Reduced dietary intake of simple sugars alters perceived sweet taste intensity but not perceived pleasantness

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ABSTRACT

Background: Individuals who adhere to reduced-sodium diets come to prefer less salt over time, but it is unclear whether sweet taste perception is modulated by reduced sugar intake.

Objective: The objective was to determine how a substantial reduction in dietary intake of simple sugars affects sweetness intensity and pleasantness of sweet foods and beverages.

Design: Healthy men and women aged 21–54 y participated for 5 mo. After the baseline month, 2 subject groups were matched for demographic characteristics, body mass index, and intake of simple sugars. One group (n = 16; 13 of whom completed key experimental manipulations) was randomly assigned to receive a low-sugar diet during the subsequent 3 mo, with instructions to replace 40% of calories from simple sugars with fats, proteins, and complex carbohydrates. The other (control) group (n = 17; 16 of whom completed the study) did not change their sugar intake. During the final month, both groups chose any diet they wished. Each month subjects rated the sweetness intensity and pleasantness of vanilla puddings and raspberry beverages that varied in sucrose concentration.

Results: ANOVA showed no systematic differences between groups in rated sweetness during the baseline or first diet month. During the second diet month, the low-sugar group rated low-sucrose pudding samples as more intense than did the control group (significant group-by-concentration interaction, P = 0.002). During the third diet month, the low-sugar subjects rated both low and high concentrations in puddings as ~40% sweeter than did the control group (significant effect of group, P = 0.01). A weaker effect on rated sweetness was obtained for the beverages. Rated pleasantness was not affected for either of the stimuli.

Conclusions: This experiment provides empirical evidence that changes in consumption of simple sugars influence perceived sweet taste intensity. More work is needed to determine whether sugar intake ultimately shifts preferences for sweet foods and beverages. This trial was registered at clinicaltrials.gov as NCT02090478.


Keywords: human, low sugar, psychophysics, sucrose, sugar reduction

INTRODUCTION

Simple sugars account for a considerable proportion of energy intake, both in industrialized and developing countries (1, 2). Although it is unclear whether the consumption of sugar within an energy-balanced diet promotes disease, overconsumption of energy-dense foods contributes to obesity (3, 4). Obesity and related health consequences, including type 2 diabetes and heart disease, are leading contributors to morbidity and mortality (3, 4). Thus, the American Heart Association and other health organizations recommend reductions in the intake of added sugars (5–8).

Of course, reducing sugar concentrations in foods and beverages can decrease palatability and consumer acceptance. One strategy to maintain palatability is to replace sugars with non-nutritive sweeteners (9). Unfortunately, nonnutritive sweeteners often have unpleasant side tastes, aftertastes, or a slower onset of sweetness than sugar. Flavors that do not taste sweet but enhance the perception of sweetness (e.g., positive allosteric modulators) are promising but can have some of the same issues as non-nutritive sweeteners (10–12).

Studies of dietary influences on taste perception suggest a potential alternative to replacing sugar. When individuals adopt a lowered-sodium diet for several weeks, they may perceive a given concentration of sodium in food to be more intensely salty than it was before the diet or come to prefer lower concentrations of sodium (13–15). In contrast, increases in salt intake increase preferred sodium concentrations (15, 16). Accordingly, some have proposed that gradual salt reduction might lead to decreases in preferred concentrations and, consequently, lowered sodium intake (17). The intake of fat may affect fat perception in a similar fashion (18, 19). Furthermore, individuals are able to taste lower sugar concentrations as being sweet, and their preferred sugar concentration decreases, after weight loss from bariatric surgery or calorie restriction (20, 21). Furthermore, urban populations in Iraq, who have diets higher in simple sugars than do their rural counterparts, also tend to prefer higher sugar concentrations in tea (22). Although another study failed to find a significant association between the intake of sweet foods and gustatory responses to sugar (23), the findings outlined above provide a solid rationale for examining whether lowering dietary sugar intake affects sweet taste intensity and pleasantness.

We tested the hypothesis that the reduced intake of simple sugars in healthy adults would increase the perceived sweetness

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intensity of fixed concentrations of sugar in foods and beverages and decrease the concentrations rated as most pleasant. Subjects rated intensity and pleasantness of vanilla puddings and raspberry beverages with various sucrose concentrations during each of 5 consecutive months. The first month provided baseline measures. For the subsequent 3 mo, 1 group of subjects (low-sugar) reduced their intake of simple sugars by \( \sim 40\% \), whereas the other group (control) maintained their current sugar intake. During the fifth month, subjects followed the diet of their choice.

**METHODS**

All procedures were approved by an institutional review board (Schulman Associates IRB). Participants provided written, informed consent on institutional review board–approved forms. The protocol is registered at clinicaltrials.gov (NCT02090478).

