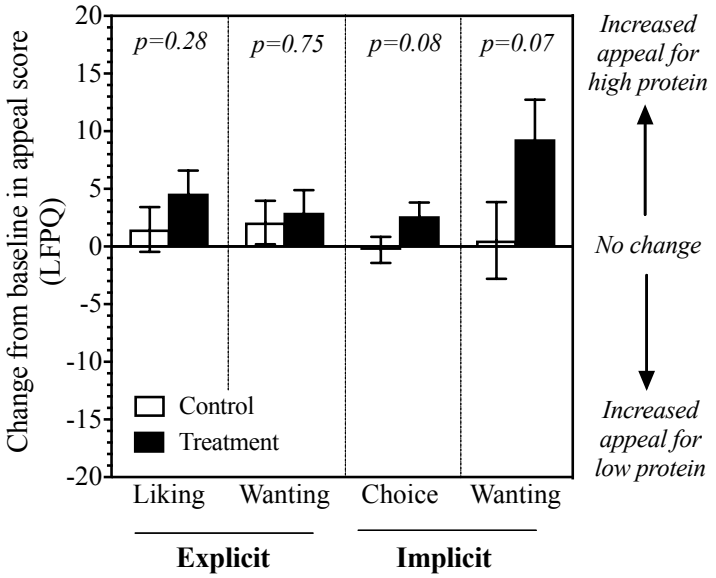

Figure 3.7
Change from baseline in high protein appeal scores following daily consumption of broth (control group) or broth with MSG (treatment group) for 4 weeks, assessed with the Leeds Food Preference Questionnaire (LFPQ). Values represent mean change and SEM, adjusted for baseline score. A positive value indicates an increased wanting or liking of high protein foods from baseline and a negative value indicates a decrease, depicted by right y-axis. P-values represent main effect of treatment from general linear models. N=58 total, 30 control, 28 treatment.

Hedonic evaluations for parmesan cheese, roasted almonds, pickles, and jam were generally favorable at baseline, with average ratings ranging between 17.7±4.2 and 27.0±3.2 on the hedonic gLMS for both groups, while sundried tomatoes were rated relatively neutral (-1.0±4.0). Treatment did not change hedonic ratings for any of the real foods that were hypothesized to be predominantly umami (effect of group: $F(1,55)=0.06$, $p=0.81$ for parmesan, $F(1,55)=1.71$, $p=0.20$ for sundried tomato; $F(1,55)=0.25$, $p=0.62$ for roasted almond), sweet ($F(1,55)=0.02$, $p=0.88$ for jam), or salty ($F(1,55)=0.03$, $p=0.86$ for pickles). This did not differ by sex for any of the foods (P-interaction≥0.10).

Prior to the intervention, 43% (n=13) of the control group preferred the sample of tomato juice with added MSG, compared to 50% (n=14) of the treatment group. Logistic regression showed that treatment did not significantly influence preference for MSG in tomato juice after the

intervention (effect of group: $X^2(1)=1.29$, p=0.26), although the treatment group tended to be more likely to chose the sample containing added MSG over the sodium-matched sample not containing added MSG (odds ratio [95% CI]: 1.87 [0.64, 5.49]), even when controlling for baseline preference. This did not differ by sex (P-interaction=0.53).

Discussion

Diminished perceived umami intensity in females after a diet high in MSG

Our data show that repeated exposure to umami taste diminishes perceived umami intensity, but selectively in females. Perceived salt taste also tended to decrease across the study period, regardless of treatment group. These results are in line with previous literature suggesting that the appetitive tastes of sweet, salt, and fat may be attenuated, or preferences shifted to more intense stimuli with a diet high in the respective taste stimuli (1–3). Equivalent associations have been reported for diets low in sugar, salt, and fat (1,6,7), suggesting an adaptive relationship that is plastic with either high or low exposure to the taste, although a diet low in umami was not assessed here.

We speculate that our results could be attributed to a down-regulation in expression of either the T1R1 or T1R3 subunit of the umami-sensing G-protein coupled receptor, analogous to that demonstrated for CD36 with repeated dietary exposure to fats in mice (8). In our study, sweet taste intensity followed a similar downward trend in those exposed to dietary glutamate compared to controls. This may imply that repeated umami exposure influences the T1R3 subunit, since umami and sweet tastes both act at least partially through this receptor (22). Preliminary research in our group supports the hypothesis of decreased expression of T1Rs with long-term exposure to MSG in mice (48), with evidence also suggesting an association between increased consumption of umami-rich foods (like meat) and impaired umami perception in a free-living human population (49).

Few studies investigating tastant exposure report testing for sex differences. Sartor et al (3) found no differential sex effects on sweet taste after one month of soft drink supplementation. Regardless, sex differences are regularly observed in taste (3,11,50,51), although many studies lack an assessment of umami (10,11,52). Circulating sex hormones such as estrogen have been hypothesized to differentially influence taste perception between sexes (51), particularly during pregnancy and certain phases of the menstrual cycle (53,54). Although none of our participants reported being pregnant, we cannot rule out the influence of phase of the menstrual cycle, which was not assessed in our design. Despite this, baseline and post-treatment testing sessions were separated by 28 days, the approximate length of a typical menstrual cycle (55). Sex differences have also been reported in umami taste (9,49), and may modify associations between taste and BMI (9) and weight change (49). This may explain some of our results since weight was gained differentially between the sexes across the study period, although this is speculative.

It is possible that dietary differences between sexes could modulate the effect of our intervention on taste. In line with previous accounts (56), males tended to report a higher intake of protein at baseline compared to females as well as greater habitual glutamate consumption. However, differences in protein or glutamate intake at baseline did not explain differences in umami taste perception. Due to the small sample size of males in the treatment group (n=8), we lacked power to assess whether males differed in taste response after prolonged dietary exposure to MSG according to relative protein intake. Even so, we reason that if males regularly consume a diet higher in glutamate, any added exposure via our treatment would have less of an effect on taste compared to females. Previous reports highlighted similar phenomena, where a high fat diet had no effect on fat sensitivity in a group of individuals that were overweight, unlike a low fat diet. Another study revealed an association between habitual protein intake and reported pleasantness of MSG stimuli, but only when participants were in a state of protein deprivation (28).

No group differences were observed on taste discrimination via the ranking task, in line with previous research that examined ranking of fatty stimuli following a high fat diet (1). We hypothesize that the ranking taste may have been too difficult initially and could limit the ability to detect a true decrease in taste discrimination. This lack of an effect adds to evidence suggesting taste intensity and discrimination may be separate components of the perception of taste (57).

