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Modulation of sweet preference by the actual and anticipated consequences of eating

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Running header: ‘sweet-calorie learning’ in humans

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Abstract

Previous research has shown that non-human animals exhibit an inverted-U pattern of sweet preference, with consumption increasing across moderate levels of sweetness and then declining for high levels of sweetness. In rodents, this pattern reflects an avoidance of the postingestive effects of consuming energy-dense sugar solutions (conditioned satiation). Here, we examined whether humans also adjust their preferences to compensate for the anticipated energy content / satiating outcomes of consuming sweetened foods. In two experiments (each N = 40), participants were asked to taste and imagine eating small (15 g) and large (250 g) portions of five novel desserts that varied in sweetness. Participants evaluated the desserts' expected satiety, expected satiation, and expected sickliness. A measure of estimated energy content was also derived using a computerized energy compensation test. This procedure was completed before and after consuming a standard lunch. Across both experiments, results confirmed that participants preferred a less sweet dessert when asked to imagine eating a large versus a small portion, and when rating the dessert in a fed versus fasted state. We also obtained evidence that participants anticipated more energy from the sweeter desserts (even in Experiment 2 when half of the participants were informed that the desserts were equated for energy content). However we found only partial evidence for anticipated satiation—expected sickliness was related systematically to increases in sweetness, but expected satiation and expected satiety were only weakly influenced. These findings raise questions about the role of sweetness in the control of food intake (in humans) and the degree to which 'sweet-calorie learning' occurs in complex dietary environments where sweetness may actually be a poor predictor of the energy content of foods.

Keywords: Satiation; Satiety; Sweet taste; Preference; Expected satiation

Introduction

Over many years researchers have shown considerable interest in the role of sweetness in the control of energy intake and bodyweight. Infants and other mammals show an inherent liking for sweetness that is present from birth (Steiner 1979, Ventura and Mennella 2011). Presumably this liking for sweetness is beneficial when sugar-rich carbohydrates are rarely encountered (Breslin and Spector 2008, Breslin 2013). However, in modern Western environments where sugar-containing foods are abundant, preference for sweet foods and drinks is often implicated in the etiology of obesity (Ludwig, Peterson et al. 2001, Salbe, DelParigi et al. 2004).

Sweet foods are generally expected to stimulate intake because they are palatable. However, research in rodents has shown that preference for a food depends not only on its taste but also on its anticipated postingestive effects. Preferences can be acquired over time as the animal learns to anticipate the nutritive and satiating effects of a food (Myers and Sclafani 2006). These learned preferences can then be further modified by moment-to-moment changes in hunger state, with satiation tending to inhibit intake. For instance, in two-bottle preference tests, rats will prefer the sweeter of two sucrose solutions when the postingestive effects of eating are minimal (i.e., when given only brief access to the stimuli or when both solutions are low in energy content), but will shift their preference to the less-sweet solution when the postingestive demands of eating are increased (i.e., in 24-hr intake tests or when the sweeter solution is particularly energy dense) (e.g., (Booth, Lovett et al. 1972, Warwick and Weingarten 1996).

This reduced preference for highly-sweet stimuli may reflect a form of *conditioned satiation*—a learned avoidance of the aversive satiating effects of consuming high-energy sugar solutions, particularly when the animal is already in a food-sated state (c.f., (Booth, Lovett et al. 1972, Warwick and Weingarten 1996). Because sweetness is correlated with the amount of energy provided by sugar, the animal learns to associate increased sweetness with increased energy content and, thus, consumes less of the sweeter solution to avoid over-satiation. This interpretation is supported by flavour-conditioning studies conducted in rats (Sclafani and Ackroff 2004) which have shown that high-energy stimuli can have aversive satiating effects that retard the development of flavor preferences. Together, these findings suggest that rats can learn to use increased sweetness as a predictor of satiation (conditioned satiation), and will moderate their preference for sweet foods depending on their current satiety state.

Although this idea has not been tested formally in humans, there is some evidence that they also rely on ‘sweet-calorie learning’ to predict and guide food intake. For example, sweet foods and fluids may become less desirable when the individual is replete (Cabanac 1971, Cabanac and Fantino 1977, Looy and Weingarten 1991, Laeng, Berridge et al. 1993). It is possible that this reduction in the reward value of sweet foods when satiated may be governed, at least in part, by learned associations between sweetness and energy content. In support of this idea, participants will often prefer an intensely-sweet food in a ‘taste-and-spit’ test (that provides minimal postingestive feedback), but will shift to preferring a less-sweet food when they are required to swallow the sample or consume an entire portion (Mattes and Mela 1986, Lucas and Bellisle 1987, Zandstra, de Graaf et al. 1999).