**Design and subjects**

Participants included healthy (by self-report) men and women aged 21–54 y. All reported consuming at least 2 sugar- or high-fructose corn syrup–sweetened soft drinks per day on average. All were able to select their own foods and control their diets. Exclusion criteria included chronic illness, major illness within the past 6 mo, daily use of medication (except for birth control pills, vitamins, or aspirin), pregnancy, change in body weight of at least 10% within the past 3 mo, and regular use of non-nutritive sweeteners. At the end of the first month, subjects were divided into 2 subsets, matched as closely as possible for age, sex, race, BMI, and proportion of total calories from sugar during the baseline month, as estimated from diet records (see Diet records and diet manipulation). One subset, randomly assigned to a control group, was instructed to maintain their intake of simple sugars for the first 4 mo of the study. The other subset, assigned to a low-sugar group, was instructed to lower their sugar intake by 40% (relative to month 1) during months 2–4. Both of the groups were allowed to follow any diet they wished during the last (fifth) month (Figure 1). The length of the diet manipulation was chosen because 3 mo with a lowered-sodium diet was sufficient to see changes in salt taste perception (13). Although changes in the rated sweetness intensity or pleasantness need not follow the same time course as changes in salt taste, the literature on salty taste offered the most comparable data because they offered the closest available parallel.

Due to the nature of the experiment, participants were aware of the condition to which they were assigned. It was also impractical for the 2 research technicians primarily responsible for executing the experiment to be blinded to group assignment, but several precautions helped mitigate possible bias. First, instruction, training, and the first month of sensory testing were conducted before group assignment occurred. An author who had no previous interactions with participants (LJF) divided the participants into subsets and the subsets were randomly assigned in a blinded manner. Second, sensory tests (see “Primary measures” section below) were conducted in sessions with small groups (\( \sim 4 \)) that included both low-sugar and control subjects. Accordingly, members of both groups received all batches of stimulus materials and group instructions during sensory testing. Third, another author (PMW) conducted blinded spot checks on scoring and entry of sensory responses.

On the basis of a similar study of the influence of sodium intake on salt taste perception (13), power analysis indicated that at least 12 subjects/group would yield a power \( (1-\beta) >0.80 \) (assuming similar effect sizes and \( \alpha = 0.05 \)) for dietary effects on rated pleasantness. Again, there was no assumption that underlying mechanisms for changes in salty and sweet taste are the same. We based the power analyses on sodium reduction data because they offered the closest available parallel.

Experimenters called 187 past participants of Monell Chemical Senses Center studies who had agreed to be contacted with regard to future studies. Fifty agreed to come in for an interview and a consent discussion. Of the 50 candidates, 8 failed to meet the screening criteria and 9 decided not to continue. The remaining 33 were divided into groups of 17 (randomly assigned to serve as controls, as described above) and 16 (randomly assigned to the low-sugar diet). One participant from the control group and 3 from the low-sugar group chose to withdraw before the diet manipulation was complete (i.e., before the end of study month 4). Thus, 13 in the low-sugar group and 16 in the control group completed the critical 3-mo diet manipulation. An additional participant in the low-sugar group withdrew during study month 5 during the return to an unrestricted diet.

Participant characteristics are shown in Table 1. Statistical tests (chi-square tests on sex and race, \( t \) tests on other variables) failed to find significant differences between groups for any characteristic. Although the sample sizes provided limited power, the results suggest that the 2 groups did not differ substantially in any of these characteristics.

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**FIGURE 1** Flowchart summarizing participant recruitment, screening, and experimental manipulation.

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TABLE 1
Baseline characteristics of participants

| Characteristic          | Low-sugar group | Control group | P*
|-------------------------|-----------------|---------------|-------
| n                       | 13              | 16            |       |
| Age, y                  | 36.7 ± 10.2     | 34.4 ± 9.7    | 0.53  |
| Female sex, %           | 53.4            | 56.3          | 0.90  |
| Race, %                 |                 |               | 0.31  |
| African American        | 69              | 56            |       |
| White                   | 23              | 31            |       |
| Other                   | 8               | 13            |       |
| Height, cm              | 168.6 ± 6.7     | 169.0 ± 8.9   | 0.90  |
| Weight, kg              | 73.4 ± 16.7     | 77.6 ± 21.1   | 0.65  |
| BMI, kg/m²              | 26.1 ± 5.5      | 27.4 ± 8.4    | 0.63  |
| Baseline energy, kcal/d | 2422.8 ± 1005.4 | 2193.9 ± 940.8 | 0.53 |
| Calories from sugars, % | 21.9 ± 8.2      | 26.9 ± 8.1    | 0.16  |

*Derived by between-groups comparisons by chi-square test (sex, race, and age) and t test (other variables).