Decreased intake of and desire for savory food with repeated exposure to umami taste

Our data suggests that desire for and intake of savory foods is diminished with repeated dietary exposure to MSG. There is mixed evidence detailing a link between MSG, appetite, and satiation. In two studies, preload soups with added MSG/IMP were rated as having a stronger flavor compared to soup without additional umami stimuli, and consumption of the preload with MSG decreased subsequent intake at a test meal (13,58), although this effect has not been consistently supported (59). While one study reported increased appetite following intake of soup with MSG (13), another reported decreased appetite (59), and a third reported no effect on the motivation to eat (58). There are consistently greater hedonic ratings for foods supplemented with umami-rich stimuli, usually attributed to enhanced flavor (58–60), with heightened positive emotions and satisfaction also reported following consumption (60). Based on these results, we initially hypothesized that the treatment group in our study perceived less umami in the savory course than they did at baseline, and had diminished appetite compared to the control group, presumably due to a lower perceived palatability of the test meal. However, we have no data on perceived umami intensity or palatability of the ad-libitum meal, and we observed no group differences for hunger, fullness, or prospective food consumption ratings at any point in the meal in this study.

Our data suggest that irrespective of treatment, attenuated umami taste at lower concentrations associated with decreased desire for savory foods following the savory course, but there is no

evidence to suggest that change in taste was linked to savory food intake. Since females primarily decreased in perceived umami intensity with repeated exposure to MSG, whereas both sexes reported decreased desire for and intake of savory food, it makes sense that perceived umami intensity does not entirely explain behaviors associated with appetite. It is possible that intake of MSG may have postingestive appetite effects beyond the peripheral taste system, as suggested by previous literature (61,62). Across the study period, changes in the appeal for high protein foods (assessed via the Leeds' Food Preference Questionnaire) also did not predict changes in food intake in the test meal. This lack of correlation is not entirely surprising since our test meal was not high in protein.

Stepping back, our results could be explained more simply, with the decreased intake in the test meal attributed primarily to a diminished desire for savory food. Indeed, this was supported in our data, where a reported decreased desire for savory food correlated with decreased intake in the savory course of the test meal, especially evident prior to the beginning of the meal. Research has shown that previous exposure to savory has an especially strong effect on ensuing appetite and food choices (63,64). We speculate that the treatment group may have been over-stimulated with umami taste during the treatment period and were simply less driven to consume savory, in line with sensory specific satiety theory (65). With this in mind, we believe that increased exposure to umami taste may have additional downstream effects on appetite, which cannot be entirely explained by changes in the peripheral taste system.

Slight gravitation towards high protein foods with a diet high in MSG

The implicit measures of liking and wanting suggested an increase in desire for high protein foods relative to baseline, with little change in the controls, although this did not reach the statistical threshold between groups. Those that consumed the broth with MSG for one month tended to be more likely to chose a high protein food over a low protein food in a forced choice measure, and had a greater implicit wanting for high protein foods following the intervention,

seemingly driven by sweet, as opposed to savory foods. Assuming that umami taste simulates for amino acid consumption, this result is in contrast to previous reports of increased implicit wanting for high protein foods after a low protein diet, and no preference after a high protein diet (43). Similar to our study, decreased perception of umami associated with decreased desire for protein (12). Meanwhile, rated liking for the select real foods assessed in this study did not differ by treatment group with the intervention. This could suggest that implicit measures may be more susceptible to change with increased dietary exposure to umami taste compared to explicit measures, either when presented with as an image or as a real food.

Limitations and future work

Results from this study are limited to relatively young, normal-weight, non-smoking, non-restrained eaters. Importantly, a randomized controlled study design limits confounding factors on taste. It should be noted however, that even though treatment groups in our study were randomized and balanced on sex and habitual glutamate consumption, and thus any influence of sex hormones or diet should be considered non-differential bias, it could be that our study was not large enough of a sample size to truly limit other confounding factors. More research is needed to elucidate sex differences in taste, specifically assessing hormonal modulation and taste changes, while controlling for differences in dietary intake. Since we investigated repeated exposure to MSG, it would be interesting to see if similar effects occur with increased intake of other umami-rich stimuli, such as disodium gluanylate (GMP) and disodium inosinate (IMP), or in combination with MSG. It should be noted that this study was powered to detect differences between treatment groups in taste intensity perception, as opposed to other secondary measures. Although our study begins to unravel the relationship between diet, umami taste, and health, umami taste is still not entirely understood. More studies are needed examining umami taste to understand additional environmental or genetic factors that may contribute to variations in perception.

Conclusion

Our results highlight a complex relationship between diet, umami taste, preferences, and appetite. Relative to controls, increased dietary exposure to MSG for 4 weeks diminished umami taste (selectively in females), decreased the desire for and intake of savory foods at an ad-libitum meal, and marginally shifted implicit liking/wanting towards higher protein, sweet foods in a computerized measure. Findings from this research could be applied to the study of food choice, a factor in the development and maintenance of diet-related diseases such as obesity, osteoporosis, and kidney disease.

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CHAPTER 4

THE EFFECT OF EMOTIONAL STATE ON TASTE PERCEPTION[4]

Introduction

Acute stress and affective manipulations have been demonstrated to influence our perception of taste (1–4). Negative emotional states also correlate with increased consumption of palatable foods with high hedonic value, potentially providing positive gratification and comfort (5). However, repeated consumption of these palatable energy-dense foods, usually high in salt, sugar, and fat, increase the likelihood of obesity, and substantiates the need to clarify how affective state can impact our health.

Several groups have demonstrated alterations in human taste perception with stressful or emotional manipulations in a laboratory setting. Following both positive and negative mood induction, suprathreshold sour solutions were rated as more intense compared to testing in neutral temperament (2). Emotional manipulation using common antidepressants that target the serotonergic and adrenergic systems also influence thresholds for sweet, bitter and sour (6), as serotonergic receptors are important in taste transduction (7). Negative affect also correlates with stress (8) and after exposure to acute stressors, participants rate umami and sweet solutions as less intense (3). Likewise, exposure to mild stressors has been associated with more intense bitter perception, as well as less intense sweet perception in a population categorized as low-pleasure participants (4). Taken together, it would seem that the more classically appetitive tastes of sweet and umami are perceived as weaker, while the aversive bitter and sour tastes are perceived stronger after exposure to stress or negative mood manipulation, highlighting the potential for a shift in the hedonic properties of food with variation in affect.

[4] An article detailing this study was published in June 2015 in the journal Appetite titled, "The effect of emotional state on taste perception," authored by Corinna Noel and Robin Dando.