These studies suggest that, like rats, people expect different postingestive effects from different levels of sweetness. To the authors’ knowledge: (1) no study has explicitly tested this hypothesis, and (2) it remains unclear whether these expectations impact preference for an optimal level of sweetness. In two studies, we explored these ideas by examining whether participants’ preferred level of sweetness (hereafter referred to as ‘optimal sweetness’) of a novel dessert changes in anticipation of different postingestive (PI) effects. Participants were asked to imagine consuming the novel dessert in two different portion sizes (small or large), while under two different levels of food deprivation (fasted and fed). This generated three levels of ‘PI demand’: a small portion consumed in a fasted state (Min PI), a large portion consumed in a fasted state (Med PI), and a large portion consumed in a fed state (Max PI). We predicted that individuals would shift their preference away from highly sweet foods and towards less sweet foods as the PI demands of eating were increased—this would indicate anticipatory compensation for the presumably higher energy content of sweeter desserts and be suggestive of ‘sweet-calorie learning’ in humans.

Studies from our lab (Brunstrom, Shakeshaft et al. 2008, Brunstrom and Rogers 2009, Wilkinson, Hinton et al. 2012, Brunstrom 2014) and others (Forde, Alexander et al. 2011) have demonstrated that people can reliably discriminate between foods based on an anticipation of their postingestive consequences. The ‘expected satiety’ (anticipated absence of hunger) and ‘expected satiation’ (fullness anticipated at the end of a meal) generated by foods appears to vary considerably (Brunstrom, Shakeshaft et al. 2008, Brunstrom and Shakeshaft 2009) and it changes as a food becomes familiar (Brunstrom, Shakeshaft et al. 2010, Irvine, Brunstrom et al. 2013). On this basis, people have been shown to discriminate between foods that are otherwise very similar (Hogenkamp, Brunstrom et al. 2012, Ferriday, Bosworth et al. 2016). These expectations are important, because they predict the energy content of self-served portions (Brunstrom and Rogers 2009, Brunstrom and Shakeshaft 2009) and the amount of food that is subsequently consumed (Wilkinson, Hinton et al. 2012). Thus, we also assessed ratings of expected satiation and expected satiety, and included a novel measure of expected “sickliness” in this study. This allowed us to determine whether any preference shifts might be attributed to an “avoidance” of the greater expected satiety associated with eating the sweetest desserts. We also explicitly assessed whether participants believed the sweeter desserts contained more energy than the less-sweet desserts using a computer-based energy compensation task.

Experiment 1

Method

Participants

Forty individuals were recruited from the University of Bristol (UK) and from the surrounding community to participate in an experiment investigating the "sensory evaluation of novel foods". Participants were 29 females and 11 males (Age: *M* = 20.88 years, *SD* = 4.34). Body mass index (BMI) ranged from 17.72 – 31.33 kg/m^2 (*M* = 22.64, *SD* = 2.85). Participants received either £15 Sterling or class credits for their assistance. Ethical approval was obtained from the local Faculty of Science Human Research Ethics Committee.

Design and Procedure

Participants attended a single 'taste test' session lasting approximately 90 minutes at the Nutrition and Behavior Unit. Sessions were scheduled between 11:30 – 13:00 or 13:30 – 15:00 and participants were told that lunch would be provided. During the session, participants were asked to rate a series of novel dessert products that varied in their sweetness intensity; all desserts were matched for energy content but this fact was not made known to the participants. Participants were asked to refrain from eating and from drinking anything other than water for three hours prior to the test session. Upon arrival, participants read an information sheet and completed a consent form, and provided baseline appetite ratings.

Each participant was then presented with a tray containing a 15 g taster pot of each of the five desserts (presentation order of the five desserts was counterbalanced across participants). Participants were first instructed to sample each dessert and to rate its sensory characteristics (sweetness, thickness). Next, participants were asked to evaluate what it would be like to eat different amounts of each dessert. Participants were shown a small (15 g) and a large (250 g) portion of each dessert in a glass dish. Using these visual aids, participants were instructed to consume a mouthful from each 15 g taster pot and to imagine consuming the small and large portion size. Participants were instructed to take into account *both* its sensory characteristics (sweetness) and the size of the portion (small or large), in order to evaluate four dimensions: 1) expected enjoyment; 2) expected satiety, 3) expected satiation, and 4) expected sickliness (see below for details). The small and large portions were presented in a counterbalanced order across participants. After completing all of the ratings for the first dessert, they rinsed their mouth with water and repeated the procedure on the next dessert in the series until all five desserts had been evaluated. The participants then completed a computerized energy compensation task (described below).

Participants were then given a standard 550-kcal lunch (bacon, lettuce and tomato sandwich and a 25 g packet of salted potato chips) which they were instructed to consume in its entirety. Twenty minutes after consuming the meal, the participants re-rated their appetite, re-evaluated the desserts as described above, and repeated the computerized energy compensation task. Measures taken before both before and after lunch enabled us to assess how responses to the sweet desserts differed across three levels of ‘PI demand’: a small portion consumed in a fasted state (Min PI), a large portion consumed in a fasted state (Med PI), and a large portion consumed in a fed state (Max PI). At the end of the experiment, a measure of height and weight was taken.