Diet records and diet manipulation
All of the participants were instructed to complete a 7-d food and activity log once each month. They were asked to record the type and amount of all foods and beverages consumed as well as their exercise during the 7-d period. The exercise level was used to help determine calorie needs to maintain energy balance during the study. Each participant was provided with an illustrated portion-size booklet [published by the Fred Hutchinson Cancer Research Center (24)] and received detailed instructions from a registered dietitian (LN). Food/activity records were returned each month and assessed by LN. Total calories and grams of sugar were determined from The Food Processor Nutrition and Fitness Software (version 10.8; ESHA Research) and were used to calculate percentage of calories from sugar by using the following equation: (grams of sugar × 4/total calories) × 100. During the first month, several subjects returned insufficiently detailed food records and were given additional instructions and asked to complete another record.

After the diet records were collected and analyzed for the first (baseline) month, LN designed individualized dietary guidelines and met with each participant. She met with participants again after the first month of the diet manipulation (second study month) to make adjustments as needed and conducted telephone meetings with participants in subsequent months to discuss progress.

Participants in the low-sugar group were provided with detailed instructions to help achieve the target (40%) reduction in calories from simple sugars while maintaining energy balance and adequate nutrition. Dietary changes for this group included replacing high-sugar foods with items higher in complex carbohydrates, protein, and/or fats and diluting sugary drinks (fruit juices, sodas, etc.) by 50% with water or seltzer and consuming the same total volume. Participants were instructed not to replace sugar with nonnutritive sweeteners.

Participants in the control group met with LN to discuss their diet using the same schedule as the low-sugar group, in part to ensure that the control and low-sugar groups had comparable contact time with the dietitian. The control group was instructed to maintain their usual (month 1) diet for the most part, with small changes suggested to achieve adequate nutrition. In particular, the control group was provided with diet recommendations designed to maintain the amount of simple sugars consumed during the baseline month. Both the low-sugar and control groups were instructed not to intentionally lose weight during the study, with accompanying diet recommendations designed to maintain energy balance.

During the 5-mo study, most participants were compliant with instructions to avoid nonnutritive sweeteners. There were a few exceptions. In the control group, 2 participants reported consuming 1 beverage [16 ounces (473 mL) each] containing nonnutritive, artificial sweeteners during study month 4 (month 3 of the diet manipulation). One participant reported consuming 6 ounces (170 g) of yogurt containing artificial sweeteners during study month 2 (first diet month) and again during study month 5 (the final study month). Another control participant reported consuming 2–4 packets of artificial sweeteners daily for 5 d during study month 3 (second month of the diet manipulation). For the low-sugar group, 2 participants reported consuming noncaloric sweeteners. One consumed artificially sweetened coffee creamer once per day for 3 d during month 2 (first week of diet manipulation). A second participant in the low-sugar group consumed one 12-ounce (355 mL) diet cola during study month 2 (first diet month) and consumed one 12-ounce (355 mL) diet cola daily for 6 d during month 5 (the final study month).

Primary measures (taste intensity and pleasantness)
Participants rated sweet taste intensity by marking 117-mm printed general labeled magnitude scales (gLMSs)4 (25). The scales included the following descriptors: “barely detectable” (1.7 mm), “weak” (7.9 mm), “moderate” (21.6 mm), “strong” (41.9 mm), “very strong” (62.2 mm), and “strongest imaginable sensation of any kind” (117 mm). Participants rated pleasantness on a 23-point category scale anchored with the labels “very unpleasant” at −11, “neutral” at 0, and “very pleasant” at +11. Below, the term “pleasantness” refers to these ratings. In addition (as described below), we determined the concentration of each compound associated with the highest pleasantness ratings (which may be thought of as the most preferred concentration). Stimuli included model foods/beverages developed by a company that specializes in novel food products (ESCA Enterprises). During an early training session, subjects received basic instructions on the use of the sensory measures and completed practice trials.

Model sweet stimuli included vanilla puddings and raspberry beverages. The puddings varied in amounts of added sucrose: 0%, 6.6%, 11%, 25%, 31%, 40%, 47%, and 52% by weight. Consistency of mouth-feel across the range of sucrose concentrations was maintained by adding complementary amounts of maltodextrin, which had little, if any, sweet taste. This manipulation resulted in a wide range of sweet intensities without large changes in texture. Pudding samples were presented at room temperature in plastic medicine cups (15-mL aliquots). The model beverages contained tasteless raspberry aroma, pink coloring, and sucrose at a range of concentrations. No other flavors (i.e., acid) were added

4 Abbreviations used: gLMS, general labeled magnitude scale; SGLT, sodium-glucose cotransporter protein; TAS1R3, taste receptor protein type 1 member 3; TAS1R2+TAS1R3, heterodimer of taste receptor protein type 1 member 2 and taste receptor protein type 1 member 3 (G protein–coupled sweet taste receptor).
to avoid changes in additional tastes with changes in sucrose amounts (0%, 2.5%, 5%, 7.5%, 10%, 12.5%, 16%, 19%, and 25% by weight). Again, complementary amounts of maltodextrin were used to maintain oral consistency. Model beverages were presented chilled (~10°C) in 10-mL aliquots in plastic medicine cups. Puddings and beverages were prepared from powder mixes at the testing center on an as-needed basis.