The majority of studies of taste and emotion take place in a controlled laboratory environment, with most focusing on stress and negative affect, utilizing precise stressors or emotional manipulations. However, humans encounter situations that evoke varying affective reactions in everyday life. It is interesting to consider the influence of real-world positive and negative emotions on taste perception, and speculate how this may affect liking and food choice. It is possible to evaluate this with a sufficiently high-powered observational field study, where emotions vary under real-life conditions contingent upon the environment. A better understanding of the association of basic taste perception and hedonics with everyday emotional events may clarify the role of the taste system in emotional eating.

Competitive sporting environments elicit powerful affective reactions. All united under a common cause, a unique group dynamic allows fans see their team as an extension of themselves, where they place a great deal of emotional significance on the success or failure of their team (9). In a competitive sports setting, victory or defeat induces a wide variety of emotional reactions among fans, ranging from shame, disgust, sadness, anger, and frustration to hope, happiness, surprise, and pride (10). Team success will usually generate positive affect, while failure will induce highly negative affect among fans. At college basketball games, team success was associated with enhanced mood and positive self-esteem of winning fans, while team failure was associated with decreased mood and negative self-esteem in fans of the losing side (9). Directly following Japanese soccer matches, fans of the losing team experienced more anger, sullenness, humiliation, resentment and stress when compared to fans of the winning team, who generally had more pleasant emotions (11). Hormones are also associated with affective reactions such as testosterone and cortisol, and vary among spectators depending on outcomes of sporting events (12,13).

While several studies have focused on how emotions or stressful situations affect taste perception or food intake in a controlled laboratory environment, there is limited research exploring the impact of emotional manipulations on basic taste perception under real-life conditions. Sporting events have been shown to consistently induce both positive and negative moods of fans depending on the outcome, thus presenting a unique environment to examine the influence of varying affective states on taste perception. This study aimed to determine how emotions arising from the outcome of college hockey games influenced the perceived intensities of sweet, salty, bitter, sour, umami, and fatty tastes, as well as a measure of hedonic responses to real foods. A supplementary study confirmed that the measure of satisfaction with game outcomes associated with true positive and negative affect using a validated affective assessment questionnaire. Ultimately, this research reveals how emotional state in a competitive environment affects our perception of taste.

Methods

All aspects of this study were reviewed and approved by the Cornell University Institutional Review Board. Verbal consent was obtained from each participant, although subjects were not informed of the true nature of the study to avoid bias. Data was collected at eight Cornell University Men's Hockey games throughout the 2013-2014 season, at Cornell's Lynah Rink in Ithaca, NY, where the vast majority of spectators were home fans. During these games, the home team won four times, lost three times, and tied once, ensuring a broad spectrum of emotional states. Participants with food allergies were excluded from the study. Complete survey data was collected from 550 attendees over the course of the season, with incomplete or illegible ballots excluded.

At the conclusion of each game, participants were asked to taste and evaluate two different samples of ice cream. Ice cream was selected as a medium to assess basic taste perception due to the reported preference of high-fat sweet foods such as ice cream in times of stress (14) and the

samples also incentive study participation. Flavor 1 was a salted caramel pretzel ice cream, while flavor 2 was a lemon/lime sorbet. Together these flavors comprised a mixture of the five basic tastes of sweet, salty, sour, bitter, umami, and fat. Ratings from flavor 1 were used to assess sweet, salty, umami, and creaminess perception while ratings from flavor 2 were used to assess sweet, sour, and bitter tastes. The samples were served in uniform clear tasting cups, identified by randomly assigned numbers (15). A paper ballot evaluated the participant's intensity perception of sweet, salty, bitter, umami, sour, and creaminess, in addition to an overall 'liking' (hedonic) rating of the flavor on a visual analog scale (VAS). The visual analog scale is a widely used psychophysical measure of taste intensity perceptions (16) as well as other non-gustatory qualities (17). As an unstructured line scale with minimum and maximum ratings for a specific attribute, the visual analog scale anchors for the intensity ratings were 'not detectable' and 'strong,' while the anchors for the hedonic ratings were 'did not like at all' and 'like extremely.' Since the general population does not fully understand the term 'umami,' the attribute label 'savory' was used in its place on the questionnaire, while the attribute label 'creaminess' acted as a surrogate for the oral sensation of fat.

In order to maintain consistency, the visual analog scale was used to measure participant satisfaction with the outcome of the game. Using a direct measure of positive or negative affect was not feasible in this study due to the time such a measurement takes, especially considering the chaotic environment at the conclusion of games when the samples were evaluated. Correctly filling out positive and negative affect scales requires time, diligence, and motivation, while visual analog scales are straightforward, easily understood, rapidly completed and have a high rate of compliance from people of all backgrounds (17). A visual analog scale was also used to capture the participant's assessment of the atmosphere at the game and their self-reported degree of fanaticism. The visual analog scale anchors were 'extremely unsatisfied' and 'extremely satisfied' for outcome satisfaction, 'subdued' and 'intense' for perceived game atmosphere, and 'not a fan' and 'huge fan' for degree of fanaticism. Each visual analog scale was 145 mm in

length and the absolute measurements of the ratings were inputted as continuous variables. Participants also reported sex and age on the questionnaire. The serving order of the samples was also recorded, so that we were able to control for adaptation or mixture suppression in our analyses (16).

Data analysis

Subjects under the age of 12 years (6.9%) were excluded from analysis because it has been shown that children below this age cannot consistently complete a visual analog scale (18). Following this, the study population consisted of 512 subjects. In order to verify that the outcome of the game (win, tie, loss) was successful in manipulating satisfaction ratings, a one-way analysis of variance was run with VAS game satisfaction ratings as the dependent variable and the outcome of the game as the independent variable. Additional analyses were run in the same fashion, examining the association of fanaticism, atmosphere, age, and liking stratified by flavor, with outcome. Given a statistically significant result, post-hoc means of the outcomes were compared using Tukey's test. Chi-squared tests determined if the proportions of gender and flavor served first differed significantly by game outcome. T-tests ascertained how hedonic ratings differed between the two flavors alone, regardless of outcome.