Novel desserts

Five gelatinous desserts were formulated using a novel combination of skimmed powdered milk, maltodextrin glucidex® 19, caster sugar (sucrose), and a commercial thickening agent (Instant ClearJel®, Bako Western, Devon, U.K.). Truvia®, a ‘zero-calorie’ sweetener derived from the extract of the stevia leaf, was added to this mixture to produce five desserts that were equated for energy content and differed only in their sweetness intensity (levels 1-5): 0% Truvia, 2% Truvia, 4% Truvia, 16% Truvia, & 16% Truvia + 0.2% sucralose. Participants sampled 15 g ‘taster portions’ of the desserts, presented in clear plastic pots (25 ml). The ingredients and macronutrient composition of these desserts are provided in **Table 1**.

Measures

Appetite: Hunger and fullness was assessed at the start of the session and after the fixed portion lunch using a 100-mm visual-analog scale (VAS): "How hungry / full [as appropriate] do you feel right now?" Ratings were anchored with the labels 'Not at all' and 'Extremely'.

Sensory ratings: Participants were presented with a 15 g taster portion of each dessert (5 portions in total). In turn, they tasted each dessert and evaluated its sweetness and thickness using a 100-mm VAS: "How sweet / thick [as appropriate] is this dessert?" (anchored: 'Not at all' and 'Extremely'). The thickness rating was included to assess differences in perceived viscosity that might otherwise influence judgments of expected satiety and expected satiation (Hogenkamp, Stafleu et al. 2011, Hogenkamp, Mars et al. 2012). To control for order effects the presentation order of the five desserts was counterbalanced across participants according to a balanced Latin-square design.

Sweet preference: While viewing a small (15 g) or a large (250 g) portion of dessert as a visual aid, participants evaluated how much they would enjoy consuming different amounts of each dessert using a 100-mm VAS: "How much would you enjoy eating this portion of food right now?" (anchored: 'Extremely Dislike' and 'Extremely Like'*).* The dessert (1-5) that received the highest rating was identified as the 'optimal sweetness level' for a given portion size. This optimal sweetness level (1-5) was the primary measure for our analysis of sweet preference.

Anticipated satiation, satiety, and sickliness: While viewing a small (15 g) or a large (250 g) portion of dessert as a visual aid, participants evaluated the postingestive effects of consuming different amounts of each dessert using the following 100-mm VAS ratings: Expected satiety - "If you ate this portion of food right now, how long would it take until you were hungry enough to eat again?" (anchored: '30 min' and '4 hours'); Expected satiation - "How full would you feel if you ate this portion of food right now?" (anchored: 'Not at all' and

‘Extremely’); Expected sickliness - “How sickly would you feel if you ate this portion of food right now? (anchored: ‘Not at all’ and ‘Extremely’). This question was included to assess other aversive effects of eating the dessert that were not captured in other measures.

Computerized energy compensation task: A more direct measure of ‘sweet-calorie learning’ was obtained using a hypothetical preload compensation test. Participants were asked to *“imagine that you are on a strict diet and have just 'cheated' by consuming one of the desserts (1-5) as an afternoon snack”*. Participants’ attention was directed to a 250 g portion of the dessert that they were instructed to use as a visual cue representing the ‘snack’. Participants were then shown an image of a meal (500 kcal) on a computer screen and were told to imagine that they would be eating it later that evening. However, *“…in order to not exceed your daily calorie limit, you need to reduce the amount of food you eat at dinner [on the screen] in order to adjust for the number of calories that were in the snack.”* In response, the participants sampled the appropriate taster pot and then adjusted the portion size on the screen using the left and right arrow keys on the keyboard. The task was completed twice, with two different evening meals; chicken tikka masala and spaghetti Bolognese. For each meal, a set of images was taken using a high-resolution digital camera. Each was photographed 50 times (numbered 1-50) on the same white plate (255-mm diameter). Lighting conditions and viewing angles were maintained in all photographs. Portions were presented in 20 kcal steps ranging from 20 kcal (smallest portion) to 1000 kcal (largest portion). Meals were presented in a randomised order. The participants adjusted the portion using the left and right arrow keys on the keyboard using a method of adjustment (Brunstrom and Rogers 2009). Depressing the left arrow-key (on the keyboard) caused the portion size displayed on screen to decrease (a smaller picture number was displayed). Depressing the right arrow-key caused the converse. The pictures were loaded with sufficient speed that continuous depression of the left or right arrow key gave the appearance that the change in portion size was 'animated.' Participants were instructed to press the 'Enter' key when they had selected an appropriate portion size. For each of the desserts, meal size was computed by calculating the average size of the test meal (kcal) that was selected across chicken tikka masala and spaghetti Bolognese.