Control (salty) stimuli included broth and soda crackers to determine whether potential effects of modification of dietary sugar amounts were specific to sweet taste. Subjects rated salt taste intensity on the gLMS and pleasantness on the 23-point category scale. The model broth varied in amount of sodium chloride (0.014, 0.06, 0.10, 0.16, 0.25, 0.39, 0.62, and 0.87 mol/L), as did the model soda crackers (0.5%, 1.2%, 2.5%, 4.5%, and 8.5% by weight). Broth samples were presented warm (46°C) in plastic medicine cups in 10-mL aliquots. Cracker samples consisted of a single cracker (0.65 g on average).

Sensory testing occurred during the last 2 wk of each month. Subjects evaluated all concentrations of all stimuli, twice each, over several test sessions. Each session consisted of multiple blocks of trials. Each block consisted of all concentrations for 1 stimulus (e.g., all sucrose concentrations for the pudding samples), in random order. Subjects began each block by rinsing their mouths 4 times with bottled drinking water before tasting the first sample. Subjects chewed solids and moved the stimuli around the mouth for ~4 s, completed all required sensory ratings, then expected the rated sample. After spitting, subjects rinsed their mouths twice with drinking water, then waited for ~30 s before taking the next sample. Within a session, breaks of at least 5 min separated successive blocks of trials. Test sessions for individuals were scheduled on the same days of the week each month, at the same time of day if possible. Subjects were instructed not to eat or drink, except for water, for at least 2 h before a test session.

Secondary measures

Height and weight were measured during month 1. Weight was measured during each month thereafter. BMI was calculated as weight in kilograms/height in meters squared.

Sucrose detection thresholds (i.e., the minimum concentration of sucrose subjects could discriminate from plain water) were measured by using an efficient version of the forced-choice ascending method of limits (26, 27). In each trial, subjects sampled a 10-mL aliquot of sucrose solution and two 10-mL water blanks, in random order. Subjects attempted to determine which sample contained the sucrose solution, guessing if necessary, and rinsed with bottled drinking water between successive trials. Sucrose amounts ranged from 0.0006 to 0.06 mol/L in twelve 1.52-fold concentration steps and were diluted in Millipore-filtered, deionized water. Each stimulus concentration was presented at most once, in ascending order. Concentrations ascended until the subject achieved 3 consecutive correct responses and gave the last correct response with high confidence. Thresholds were defined as the geometric mean of the concentration associated with the first of the 3 consecutive correct trials and the concentration associated with the last incorrect response. Thresholds were measured 4 times each month (i.e., twice in each of 2 test sessions). When thresholds and ratings of model foods and beverages were conducted in the same experimental session, thresholds were always measured first.

Sham thumb scan

A sham test was conducted each month to encourage compliance. Participants were told that experimenters were tracking blood sugar (relative to a baseline measurement made during the first month of the study) by scanning their thumbs with the use of infrared optics. A pad on which subjects placed their thumbs generated clicks and some harmless light effects. A computer monitor showed a trace, with various effects to make the sham test more credible. Subjects were debriefed after the experiment, and none reported having been aware that the test was a sham.

Data analysis

Statistical analyses were conducted by using Statistica software (version 10; Statsoft). Effects of diet were assessed by using mixed within-between-subjects ANOVA models, with a significance criterion of α < 0.05. For all measures, the results of replicate measurements (either rated sweetness intensity or rated pleasantness) were averaged within subjects by using the arithmetic mean. Ratings of sweetness intensity were positively skewed across subjects, as is often true of intensity ratings made with the use of similar methods (25, 28). Accordingly, intensity ratings were log-transformed before inferential analyses. Ratings of pleasantness, which appeared to be more normally distributed, were not transformed before inferential analyses. In addition to analyses of pleasantness, analyses were also conducted on the concentration associated with the highest pleasantness rating over the range of concentrations presented (29). In one set of analyses, second-order polynomials were fit to pleasantness functions for individual subjects. Fitted functions were used to calculate the concentration associated with peak pleasantness. In another, nonparametric set of analyses, the concentration associated with the highest actual ratings was defined as the most preferred (if ≥2 ratings tied for highest, the average of the associated concentrations was estimated). The 2 analyses produced comparable results (approximate correlations of r = 0.80), and ANOVAs on parametric and nonparametric values supported the same conclusions. Accordingly, only the results of the parametric analyses are reported below.