In order to assess the association between satisfaction with the game outcome and taste intensity and hedonics, separate mixed model regression analyses were performed. Each regression model accounted for a different taste quality as the outcome, specifically sweet, salty, sour, bitter, umami, and creamy tastes, in addition to hedonic ratings for the two flavors. The taste intensity ratings for bitter underwent a square root transformation to satisfy the assumption of normally distributed residuals (19), while the continuous variables of age and outcome satisfaction were centered around the mean for easier interpretation. In each regression, a random game effect was included, as were the potentially confounding covariates of gender, age, atmosphere, hockey fan, and first flavor served. For consistency across models, all fixed effects and their second order

interactions were initially included. Backwards stepwise regression then eliminated any interaction terms with p-values greater than 0.10. These interactions tested for effect modification of the fixed effects. Since sweet ratings were collected from both samples, a random subject effect was nested within the random game effect for the sweet model. Due to sporadic missing data and repeated measures for sweet, taste analyses utilize different number of data points: sweet n=1021, salty n=512, umami n=506, sour n=509, bitter n=508, creamy n=512, flavor 1 liking n=511, and flavor 2 liking n=508. The continuous variables of degree of fanaticism and perceived atmosphere at the game were considered categorical variable of three levels for inclusion in the model. Least square means with Tukey's correction for multiple comparisons were obtained to determine effect estimates and which levels of categorical variables and interactions were significant. SAS version 9.4 (SAS Institute Inc., Cary, NC, USA) facilitated the analysis. Statistical significance was judged at $\alpha<0.05$.

Affect validation study

To ensure that our measure of satisfaction correlated with true affect, a supplementary study assessed the association of outcome satisfaction with positive and negative affect in a competitive environment. Representing two of the major affective dimensions in psychological theory that can be captured in self-report measures (20), positive affect is related to satisfaction and pleasurable events, while negative affect is related to stress and unpleasant events (8).

42 participants were recruited and offered a monetary incentive for participation. Prior to engaging in a card game task, participants signed a consent form, received detailed instructions, and were directed to play a practice round to ensure that they understood the rules of the game. Randomly paired participants then played a series of competitive card games against his or her partner, where one player was ultimately deemed the winner and the other was deemed the loser. This resulted in the decisive success or failure of the game task, ensuring a variety of affective reactions (21). The winner received a larger monetary award than the loser, incentivizing the

competition. Following the card games, participants filled out a paper survey assessing their satisfaction with the outcome of the card game task in addition to positive and negative affect, which was measured on the short form of Positive and Negative Affect Schedule (PANAS) (22). This form is shown to be as valid and reliable as the complete PANAS and takes only half the time to complete, minimizing scale fatigue. Outcome satisfaction was quantified on the same 145mm VAS used in the field study.

Those with missing or illegible scale data (n=3) were excluded from analysis. T-tests were used to assess the manipulation of PANAS scores and satisfaction ratings between wins and losses, as well as to assess the effect of gender on scale usage. To evaluate the association of the visual analog scale of outcome satisfaction with positive and negative affect, as well as the impact of age on scale usage, Pearson's product-moment correlation coefficients were computed.

Results

Positive and negative affect correlate with outcome satisfaction measures

A win or loss of the card game successfully manipulated positive affect scores ($p=0.049$), negative affect scores ($p=0.029$), and satisfaction ratings ($p<0.0001$). There were no effects of gender or age on positive affect, negative affect, or satisfaction ratings (all $p\geq0.05$). Pearson's product-moment correlations revealed that VAS outcome satisfaction ratings positively correlated with positive affect and negatively correlated with negative affect (**Table 4.1**). In general, when the participant reported a win, higher positive affect scores correspond with higher satisfaction ratings, while when the participant reported a loss, higher negative affect scores correspond with lower satisfaction ratings.

Table 4.1
Correlation of positive and negative affect with visual analog scale ratings and associated p-values. Pearson-product correlation computed between variables following a competitive card game task. [1]Visual Analog Scale (VAS) ratings of game outcome satisfaction, with values representing absolute measurements on a 145mm line scale; [2]Postive Affect (PA) score computed from PANAS-SF (Positive Affect and Negative Affect Schedule-Short Form); [3]Negative Affect (NA) score computed from PANAS-SF. N=39.

	Correlation (r)	p
VAS[1] – PA[2]	0.45	<0.01
VAS[1] – NA[3]	-0.52	<0.01

Emotional manipulation depends on game outcome

The population at the hockey games was relative young, primarily self-identified hockey fans, with similar proportions of males and females (**Table 4.2**). Since game outcome was the main emotional manipulator in the field study, we examined how a win, tie, or loss affected the variable of outcome satisfaction, in addition to the covariates of atmosphere, fanaticism, gender, age, and sample order. Analysis revealed that outcome satisfaction and the perceived atmosphere at the game significantly differed depending on the game outcome, as expected (**Figure 4.1**). Wins were rated as the highest outcome satisfaction and more intense atmosphere, while losses were rated as the lowest outcome satisfaction and most subdued atmosphere.

Table 4.2
Characteristics of study population. Values shown are mean ± SD or count (%) of participants surveyed at hockey games. N=512.

	Mean ± SD *or* count (%)
Age (years)	29.3 ± 16.1
Sex	
Men	234 (45.7%)
Women	278 (54.3%)
Reported hockey fanaticism	
Not a fan	56 (10.9%)
Neutral	150 (29.3%)
Huge fan	306 (59.8%)

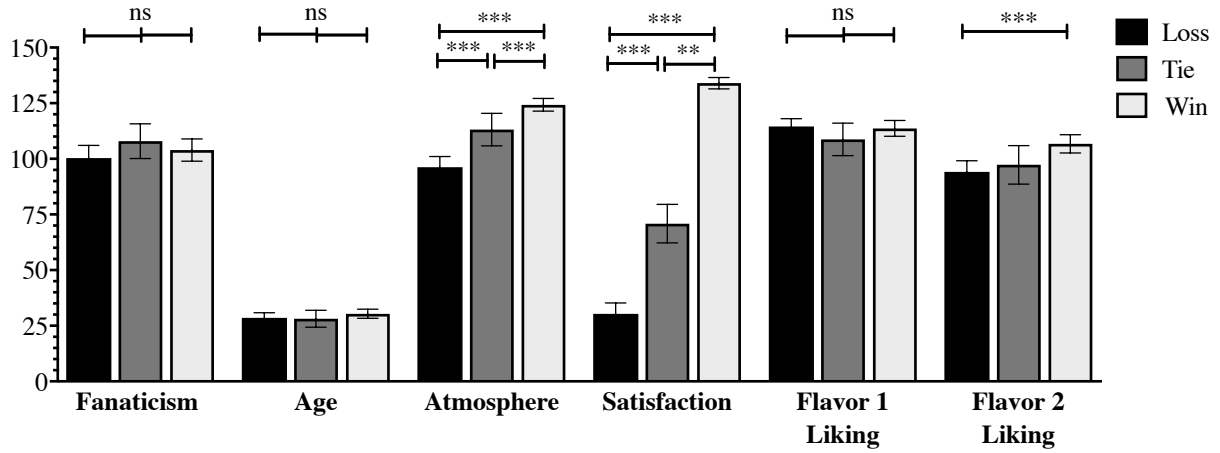

Figure 4.1
Reported degree of fanaticism, age of participants, game atmosphere, satisfaction with game outcome, and liking following game win, tie, or loss. Bars represent mean ± 95% confidence interval, with values of fanacitism, atmosphere, outcome satisfaction, and hedonic ratings signifying absolute measurements on a 145mm visual analog scale at the conclusion of college hockey games. Age was self-report in the unit of years. White bars represent ratings after a win (n=261), grey bars represent a tie (n=71), and black bars represent a loss (n=180). Stars show statistical significance between outcomes from ANOVAs: *p<0.05, ** p<0.01, *** p<0.001;,ns p≥0.05.