Statistical analysis

To ensure that the 550-kcal lunch produced a reliable increase in fullness, we assessed changes in appetite (pre- to post- lunch) using paired-samples *t*-tests. Sensory ratings (e.g., thickness, sweetness) were analyzed with repeated-measures ANOVAs with Deprivation State (Fed, Fasted) and Sweetness Level (1-5) as within-subjects factors to ensure that participants could discriminate the sweetness levels of the five desserts. The key measure in this study was optimal sweetness, which was derived from the anticipated enjoyment ratings associated with consuming a small portion in a fasted state (Min PI); when consuming a large portion in a fasted state (Med PI); and when consuming a large portion in a fed state (Max PI). The dessert (1-5) that received the highest anticipated enjoyment score was selected as the 'optimal' level of sweetness for that particular PI state. Three participants gave the same enjoyment rating for two desserts (dessert 3 and dessert 4 were given the same VAS rating); on these occasions, the highest level of sweetness was chosen as the participants 'optimal' level of sweetness. To examine the extent to which optimal sweetness changed with PI demand, optimal sweetness scores were analyzed using a repeated-measures ANOVA with PI demand (Min, Med, Max) as a within-subjects factor. We predicted that optimal sweetness would decline with increased PI demand.

To complement this analysis and to obtain evidence of anticipated satiety, we examined whether our participants anticipated a greater postingestive effect from sweeter samples. Using the expected sickliness, expected satiation, and expected satiety VAS ratings that were collected for the large portion of dessert, we conducted repeated-measures ANOVA with Deprivation State (Fed, Fasted) and Sweetness Level (1-5) as within-subjects factors. In this analysis, we predicted that ratings of expected sickliness, satiation and satiety would be higher for sweeter desserts (*i.e.*, a main effect of sweetness).

We also assessed whether participants believed that the sweeter desserts contained more energy than the less-sweet desserts using a computerized energy compensation task. The meal size (average portion size of the test meal, in kcal) participants selected after tasting each of the novel desserts was entered into a repeated-measures ANOVA with Deprivation State (Fed, Fasted) and Sweetness Level (1-5) as within-subjects factors. We expected that participants would select a smaller meal (kcal) in response to the sweeter 'preload'.

Results

Hunger manipulation

Participants arrived at the lab moderately fasted and hungry (baseline hunger (in millimeters): *M* = 65.1, *SD* = 16.8; baseline fullness (in millimeters): *M* = 20.4, *SD* = 16.8). After consuming the test food, hunger was reduced (*M* = 13.5, *SD* = 12.6; *t*(1, 39 = 17.2, *p*<.0001) and fullness was increased (*M* = 73.8, *SD* = 17.5; *t*(1, 39) = 15.7, *p*<.0001).

Sensory ratings

As shown in **Figure 1**, sensory ratings confirmed that the desserts indeed differed in their perceived sweetness (range 33.3 mm - 84.6 mm; main effect of Sweetness Level, F(4, 156) = 62.32, $p < .0001$, $\eta_p^2 = 0.62$). *Post-hoc* Newman-Keuls test confirmed that all desserts significantly differed from one another in sweetness (*p*'s ≤ 0.01). Participants rated all of the desserts as slightly sweeter after lunch (main effect of Deprivation State, F(1, 39) = 9.87, $p < .01$, $\eta_p^2 = 0.20$), but this occurred irrespective of sweetness level (NS Deprivation State x Sweetness Level Interaction (F(4, 156) = .619, $p = .65$, $\eta_p^2 = 0.02$).

Thickness ratings were also collected in order to account for any differences in texture across the five desserts. Unexpectedly, we found a significant main effect of Sweetness Level (F(4, 156) = 13.15, $p<.0001$, $\eta_p^2 = 0.25$) on perceived thickness. Respectively, for desserts 1 - 5, perceived thickness ratings (mm) were 66.74 ± 2.92, 57.35 ± 3.14, 73.83 ± 2.12, 75.95 ± 2.12, and 76.58 ± 2.84 (*M* ± *SE*)). *Post-hoc* Newman-Keuls test revealed that the second dessert (sweetness level 2) was perceived to be significantly thinner ($p < .05$) than the other four desserts, which did not differ from one another. The effect of deprivation state (F(1, 39) = .21, $p = .65$, $\eta_p^2 = 0.01$), and the interaction between sweetness and deprivation state (F(4, 156) = 2.15, $p = .08$, $\eta_p^2 = 0.05$), were not significant.