RESULTS

Dietary sugar amounts from diet records

Overall, analysis of the diet records supported a successful diet manipulation (Figure 2). An ANOVA on the percentage of reduction in calories from simple sugars (relative to the baseline month) for the 3 mo of the diet manipulation (treatment group × month) yielded a significant effect of group [F(1, 27) = 25.98, P = 0.0002, ηp2 = 0.49]. The effect of month and the interaction were nonsignificant. An analysis of all months (n = 11 for the low-sugar group, n = 15 for the control group due to missing sensory ratings or diet records for month 5) found a weaker effect of group [F(1, 24) = 12.76, P = 0.002, ηp2 = 0.35] due, in part, to the tendency for subjects in the low-sugar group to increase sugar intake during month 5. The increase in sugar consumption by the low-sugar group is important in interpreting ratings of sweetness during month 5, as discussed later. To facilitate the interpretation of results,
energy and macronutrient intakes by diet month are presented in Table 2.

BMI and weight

BMI and weight were analyzed between the 2 groups by using ANOVA: treatment group (control compared with low-sugar) × month (months 1–5). For both BMI and weight, both the main effects and the interactions were nonsignificant. Although the sample sizes provided limited power, the results suggest that the 2 experimental groups did not differ greatly in BMI and that the diet manipulation did not cause a large amount of weight loss in the low-sugar group (Figure 3).

Sucrose detection thresholds

Thresholds were measured in 2 sessions each month. Test-retest correlations for the 5 mo ranged from 0.39 to 0.71 with an average of 0.52. This level of reliability was within the range expected for an efficient threshold test (27). Replicate threshold measurements for each month were averaged and analyzed by using ANOVA: group (low-sugar compared with control) × month (months 1–5). Both the main effects (P = 0.12 and 0.92, respectively) and interaction (P = 0.41) were nonsignificant. The average (across months) threshold was 0.016 (SD = 0.010) mol/L for the low-sugar group and 0.013 (SD = 0.005) mol/L for the control group. Thus, the diet manipulation had no measurable effect on sucrose thresholds.

Ratings for the added-sugar stimuli

Both the vanilla puddings and the raspberry beverages included a zero sugar concentration (blank) that should be rated as very low in sweetness intensity if the ratings were valid. In preliminary analyses, ratings for the blanks for both stimulus types were analyzed by using 2-factor ANOVAs: group (low-sugar compared with control) × month (months 1–5). In both the pudding and beverage analyses, neither the main effects nor the interactions were significant (P values ranged from 0.26 to 0.93). Intensities were close to “barely detectable” on the gLMS: means ± SDs (across months) were 1.67 ± 0.10 and 2.54 ± 0.52 for the puddings and beverages, respectively. Because the blanks had very little sweetness (as expected), ratings for these zero-sugar-added stimuli were excluded from subsequent analyses.

For the remaining sugar-added stimuli, we first analyzed data for the first 4 diet months (i.e., the baseline month plus the full 3 mo of the diet manipulation). Data from month 5 were analyzed separately for 2 reasons. First, because subjects were not instructed to follow a specific diet, we had no a priori predictions with regard to how the 2 groups might differ during the last (postmanipulation) month (this decision was made before the study began). Second, the last month was difficult to record because of missing diet records for the last month.

In summary, the diet manipulation did not cause a large amount of weight loss in the low-sugar group (Figure 3).

Table 2

Macronutrient intakes across the study

<table>
<thead>
<tr>
<th>Nutrient and group</th>
<th>Study month</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Ethanol, g</td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>5.0 ± 7.2</td>
</tr>
<tr>
<td>Low-sugar</td>
<td>5.1 ± 11.9</td>
</tr>
<tr>
<td>Carbohydrate, g</td>
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</tr>
<tr>
<td>Control</td>
<td>306.4 ± 168.4</td>
</tr>
<tr>
<td>Low-sugar</td>
<td>283.3 ± 84.5</td>
</tr>
<tr>
<td>Fat, g</td>
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</tr>
<tr>
<td>Control</td>
<td>71.6 ± 25.8</td>
</tr>
<tr>
<td>Low-sugar</td>
<td>100.5 ± 73.6</td>
</tr>
<tr>
<td>Protein, g</td>
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</tr>
<tr>
<td>Control</td>
<td>80.3 ± 28.6</td>
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<tr>
<td>Low-sugar</td>
<td>91.3 ± 51.8</td>
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<tr>
<td>Energy, kcal</td>
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</tr>
<tr>
<td>Control</td>
<td>2194 ± 941</td>
</tr>
<tr>
<td>Low-sugar</td>
<td>2423 ± 1005</td>
</tr>
</tbody>
</table>

1Values are means ± SDs; n = 16 for the control group (with the exception of month 5: n = 15), and n = 13 for the low-sugar group (with the exception of month 5: n = 11).