Fanaticism and age did not vary by the game outcome (Figure 4.1), nor did the proportion of males and females (χ^2 =0.056, p=0.973). It was revealed that sample order was appropriately randomized by game, since there were no significant differences based on outcome (χ^2=0.820, p=0.664). Therefore, any significant differences revealed in the more complex model can be attributed to the main predictor variable of satisfaction, and the accompanying covariates, as opposed to systematic differences of these select participant characteristics.

Preliminary analysis revealed that flavor 1 had consistently higher hedonic ratings compared to flavor 2, regardless of the outcome (p<0.0001), indicating that flavor 2 was less well liked overall compared to flavor 1. Interestingly, depending on the outcome, hedonic ratings selectively differed between the 2 samples evaluated (Figure 4.1). Specifically, hedonic ratings for the less-liked flavor 2 showed significant variation with game outcome, while there were no significant difference between outcomes for the more liked flavor 1's hedonic ratings. Flavor 2, looked on less favorably, was liked significantly more when the home team won. This suggests

that this less-preferable stimulus becomes more acceptable in a positive affect, and less acceptable in a negative affect. The outcome of this analysis prompted the decision to examine each flavor's hedonic ratings in separate linear models.

Game outcome satisfaction is associated with differences in taste intensity perception

Sweet, sour, and creaminess intensity were influenced by satisfaction with game outcome, while salty, umami, and bitter tastes were negligibly affected **(Figure 4.2**, **Table 4.3**). As signified by the solid regression lines in Figure 4.2A, sweet displayed a positive association, while sour negatively associated with outcome satisfaction. That is, as satisfaction ratings increased, sweet intensity perception was reported as more intense, and sour less so. Furthermore, the effect of outcome satisfaction on creamy sensation was modified by gender and perceived atmosphere levels (Figure 4.2C). A more negative association was observed in males compared to females and those reporting a subdued atmosphere compared to those reporting a more intense atmosphere. Reported fanaticism did not modify the outcome satisfaction–taste intensity perception association for any of the basic tastes ($p \geq 0.05$).

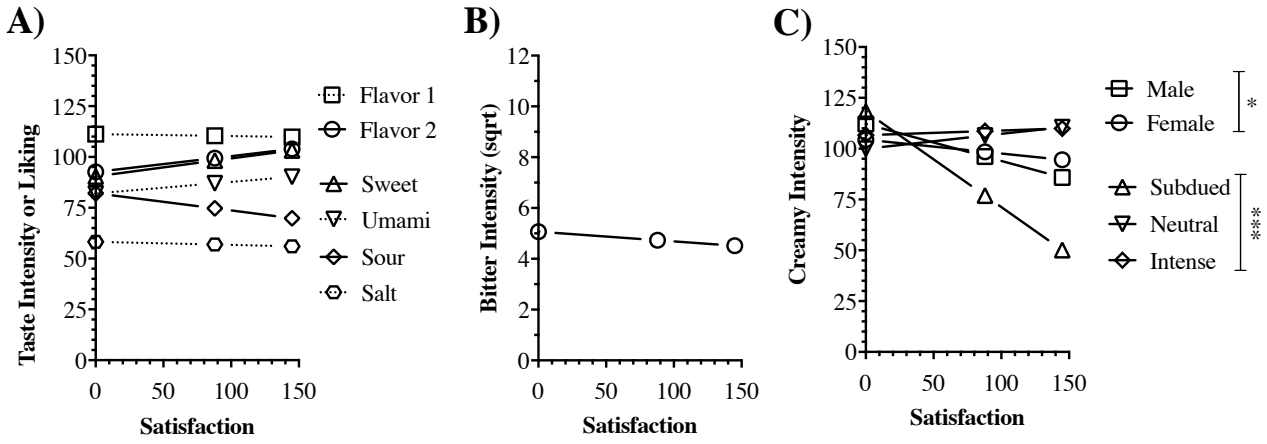

Figure 4.2
Effect of outcome satisfaction on taste intensity and hedonic ratings. Outcome satisfaction and taste intensity and liking ratings evaluated on a 145 mm visual analog scale following college hockey games. 4.2A/4.2B solid lines represent significant regression estimates of the association ($p<0.05$); dotted lines represent non-significant effects ($p\geq0.05$). 4.2C sex (male, female) and atmosphere level (subdued, neutral, intense) modify creamy intensity–outcome satisfaction relationship; statistical significance of the interaction terms: *$p<0.05$, **$p<0.01$, ***$p<0.001$. Effect estimates and SEM at satisfaction lower limit (0.0), mean (88.0), and upper limit (145.0) were obtained from LSM of the regression models. At satisfaction mean=88.0, mean intensity/hedonic ratings (SEM) were: flavor 1 liking 110.4(2.6), flavor 2 liking 99.5 (3.0), sweet 98.2 (2.3), umami 87.0 (4.1), sour 74.7 (3.4), salty 56.9 (3.5), square root bitter: 4.7 (0.3); creamy female 98.5 (3.4), creamy male 96.2 (3.5), creamy subdued 76.9 (8.5), creamy neutral 106.4 (3.5), creamy intense 108.6 (1.9). Sweet n=1021 (repeated measurement), Salty n=512, Umami n=506, Sour n=509, Bitter n=508, Creamy n=512, Flavor 1 liking n=511, Flavor 2 liking n=508.