Sweet preference

Participants became less accepting of the sweeter desserts as the PI demands of eating increased. Participants preferred a moderate-to-high level of sweetness when rating the smallest portion of dessert under a mild food deprivation (Min PI, *M* = 3.5, *S.E.* = 0.17). However, they preferred a lower level of sweetness when asked to imagine eating a larger portion of the same dessert (Med PI, *M* = 3.1, *S.E.* = 0.21), and the optimal level of sweetness was further reduced when participants were asked to imagine eating the large portion of dessert in a sated state (Max PI, *M* = 2.44, *S.E.* = 0.23). This effect was confirmed by a significant main effect of PI demand (F(2, 78) = 8.38, $p < .001$, $\eta_p^2 = 0.18$). *Post-hoc* Newman-Keuls tests confirmed that sweet preference was significantly reduced between the Max PI vs. Med PI ($p = .02$) and Max vs. Min PI conditions ($p < .001$); however, the difference between the Min PI vs. Med PI conditions did not reach significance ($p = .10$).

Another way to visualize this shift in preference is to consider the frequency with which participants identified each dessert as having optimal sweetness. As shown in **Figure 2**, most participants preferred a high level of sweetness when the PI demands of eating were minimal (Min PI); however, their preference shifted towards less-sweet desserts as the PI demands of eating increased (Max PI).

Anticipated satiation, satiety, and sickliness

Although a significant shift in preference was observed in response to increased PI demand, we observed only partial evidence of a relationship between sweetness and anticipated satiation. A significant main effect of Sweetness Level was observed for expected satiety (main effect of Sweetness Level, F(4, 156) = 2.93, p = .02, η_p^2 = 0.07), but the pattern of data is difficult to interpret because we failed to observe any evidence for a monotonic relationship between sweetness level and expected satiety **(Figure 3, panel a)**. Indeed, *post-hoc* Newman-Keuls tests failed to find a significant difference between any sweetness level (smallest p = .05 between dessert 3 and 4). Expected satiation also did not vary as a function of sweetness intensity (main effect of Sweetness Level, F(4, 156) = 1.46, p = .22, η_p^2 = 0.04) **(Figure 3, panel b)**. Notably, a positive relationship with sweetness intensity was observed for expected sickliness (**Figure 3, panel c)** (main effect of Sweetness Level, F(4, 156) = 18.36, p < .00001). Indeed, *post-hoc* Newman-Keuls tests confirmed significant differences across all levels of sweetness except between dessert 1 and 2 (p = .64), and between dessert 4 and 5 (p = .05). Further, while the lunch did increase participants' ratings of expected satiety, satiation, and sickliness (main effect of Deprivation State, p's<.05; smallest F = 6.49), there was no evidence that it selectively increased their expectations about the sweetest desserts (all Sweetness Level x Deprivation State interactions were non-significant; the largest effect was for sickliness (F(4, 156) = 0.38, p = .82, η_p^2 = 0.01)).

Computerized energy compensation task

The computer-based energy compensation task confirmed that participants associated increased sweetness with increased energy content. As shown in **Figure 4**, a linear reduction in anticipated portion selection occurred as the sweetness of the preload increased. In other words, smaller dinners were selected after imagining eating 250 g of a sweeter dessert compared to when imagining eating the same sized portion of a less-sweet dessert (an 85 kcal difference between the most and least sweet desserts). This result was confirmed by ANOVA which yielded a significant main effect of Sweetness Level (F(4, 156) = 19.24, $p<.00001$, $\eta_p^2 = 0.33$). *Post-hoc* Newman-Keuls tests confirmed significant differences across all levels of sweetness except between dessert 1 and 2 ($p = .27$), and between dessert 3 and 4 ($p = .07$). Neither the main effect of Deprivation State (F(1, 39) = 1.35, $p=.25$, $\eta_p^2 = 0.03$) nor the Deprivation State x Sweetness Level interaction (F(4, 156) = 1.33, $p=.26$, $\eta_p^2 = 0.03$) reached significance.

Interim discussion

Previously, research in both humans (Mattes and Mela 1986, Lucas and Bellisle 1987, Zandstra, de Graaf et al. 1999) and non-human animals (Booth, Lovett et al. 1972, Warwick and Weingarten 1996) has demonstrated a reduced preference for highly-sweet stimuli when participants expect a greater post-ingestive effect (e.g., when fed or when imagining consuming a larger portion). Based on this literature, we predicted that preferred sweetness level (optimal sweetness) would be moderated by the expected effects of consuming a dessert with a higher or lower anticipated energy content (large or small portion), and by current PI demand (fed or fasted). Consistent with this hypothesis, optimal sweetness depended on both the participants' deprivation state and the portion size of the dessert that they were evaluating – participants preferred a highly-sweet dessert when fasted, but preferred a less-sweet dessert when they were challenged to consume a larger portion or to consume the portion when they were already sated.