2Based on 1-factor (study month) within-subjects ANOVA.
The 3-factor interaction (group × added-sucrose concentration × month) was also significant \( F(18, 486) = 1.63, P < 0.05, \eta^2 = 0.06 \). Separate 2-factor (group × concentration) ANOVAs for each month did not show significant effects of group or significant interactions for months 1 and 2 (\( P \) values ranged from 0.50 to 0.87). However, for month 3 (second diet month), the interaction was significant \( F(6, 162) = 3.70, P = 0.002, \eta^2 = 0.12 \). The low-sugar group rated low-concentration samples as sweeter than did the control group. The main effect of group was nonsignificant (\( P = 0.32 \)). For month 4
(third diet month), the main effect of group was significant \( F(1, 27) = 7.76, P < 0.01, \eta_p^2 = 0.22 \), but the interaction was nonsignificant \( (P = 0.44) \). Across concentrations, the low-sugar group rated the pudding samples as \( \sim 40\% \) more intense than during month 1 (Figure 5). In short, the 2 groups did not differ during the baseline month or during the first month of sugar restriction, but low-sugar subjects began to rate weak samples as more intense during the second month of sugar restriction and rated a wide range of samples as more intense during the third month of sugar restriction.

Ratings for the beverage samples

Group differences were more modest for ratings of beverage sweetness but were consistent with rated sweetness for the pudding samples (Figure 4, second row of graphs). The low-sugar group rated low concentrations of the beverages as sweeter than did the control group during month 4 (the last month of sugar reduction), and no systematic differences in pleasantness ratings were apparent.

Ratings of sweetness were analyzed by using a 3-factor ANOVA: group (low-sugar compared with control) \( \times \) added-sucrose concentration (8 amounts) \( \times \) month (diet months 1–4). The effect of sucrose concentration was significant \( F(7, 189) = 102.93, P < 0.00001, \eta_p^2 = 0.79 \). Again, ratings of sweetness faithfully tracked relative sucrose concentration. The other main effects of group and month were not significant \( (P = 0.66 \) and 0.18, respectively). The month \( \times \) group interaction was marginal \( F(3, 81) = 1.66, P = 0.06, \eta_p^2 = 0.086 \). Further analyses (2-factor ANOVAs for each month) did not find significant main effects or interactions for months 1–3 \( (P \) values ranged from 0.40 to 0.75). For month 4, the effect of group was marginal \( F(1, 27) = 3.57, P = 0.07, \eta_p^2 = 0.12 \); nominally, the low-sugar group rated samples as sweeter than did the control group overall. The sugar concentration \( \times \) group interaction was significant \( F(7, 189) = 3.50, P < 0.002, \eta_p^2 = 0.11 \); the low-sugar group rated the lower concentrations of added sucrose as sweeter than did the control group.

Ratings of pleasantness were analyzed by using a parallel ANOVA. The effect of sugar concentration was significant \( F(7, 189) = 8.34, P < 0.00001, \eta_p^2 = 0.24 \). A significant quadratic trend \( F(1, 27) = 38.34, P = 0.00001 \) indicated that pleasantness was nonlinear with respect to concentration (Figure 6, second row of graphs). No other effect was significant \( (P \) values ranged from 0.28 to 0.84). In a group \( \times \) month ANOVA on the most preferred concentration, neither the main effects nor the interaction was significant \( (P \) values ranged from 0.67 to 0.98). The most preferred concentrations [averaged across months \( (\pm SDs) \)] were 13.46% \( \pm 5.54\% \) sucrose for the low-sugar group and 13.88% \( \pm 4.79\% \) sucrose for the control group. Thus, the diet manipulation had no measurable effect on ratings of pleasantness for the model beverages.

Effects of the diet manipulation on rated sweetness during diet month 4 were no longer apparent during the month after the diet manipulation. Ratings of sweetness during study month 5 were submitted to a group \( \times \) concentration ANOVA. Neither the main effect of group nor the interaction was significant \( (P = 0.53 \) and 0.87, respectively). A parallel ANOVA on ratings of pleasantness also did not show a significant effect of group or a significant concentration \( \times \) group interaction \( (P = 0.48 \) and 0.95, respectively), and a between-subjects \( t \) test showed no significant effect of group for the most preferred concentration \( (P = 0.54) \).

Ratings of the added-salt stimuli

Ratings for cracker samples

As expected, the diet manipulation had no apparent effects on ratings of the cracker samples (Figure 4, third row of graphs). Log-transformed ratings of saltiness were analyzed by using a 3-factor ANOVA: group (low-sugar compared with control) \( \times \) sodium

![FIGURE 5](image-url)
The effect of sodium chloride concentration was significant \( F(4, 108) = 173.29, P < 0.00001, \eta^2 = 0.87 \). Ratings of saltiness faithfully tracked relative sodium chloride concentration. The other main effects and the interactions were not significant (\( P \) values ranged from 0.15 to 0.93). Ratings of pleasantness were analyzed by using a parallel ANOVA. The effect of sodium chloride concentration was significant \( F(4, 108) = 15.51, \eta^2 = 0.58 \).
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A significant quadratic trend \( F(1,27) = 35.84, P = 0.000002 \) indicated that pleasantness ratings were nonlinear with respect to concentration (Figure 6, third row of graphs). The effect of group and all interactions involving group were not significant (\( P \) values ranged from 0.32 to 0.49). Furthermore, in a month × group ANOVA on the most preferred concentration, neither the main effects nor the interaction was significant (\( P \) values ranged from 0.54 to 0.92). The most preferred concentrations [averaged across months (±SD)] were 2.17% ± 0.86% NaCl for the low-sugar group and 2.14% ± 1.21% NaCl for the control group.