Interestingly, the hedonic ratings of the overall less-liked flavor 2, but not flavor 1, significantly increased as satisfaction with the game's outcome increased (Figure 4.2A). Consistent with the modulation of sour and sweet tastes observed with the affective manipulation (Table 4.3), the primarily sweet and sour flavor 2 appeared to taste best when satisfaction was highest, and taste worst when satisfaction was lowest. No significant changes were observed in the hedonic ratings of the more-liked flavor 1. This agreed with the results obtained from the outcome analysis (Figure 4.1), where the greatest hedonic ratings for flavor 2 were observed when the home team won and the lowest hedonic ratings were observed when the home team lost. This further supports the effect of outcome satisfaction observed on sour and sweet tastes, as these were the

predominant basic tastes in flavor 2. See **Table 4.4** for more detailed effect estimates and standard errors in each model.

Table 4.3
Regression estimates for effect of game outcome satisfaction on taste intensity and hedonic ratings. Data represents effect estimate, 95% confidence interval (CI) and corresponding p-value from linear regression models. Bitter outcome is square-root transformed. All models adjust for sex, age, flavor serving order, and reported atmosphere and fanaticism, in addition to relevant interactions. Due to missing data and repeated measures (sweet), analyses have different number of subjects: Sweet n=1021 (random subject effect), Salty n=512, Umami n=506, Sour n=509, Bitter n=508, Creamy n=512, Flavor 1 liking n=511, Flavor 2 liking n=508. [A]Outcome satisfaction-taste intensity relationship is modified by sex (male, female) and perceived atmosphere (subdued, neutral, intense); more detail provided in Table 4.3. *Bolded estimates highlight statistical significance at $p<0.05$.

	Estimate (95% CI)	p
Sweet	**0.09 (0.04, 0.14)***	**<0.01**
Umami	0.06 (-0.03, 0.15)	0.22
Salty	-0.02 (-0.09, 0.06)	0.69
Sour	**-0.08 (-0.16, -0.01)**	**0.03**
Bitter	0.00 (-0.01, 0.00)	0.29
Creamy[A]	*Modified*	
Flavor 1 liking	-0.01 (-0.07, 0.05)	0.75
Flavor 2 liking	**0.08 (0.01, 0.14)**	**0.02**

Additional factors influence taste intensity perception

Sweet, salty, and sour taste intensity perceptions were independently influenced by sample order (Table 4.4). Specifically, if the participant evaluated flavor 2 (predominantly sweet/sour) before flavor 1, salty and sour were perceived as less intense compared to the opposite, possibly due to carry over and/or mixture suppression (16). Males rated umami and bitter tastes as more intense compared to females, and lower taste intensities were usually reported with increases in age, especially in bitter taste (Table 4.4).

Table 4.4
Regression estimates of taste intensity and liking linear models. Values represent regression effect estimates and standard error of effect (row) in each taste or liking model (column). The continuous variable bitter was square root transformed. Levels of categorical variables were compared to reference levels (*ref*). Only interaction terms of $p<0.10$ were included in each model; exclusion in the model is indicated by – in cells. Interaction terms that were not significant in all models were not included in this table. Due to missing data, analyses have different number of data points: Sweet n=1021, Salty n=512, Umami n=506, Sour n=509, Bitter n=508, Creamy n=512, Flavor 1 liking n=511, Flavor 2 liking n=508. *Bolded/shaded estimates highlight statistical significance of coefficient at $p<0.05$.

		Sweet	Salty	Umami	Sour	Bitter	Creamy	Flavor 1 Liking	Flavor 2 Liking
Satisfaction		**0.09 (0.03)***	-0.02 (0.04)	0.06 (1.05)	**-0.08 (0.04)**	-0.00 (0.00)	-0.53 (0.13)	-0.01 (0.03)	**0.08 (0.03)**
Age		0.10 (0.11)	0.51 (0.32)	-0.14 (0.12)	0.01 (0.11)	**-0.04 (0.01)**	0.134 (0.12)	**-0.28 (0.08)**	0.13 (0.10)
Gender	Female	-1.92 (2.04)	1.97 (3.34)	**-13.99 (3.59)**	-3.56 (3.33)	**-0.62 (0.31)**	2.00 (2.61)	2.65 (2.40)	-1.91 (3.05)
	Male	*ref*	*ref*	***ref***	*ref*	***ref***	*ref*	*ref*	*ref*
Atmosphere level	Intense	-10.53 (4.89)	-3.63 (8.04)	**-20.61 (8.60)**	8.64 (7.92)	1.73 (0.73)	31.87 (8.65)	**2.85 (5.78)**	2.55 (7.25)
	Neutral	-9.57 (5.09)	-4.53 (8.42)	**-24.66 (8.99)**	2.10 (8.23)	1.36 (0.75)	29.66 (9.21)	**-5.45 (6.04)**	0.34 (7.53)
	Subdued	*ref*	*ref*	***ref***	*ref*	*ref*	*ref*	***ref***	*ref*
Fan level	Huge Fan	1.51 (3.33)	**5.90 (5.53)**	-1.41 (5.91)	9.62 (5.39)	0.45 (0.49)	3.22 (4.29)	**2.88 (3.94)**	2.03 (4.93)
	Neutral	1.51 (3.58)	**3.91 (6.05)**	-2.64 (6.33)	3.19 (5.81)	0.55 (0.53)	-1.35 (4.61)	**-6.81 (4.23)**	0.91 (5.32)
	Not a Fan	*ref*	***ref***	*ref*	*ref*	*ref*	*ref*	***ref***	*ref*
Flavor served first	Flavor 1	1.79 (2.02)	**7.38 (3.33)**	-5.35 (3.56)	**7.01 (3.30)**	0.42 (0.30)	-2.36 (2.60)	3.95 (2.39)	3.03 (3.02)
	Flavor 2	*ref*	***ref***	*ref*	***ref***	*ref*	*ref*	*ref*	*ref*
Satisfaction x atmosphere	Intense	-	-	-	-	-	**0.49 (0.13)**	-	-
	Neutral	-	-	-	-	-	**0.54 (0.13)**	-	-
	Subdued	-	-	-	-	-	***ref***	-	-
Satisfaction x gender	Female	-	-	-	-	-	**0.11 (0.05)**	-	-
	Male	-	-	-	-	-	***ref***	-	-
Age x gender	Female	**-0.33 (0.13)**	-	-	-	-	**-0.59 (0.16)**	-	-
	Male	***ref***	-	-	-	-	***ref***	-	-
Age x fan level	Huge Fan	-	-0.7 (0.35)	-	-	-	-	-	-
	Neutral	-	-0.13 (0.41)	-	-	-	-	-	-
	Not a Fan	-	*ref*	-	-	-	-	-	-
Age x flavor served first	Flavor 1	**-0.28 (0.13)**	-	-	-	-	-	-	-
	Flavor 2	***ref***	-	-	-	-	-	-	-