If sweetness is expected to signal greater energy content, then this tendency for individuals to prefer lower levels of sweetness when sated is consistent with a relative aversion to excess energy consumed in the sated state. This indeed appears to be the case for our participants. A novel element of our study was the inclusion of explicit tests to determine whether a manipulation of sweetness intensity affects participants' judgments about the postingestive effects of a food and whether these judgments are moderated by PI demand. In the computerized energy compensation task, participants selected smaller meals after imagining consuming a sweeter preload compared to a less-sweet preload of the same portion size. This effect was robust and linear, resulting in an 85 kcal difference between the most and least sweet desserts. Thus, our participants appeared to rely on sweetness intensity when estimating the energy content of food.

However, and contrary to our expectations, we saw little evidence that these shifts in preference were due to anticipated satiation—neither expected satiety nor expected satiation ratings differed consistently across the desserts, despite the perceived differences in their energy content. On the other hand, increased sweetness was associated with perceptions of increased 'sickliness', suggesting a potential link between perceived energy content and aversive consequences such as over-satiation.

In Experiment 2, we devised a second test to determine whether the shift in preference (with PI demand) could be attributed to an anticipatory avoidance of the greater energy expected from the sweeter desserts. If this is the basis of avoidance of sweeter stimuli when sated, then we should be able to reduce or eliminate the shift in preference simply by telling participants that the desserts do not vary in energy content (i.e., because the postingestive effects of the desserts are the same, there is no reason to avoid the sweeter dessert). In Experiment 2 this was accomplished by comparing a control group (replication condition) with a second group of participants who were told in advance that the desserts were equated for energy content.

Experiment 2

Method

Participants

Forty individuals were recruited from the University of Bristol (UK) and surrounding community to participate in the experiment. Twenty participants were allocated to the ‘Equicaloric’ group (10 F / 10 M; Age: *M* = 24.5 years, *SD* = 5.67; BMI: *M* = 23.04 kg/m^2, *SD* = 2.76) and twenty participants were allocated to the ‘No Info’ group (10 F / 10 M; Age: *M* = 23.75 years, *SD* = 6.11; BMI: *M* = 22.62 kg/m^2, *SD* = 2.68). Both groups were equated on the ratio of males and females, age, and BMI. Participants received £7 Sterling for their assistance. Ethical approval was obtained from the local Faculty of Science Human Research Ethics Committee.

Materials and procedure

Testing took place between 11:30 and 14:30. The materials and procedures were identical to Experiment 1 except that half of the participants were informed that the desserts were equated for energy content (‘Equicaloric’ group; *n* = 20). The experimenter told the participants at the start of the session that *“While looking at the taste ratings that were collected during a pilot test, it came to our attention that some individuals believed that some of the desserts contained more calories than the others-- this isn’t true. Actually, all five desserts contain the same number of calories. Try to keep this in mind while you complete your ratings, in case it affects your judgments.”* The remaining participants were not provided with this information but were tested as a replication of Experiment 1 (‘No Info’ group; *n* = 20). The computerized energy compensation task was only conducted once (prior to lunch) and was not repeated because the results of Experiment 1 indicated that there was no difference in meal size (kcal) before- versus after-lunch.

Statistical analysis

Changes in appetite related to the hunger manipulation were assessed with paired samples t-tests. To confirm that participants were able to discriminate the sweetness of the five desserts, sensory ratings (e.g., thickness, sweetness) were analyzed with separate repeated-measures ANOVA, with Deprivation State (Fed, Fasted) and Sweetness Level (1-5) as within-subjects factors and Group (Equicaloric, No Info) as a between-subjects factor. The same analysis strategy was used to analyze meal size (kcal) selection during the computerized energy compensation task and also ratings of expected sickliness, expected satiation, and expected satiety. Preference shifts were analyzed with repeated-measures ANOVA, with PI demand (Min, Med, Max) as a within-subjects factor and Group (Equicaloric, No Info) as a between-subjects factor.

Results

Hunger manipulation

Participants in the ‘No Info’ and the ‘Equicaloric’ groups reported a similar level of hunger at baseline (respectively, *M* = 61.5 mm, *SD* = 19.9; *M* = 64.9 mm, *SD* = 15.0) and after consuming the lunch (respectively, *M* = 10.7 mm, *SD* = 3.4; *M* = 13.5 mm, *SD* = 3.4). The interaction between Deprivation State and Group failed to reach significance, F(1, 38)=.03, $p = .87$, $\eta_p^2 < .01$).