There were also no effects of group during study month 5 (after the diet manipulation). Ratings of saltiness during study month 5 were analyzed by using a group × concentration ANOVA. Neither the main effect of group nor the interaction was significant (\( P = 0.32 \) and 0.97, respectively). A parallel ANOVA on ratings of pleasantness did not show a significant effect of group or a significant concentration × group interaction (\( P = 0.90 \) and 0.71, respectively), and a between-subjects \( t \) test showed no significant effect of group for the concentration associated with the highest pleasantness rating (\( P = 0.64 \)).

Ratings for broth samples

The diet manipulation also had no apparent effect on ratings of broth samples (Figure 4, bottom row of graphs). Log-transformed ratings of saltiness were analyzed by using a 3-factor ANOVA: group (low-sugar compared with control) × sodium chloride concentration (8 amounts) × month (diet months 1-4). The effect of salt concentration was significant \( F(7, 189) = 176.57, P < 0.00001, \eta_p^2 = 0.87 \). Ratings of saltiness faithfully tracked relative sodium chloride concentration. The other main effects and the interactions were not significant (\( P \) values ranged from 0.14 to 0.86). Ratings of pleasantness were analyzed by using a parallel ANOVA. The effect of sodium chloride concentration was significant \( F(7, 189) = 47.28, P < 0.00001, \eta_p^2 = 0.64 \). A significant quadratic trend \( F(1, 27) = 96.33, P < 0.00001 \) suggested that pleasantness was nonlinear with respect to concentration (Figure 6, bottom row of graphs). The effect of group and all interactions involving group were not significant (\( P \) values ranged from 0.10 to 0.81). Furthermore, in a month × group ANOVA on the most preferred concentration, neither the main effects nor the interaction was significant (\( P \) values ranged from 0.19 to 0.45). The most preferred concentrations [averaged across months (±SDs)] were 0.19 ± 0.10 mol NaCl/L for the low-sugar group and 0.18 ± 0.06 mol NaCl/L for the control group.

There were also no effects of group during study month 5 (after the diet manipulation). Ratings of saltiness during study month 5 were analyzed by using a group × concentration ANOVA. Neither the main effect of group nor the interaction was significant (\( P = 0.67 \) and 0.48, respectively). A parallel ANOVA on ratings of pleasantness also did not show a significant effect of group or a significant concentration × group interaction (\( P = 0.51 \) and 0.68, respectively), and between-subjects \( t \) tests showed no significant effect of group for the most preferred concentration (\( P = 0.80 \)).

**DISCUSSION**

Relative to a control group who were instructed not to change their intakes of simple sugars, the experimental group rated the pudding samples as sweeter after 2–3 mo following a diet with a substantially lowered sugar intake. A similar but weaker effect was seen for the beverage samples. These results are consistent with our hypothesis that lowering the intake of simple sugars would increase the perceived sweetness of sugar-added foods. A second prediction, that there would be a parallel change in the sucrose concentration rated as most pleasant, was not supported by the data.

Of course, we may have failed to see significant effects on ratings of pleasantness because of greater variability in pleasantness ratings than in intensity ratings. As others have observed (29, 30), individuals differ not only in the magnitude of pleasantness ratings but also in how pleasantness changes with concentration. Some participants showed classic quadratic trends with a clear optimal level, whereas others showed monotonic increases in pleasantness as sucrose concentration increases. These differences could make it more difficult to observe significant effects of diet group for ratings of pleasantness. If pleasantness truly was not affected by the diet manipulation, even though rated intensity was, then the result would be inconsistent with the idea that sweet intensity drives pleasantness (31, 32). Furthermore, in this study there were differences between the 2 groups in overall pleasantness even before the diet manipulation, without corresponding differences in rated intensity. The 2 groups were matched on demographic and biometric criteria rather than on psychophysical responses. Because all of the subjects were treated the same before the diet manipulation, initial differences in rated pleasantness between groups could be a quirk of group assignment.