Discussion

Outcome satisfaction is associated with positive and negative affect

As expected, game satisfaction ratings differed significantly depending on the outcome of the hockey game. Losses were rated as the least satisfactory, wins the most satisfactory, and ties falling between the two. Since VAS satisfaction ratings in the affect validation study negatively correlated with negative affect scores and positively correlated with positive affect, it is likely that the emotional manipulation at the hockey games was due to a change in affect. This true change in affect reflected on the Positive Affect and Negative Affect Schedule in the validation study would have been impractical to fully measure at the hockey games due to the level of concentration needed to complete the questionnaires. However, previous reports support the supposition that wins lead to higher positive affect and losses to higher negative affect (9,11), as our results showed. Our conclusions agree with the widely accepted theory that high positive affect is a state of high-energy, pleasurable engagement and activity, while high negative affect is a state of high-energy, unpleasant engagement and distress (8). Therefore, we propose that it is feasible to use a sporting event, such as the one in this field study, as an effective emotional manipulation to assess how the taste system varies with everyday changes in positive or negative affect.

Perceived taste intensity varies with emotional state

In the main study, satisfaction with the game's outcome was positively associated with sweet intensity ratings and negatively associated with sourness ratings, while there was no significant influence on umami, salty, or bitter tastes. In some cases, a negative association of outcome satisfaction with creamy ratings was also observed. The results demonstrate that taste intensity perception is subject to variation with emotional state elicited by everyday events. This is in line with previous research suggesting that basic tastes can be influenced by changes in affect and stress (1,2). Importantly, our study revealed that affective manipulations associate with

variations in taste in an observational field study, demonstrating its applicability in a real-world setting, as opposed to previous work within a laboratory setting.

The appetitive taste of sweet, as well as the innately aversive sour taste (at high, single stimulus concentrations) is associated with alterations in emotional state. Specifically, our data show that sweet intensity increases with positive affect and decreases with negative affect. An opposite relationship is observed with sour intensity ratings. Since positive affect is generally correlated with pleasurable events and negative affect is linked with stress and coping of unpleasant events (8), it is plausible that experiencing a pleasurable event may correlate with enhanced sweet and diminished sour intensity, while stress or experiencing an unpleasant event may associate with diminished sweet and enhanced sour intensity perception. In agreement of our findings, Heath et al. (6) demonstrated that elevated levels of serotonin (attributed to feelings of wellbeing and happiness) are associated with enhanced sweet acuity, while elevated levels of the stress hormone noradrenaline result in increased sour perception. Furthermore, previous studies demonstrated that mild stressors or negative affect correspond with lower intensity ratings of sweet stimuli (3,4) and mood manipulations associate with a variation in the perceived intensity of sourness (2). Importantly, the results of our study expand upon the conclusions of the aforementioned studies, indicating sour and sweet intensity perception are two dimensional: in addition to the effects seen with negative affect, there is a contrary relationship with positive affect.

Differences in taste intensity perception between sexes and age groups have been reported extensively in the past (23,24). Panelist age significantly influenced perceived sweet, bitter, creamy, and salty intensities, as well as the hedonic ratings of flavor 1, while sex significantly affected sweet, bitter, creamy, and umami acuity, although interaction effects with other variables in the model complicated some of these relationships (Table 4.3). Notably in this study, there was a significant negative association of age with bitter intensity ratings, as reported

previously (25,26). When examining trends among sexes, males of all ages appear to rate bitter and umami as more intense compared to their female counterparts, while older males rate sweet and creamy as more intense compared to females of the same age. This observation is somewhat contrary to a previously reported result from epidemiological study, where females rated all tastes as more intense compared to their male counterparts (27). This supports the notion that taste intensity perception varies not only due to systematic differences between individuals, but also with environmental exposures encountered in everyday life.

Selective modulation of hedonic ratings

Since perceived taste intensities of both appetitive sweet and aversive sour taste were associated with variation in emotion, some shift in hedonics would be expected. Indeed, the more moderately liked flavor 2 was rated as more pleasant after a positive event (a win, higher positive affect) and less pleasant after a negative event (a loss, higher negative affect). It has been suggested that hedonic capacities and food preferences are not stable and can be influenced by emotional state (28,29). As seen in our study, positive emotions may increase hedonic ratings of food, while negative emotions decrease food pleasantness (29,30). It is likely that the increased hedonic value of flavor 2 under positive emotions is driven by the increased sweet and decreased sour intensity perception.

Alternatively, the hedonic ratings of the more pleasantly perceived flavor 1 remained unchanged with varying emotions. Our analysis indicated that flavor 1 had overall greater hedonic scores compared to flavor 2, regardless of outcome ($p<0.0001$). It is possible that we did not observe a significant increase in hedonic scores of flavor 1 due to ceiling effects of the VAS scale. Regardless, our findings are noteworthy as they indicate that the hedonic response of a more liked food may not significantly fluctuate with changes in positive or negative affect, while a less liked food may be perceived as less palatable in times of unhappiness and more palatable in times of happiness.

This result suggests that the emotions experienced in everyday life correlate with variations in hedonic experience of less palatable food, potentially providing a link to emotional eating. Both positive and negative emotions have been shown to influence eating behavior (5,30–32). During times of negative affect in our study, foods of a less pleasurable nature are reported as even more unappealing, whereas more hedonically pleasing foods remain pleasurable. Under negative emotions or stress, it has been proposed that people are more likely to eat hedonically pleasing. These foods are likely unhealthy foods, highlighted by increased preference for palatable and energy-rich snack foods during these times (5,28,32). Previous research suggests that negative affective states associate with eating as a strategy to regulate emotions, by increasing intake of sweet foods (30,33). It is possible that the diminished sweet and amplified sour intensities perceived under negative emotions in this study could explain some of the compensatory increased intake and simultaneous preference for sweet, palatable, and energy-dense foods, although this was outside of the scope of our study.

Limitations

There are notable differences in the circumstances under which the affect validation study was conducted, with an interactive competitive card game task compared to spectators' experiences at college hockey games. However, the hectic environment after the hockey games was not a feasible setting to run an affect validation study, even with a small subset of fans. Supporting our decision to use a card game task, research has shown that a personal success-failure task is feasible to measure the association of outcome satisfaction and positive and negative affect scales in a competitive environment, as team success or failure is often observed as personal success or failure (9). Card game tasks have been demonstrated to induce both positive and negative affect (21), with winners and losers experiencing differing emotions contingent on game outcome (34).