Sensory ratings

The five desserts differed in rated sweetness (range 37.0 mm - 84.6 mm; main effect of Sweetness Level, F(4, 152) = 67.45, $p < 0.0001$, $\eta_p^2 = 0.64$). *Post-hoc* Newman-Keuls confirmed that all desserts significantly differed from one another (*p*’s < .05). Participants rated the desserts as being slightly sweeter after eating lunch (main effect of Deprivation State, F(1, 38) = 13.25, $p < .001$, $\eta_p^2 = 0.26$), and participants in the ‘No Info’ condition tended to perceive the desserts as being sweeter post-lunch than participants in the ‘Equicaloric’ condition (Deprivation State x Sweetness Level x Group interaction, F(4, 152) = 2.36, $p = .06$, $\eta_p^2 = 0.06$). Analysis of the thickness ratings revealed a relatively small but significant effect of Sweetness Level on perceived thickness, where thickness increased in tandem with sweetness (main effect of Sweetness Level (F(4, 152)=14.30, *p* < .00001, η_p^2 = 0.27). Respectively, for desserts 1 - 5, perceived thickness ratings (mm) were 69.76 ± 2.47, 71.86 ± 2.53, 76.89 ± 1.93, 78.88 ± 1.94, and 81.00 ± 1.96 (*M* ± *SE*). *Post-hoc* Newman-Keuls tests indicated that dessert 1 and 2 were significantly different in thickness from desserts 3, 4, and 5 (*p*’s < .001), the latter of which did not differ from each other (*p*’s > 0.06). No other effects were significant (main effect of Deprivation State, *p* = .37; Deprivation State x Sweetness Level x Group interaction, *p* = .81).

Sweet preference

As shown in **Figure 5**, we replicated the shift in preference observed in Experiment 1 - optimal sweetness declined as the PI demands of eating increased (Min PI: 3.38 ± 0.21; Med PI: 2.91 ± 0.22; Max PI: 2.75 ± 0.27 (*M* ± *SE)*). This was supported by a borderline significant main effect of PI demand (F(2, 76) = 3.07, *p* = .05, η_p^2 = 0.08). *Post-hoc* Newman Keuls tests confirmed that optimal sweetness was lower in the Max PI condition than the Min PI condition (*p* = .05); however, the difference between the Min PI and Med PI conditions did not reach significance (*p* = .08). Unlike Experiment 1, there was no significant decline in sweet preference between the Med PI and Max PI conditions (*p* = .54). Contrary to our prediction that the preference shift would be abolished by informing participants that the desserts were equated for energy content, we failed to obtain a significant difference in preference between the ‘No Info’ and the ‘Equicaloric’ group (non-significant PI demand x Group interaction, F(2, 76) = .92, *p* = .41, η_p^2 = 0.02).

Anticipated satiation, satiety, and sickliness

As shown in **Figure 6,** expected satiation, satiety, and sickliness ratings all increased after consuming the lunch (main effects of Deprivation State were all *p* < .05; smallest F = 8.42, η_p^2 = 0.18). As in Experiment 1, there was no evidence that increasing the PI demands of eating preferentially affected participants’ expectations about the sweeter desserts (all

Sweetness Level x Deprivation State interactions were non-significant; largest F=1.70, η_p^2 = 0.04). There was a small but significant tendency for participants to expect greater postingestive outcomes from the sweeter desserts (all main effects of Sweetness Level were $p < .05$; smallest F = 3.52, η_p^2 = 0.09), but this occurred regardless of whether they were told that the desserts were equated for energy content (all Sweetness Level x Deprivation State x Group interactions were non-significant; largest F = 1.75, η_p^2 = 0.04). *Post-hoc* Newman Keuls tests confirmed that these main effects were driven primarily by dessert 5 which significantly differed from desserts 1-3 and desserts 2-4 in anticipated satiety and satiation, respectively (*p*’s < .05). For anticipated sickliness, both dessert 4 and 5 were significantly different than the others (*p*’s < 0.01). No other post-hoc comparisons were significant.

Computerized energy compensation task

One potential explanation for why participants in the ‘Equicaloric’ condition exhibited the same pattern of preference as participants in the ‘No Info’ condition is that we did not effectively alter participants’ beliefs about sweetness by informing them that the desserts were equated for energy content. To test whether participants in the ‘Equicaloric’ condition did, indeed, treat the desserts as if they were identical in energy content, we administered the same computer-based energy compensation task from Experiment 1. As shown in **Figure 7,** both groups of participants demonstrated a linear reduction in meal size (kcal) as the sweetness of the ‘preload’ increased. This result was confirmed by ANOVA which yielded a significant main effect of Sweetness Level (F(4, 152) = 18.87, $p < .00001$, η_p^2 = 0.33) and a non-significant Sweetness Level x Group interaction (F(4, 152) = 2.10, $p = .08$, η_p^2 = 0.05). *Post-hoc* Newman Keuls test confirmed that dessert 4 and dessert 5 differed significantly from all of the other desserts (*p*’s < 0.01), the latter of which did not differ from one another (smallest $p = 0.33$). This finding suggests that our manipulation was not effective at altering participants’ expectations, and potentially accounts for why the ‘Equicaloric’ group still exhibited a shift in preference.