**Potential mechanisms**

The mechanisms that underlie sweetness enhancement for participants in the low-sugar group remain unclear. That ratings of salt were unaffected suggests that the enhancement may be specific to sweet taste (although a broader array of stimuli would be needed to firmly establish specificity). If so, sweet taste transduction mechanisms would be reasonable candidates: for example, changes in expression of heterodimer of taste receptor protein type 1 member 2 and taste receptor protein type 1 member 3 (TAS1R2+TAS1R3; heterodimeric sweet receptor protein) or changes in the second messenger cascade. To the best of our knowledge, no published studies have examined the effect of dietary sugar on sweet transduction mechanisms in the mouth. However, rats made obese by being fed a high-fat diet showed decreased expression of taste receptor protein type 1 member 2 and taste receptor protein type 1 member 3 (TAS1R2+TAS1R3; component of the sweet receptor) in taste buds relative to nonobese controls, which shows that diet or the metabolic consequences thereof can affect receptor expression (33; also see 34). Sodium-glucose cotransporters (SGLTs), which are expressed in both the intestine and in taste receptor cells, may also play a role in transduction of simple sugars (35, 36). In mice, a high-sugar diet upregulated the expression of SGLT type 1 in the gut, a process dependent on TAS1R3 and α-gustducin (37). Accordingly, dietary effects on sweet transduction mechanisms are plausible.

On the other hand, if peripheral mechanisms are responsible for the observed sweet taste enhancement, we might expect that all sucrose-containing stimuli would be affected in a similar fashion. In this case, the finding that sweetness enhancement seemed more robust for the pudding samples than for the beverages is more difficult to explain, but research suggests that there
may be some differences in how solids and liquids are processed. In particular, beverages tend to be less satisfying than calorie-matched solid foods and have different effects on postprandial sugar metabolism (38–40). Furthermore, the beverages may have been less realistic models than the pudding samples. The highest amounts of sucrose made the beverages somewhat viscous, with the approximately matching oral consistency at all concentrations due to added maltodextrin. The lack of acids or other flavorings one would expect in a fruit drink may also have given the model beverages atypical sensory properties. Thus, the beverages may have provided a somewhat different context relative to typical items in subjects’ diets.

With regard to context, short-term studies have shown that the perceived intensity of sweeteners is influenced by the distribution of sweetness amounts in stimulus sets. That is, when the intensity of a particular concentration of sucrose is judged in the context of many sweeter concentrations, it is judged to be less intense than when it is judged when presented together with many less-sweet concentrations (32). Such context effects are seen with many classes of stimuli and may play a role in the sweetness enhancement observed in the current experiment. However, in short-term studies, the optimal (most preferred) concentration of sweetener shifts in parallel with intensity (32), whereas no systematic shift in pleasantness ratings was observed in the current experiment. Furthermore, shifts in intensity only occurred after 2–3 mo with a low-sugar diet, whereas classic context effects can be observed within a single experimental session. Accordingly, a low-sugar diet may function as a low-sweetness context, but it is unclear how the current results relate to classic context effects.

Future work

One important research need is to replicate the effect with larger subject samples. Having verified sweetness enhancement associated with a low-sugar diet, it would be informative to study nonnutritive sweeteners to help determine whether the observed effects are driven by sweetness per se or by exposure to simple sugars. To simplify the current experiment, we chose subjects who did not typically use nonnutritive sweeteners, instructed them not to use such sweeteners during the diet manipulation, and replaced sugar calories with fats, protein, and complex carbohydrates to maintain calorie balance. Future work could determine whether a low-sugar diet also affects the taste of nonnutritive sweeteners and whether replacing dietary sugar with nonnutritive sweeteners during a diet manipulation counters sweetness enhancement. Other studies could begin to differentiate between taste and postingestive effects by using encapsulated stimuli (e.g., subjects could swallow sugar capsules to maintain dietary sugar levels while reducing perceived sweetness). Parallel diet manipulations in animal models could facilitate studies of receptor expression and other molecular mechanisms, although it may also be possible to observe peripheral effects in humans with the use of tongue biopsy. Functional imaging might also elucidate potential central effects.

Practical significance

Can people grow accustomed to lower amounts of dietary sugar, eventually accepting lower amounts of sugar in their foods and beverages? On the one hand, the observed changes in perceived intensity are encouraging and warrant further investigation. However, the lack of an effect on hedonic ratings leaves some doubt with regard to how the observed changes in perceived intensity would affect eating behavior (41). Of course, the relation between hedonic ratings and actual consumption is itself a complicated issue (42–44). In addition, when allowed to choose their own diet during diet month 5, subjects in the low-sugar group quickly increased their sugar intake [month 5 sugar amounts were close to baseline (month 1) amounts] and the sweetness enhancement effect was no longer apparent. Would one obtain more robust and lasting effects with a more extended diet manipulation, with a more drastic reduction in sugar intake, or with a more gradual reduction in sugar intake? These are open questions, the answers to which will help determine the practical potential of using lower-sweet diet manipulations as a strategy for ultimately reducing added sugar in our diets while maintaining palatability.

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