As an observational field study, a potential limitation was that there was less control over the testing environment compared to traditional studies in sensory evaluation centers. Some participants may have been rushed to complete the evaluation in the chaotic environment after the hockey games. However, it is important to note that this possible carelessness or confusion is experienced with any self-report of emotion (20). To control for the potential pitfalls that may be associated with a field study, a large sample size was recruited throughout the season to ensure there was appropriate power to assess variation among affective states. At the same time, the observational nature of our study fills a void in the literature examining the relationship between the taste system and emotion in a nonclinical population under real-life conditions. Oftentimes, laboratory studies do not stimulate complex emotions comparable with those experienced in real life and therefore may be less intense affective reactions (35,36). Importantly, this field study showed real-life emotional manipulations might influence the taste system. Due to the observational nature of the study, these results have greater external validity in assessing the impact of emotional change on taste perception in the general population, and may highlight behavior occurring with emotional variation on a daily basis that could be masked in a laboratory setting. Future research should elucidate the impact of emotional manipulation on the taste system and more specifically how it influences food choice.

Conclusion

The results of our study indicated that real-life emotional manipulations correlate with variations in perceived taste intensities. Positive emotions associated with enhanced sweet and diminished sour intensity perception, while negative emotions showed the opposite. For the flavor that primarily encompassed these sweet and sour tastes (the less-liked flavor), hedonic ratings increased with positive emotions. Therefore, our results reveal that it is plausible that everyday emotional manipulations in the form of pleasurable or unpleasant events could influence our taste intensity perceptions. This may shift the hedonic ratings of less acceptable foods,

suggesting that the interaction of affect and the taste system could play a role in emotional eating.

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CONCLUDING REMARKS

This research valuably contributes to the available evidence elucidating the links between taste and obesity. First, we provided support that those with a weakened sense of taste may desire more intensely tasting foods, a commonly made assumption that lacked empirical evidence. Second, we examined the influence of factors connected to obesity (weight gain, diet, and emotions) on the taste system, again linking variations in taste to food liking, preferences, appetite, and satiation. We return to the schematic diagram that illustrates our findings (**Diagram 2**), highlighting the complex relation between factors related to diet, taste, and human health evaluated in our work.

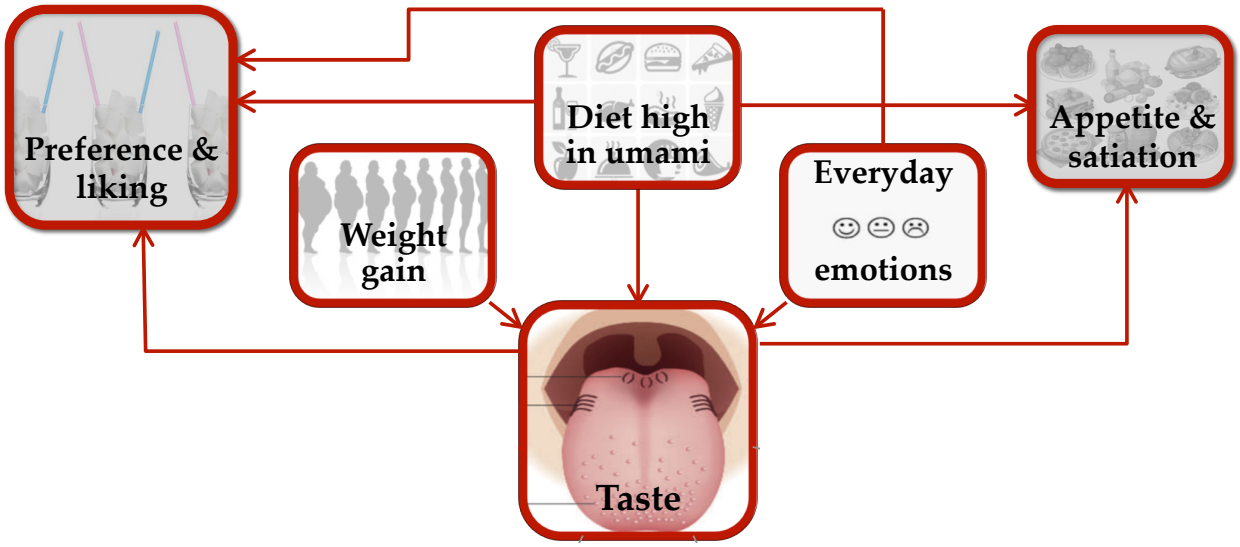

Diagram 2
Taste and health: A complex relationship. Schematic depicts relationships investigated in dissertation research; Red lines show main associations observed between factors, while arrows illustrate hypothesized direction of associations.

Taken together, our work shows that a modest weight gain, a diet high in umami, and everyday experienced emotions correlate with a weakened sense of taste in certain populations. Further, it suggests those with decrements in appetitive tastes gravitate towards more intense, usually

higher calorie foods. These factors also associate with differences in food liking, preferences, and appetite. Since higher caloric intakes are proposed to contribute to insufficient energy balance and obesity (1,2), our research provides support that taste and taste dysfunction should be considered in the complex multicomponent etiology and maintenance of obesity.

Future research should focus on evaluating whether these observed variances in the taste system translate to alterations in dietary intake in free-living populations, and whether the risk of diet-related diseases differs based upon variations in the taste system. It would be beneficial to conduct epidemiological studies examining associations between taste and health outcomes such as cancer, diabetes, and cardiovascular disease. More research would improve generalizability and the ability to detect taste and/or risk differences in nationally representative samples.

Through our work, we have recommendations for future research in taste psychophysics. We consistently observe that males and females perceive tastes differently. In line with this, we see that sex plays an important role in modifying the effect of environmental and biological influences on taste. We urge researchers to evaluate the effect modification of sex on taste outcomes in their analyses. Additionally, it has been previously established that the general Labeled Magnitude Scale (gLMS) reliably detects taste differences in groups of people, although adjustment for scale usage has been suggested to aid in parsing out differences. This was apparent in our research, where scale usage consistently accounted for unexplained variation in the outcome. We recommend that researchers control for variations at baseline (or change over time) in usage of the gLMS by including it as a covariate in statistical models. Finally, due to the abundance of environmental and behavioral factors influencing taste, it is important to control for potentially confounding variables such as diet, sex, and BMI in observational studies. This, along with careful study design, will assist in evaluating variations in taste relating to other biological or environmental factors.

Overall, this body of research contributes to the field of taste psychophysics and human health by highlighting modifiable factors that correlate with variations in taste and corresponding responses to real food. Although there is still much to be understood in the world of taste research, the work described in this dissertation adds to our understanding of the complex relationship between diet, taste, and human health, and clarifies role of the taste system in obesity.

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