General Discussion

Although sweet foods are thought to promote overconsumption due to the innate attractiveness of sweetness, evidence from non-human animals suggests that animals can also learn to use sweetness intensity to anticipate, and compensate for, the energy contained in sweet foods and fluids. Here we sought to explore whether humans also exhibit behavior consistent with ‘sweet-calorie learning’; that is, whether humans also anticipate greater energy content from sweeter foods and can utilize this information in decisions relating to food intake control. The ability to predict the energy content of food from its sweetness might be helpful because this information can be used to adjust energy intake from one meal to the next.

Our results provide support for this idea—individuals preferred lower levels of sweetness when PI demands were higher. When the PI effects of eating were minimal (e.g., when eating a very small portion in a food-deprived state), participants preferred a sweeter dessert. However, participants’ preference shifted towards a *less*-sweet alternative when the PI demand of eating increased (i.e., by having participants imagine consuming a larger portion, and to imagine eating that portion immediately after eating a 550 kcal meal). One possibility is that our findings might be attributed to a specific form of sensory specific satiety (Hetherington 1996). Others have shown that repeatedly imagining consuming a food can promote this process (Morewedge, Huh, & Vosgerau, 2010). Nevertheless, procedural differences make this account unlikely. In particular, we note that our participants were instructed to imagine consuming each dessert only once (thereby limiting the opportunity for sensory specific satiety). Moreover, accumulative and dessert-specific effects would seem implausible because we administered the stimuli in a counterbalanced order.

We note that the desserts also varied in perceived thickness. This variation was much smaller than the differences in perceived sweetness, but nonetheless may have contributed to the judgment of greater energy content of the sweeter (and apparently thicker) desserts in Experiment 2, as well as to the shifts in preference that were observed in response to PI demand. It is possible that this relationship between perceived thickness and perceived sweetness reflects a pre-existing learned association in our participants (i.e., viscosity may be positively correlated with sugar content in real foods, which led to participants entering into the study with this pre-existing association). However, this possibility remains to be formally tested in future experiments. That said, it is worth pointing out that the same pattern of results was observed in Experiment 1 where systematic differences in viscosity were *not* observed (only dessert 2 differed in perceived thickness; the other four were matched according to sensory ratings); this finding argues against viscosity as the basis of the effects observed here.

This shift in preference away from higher levels of sweetness under increasing levels of PI demand mirrors the results of our computerized energy compensation task. When participants were asked to imagine eating a 250 g portion of each dessert and to adjust their intake of a hypothetical dinner by the amount needed to compensate for the energy in each dessert, a strong linear relationship was observed between the sweetness of the dessert and self-selected meal size (kcal). Notwithstanding this point, we note that the absolute difference between the sweetest and the least sweet desserts was fairly small (85 kcal in Experiment 1 and 70 kcal in Experiment 2). It may be relevant that our sample comprised participants exposed to a Western diet. It has been suggested that exposure to low-energy sweeteners and fat replacers compromises animals’ capacity to use taste quality to predict the energetic content of foods (Davidson and Swithers 2004). Consistent with this idea, Viskaal-van Dongen *et al.* (2012) have shown that the relationship between ratings of sweetness and sugar content is degraded in highly processed foods.

Even without consumption of low-energy sweeteners and fat replacers, it is not clear that sweetness predicts much of the variance in the energy content of foods in the (complex) Western diet. Compare, for example, the energy content of sweet high-fat foods (e.g., cheesecake or chocolate) with equally sweet, low-fat foods (e.g., yoghurt or candy, such as ‘wine gums’ or ‘gummy bears’). Two foods may have equivalent energy and carbohydrate content but differ substantially in sweetness because of a difference in their relative sugar to non-sweet carbohydrate content. One way to address this issue of the potential impact of dietary complexity in blurring the relationship between sweetness (and other orosensory attributes) and energy content of foods might be to perform a cross-cultural comparison involving participants who have never been exposed to a complex Western diet (e.g., (Brunstrom, Rogers et al. 2015). However, the results from our participants (predominantly female undergraduate students) who come from a complex dietary environment lend support to the idea that humans can predict that higher sweetness signals higher energy content. This is consistent with ‘sweet-calorie learning’ demonstrated in animals, but potentially it might also reflect an innate disposition, as does liking for sweetness (Steiner 1979, Ventura and Mennella 2011). Such a disposition may ‘break-through’ despite the absence of a reliable relationship between sweetness and energy content in the individual’s diet. Future studies are needed to determine whether these effects generalize to other populations (e.g., men), or differ for certain groups (e.g., low-energy sweetener consumers).

While we obtained evidence that participants anticipated greater energy from the sweeter desserts, we found only partial evidence for conditioned satiation—expected sickliness was related to increased sweetness, but expected satiation and expected satiety were only weakly affected (only significantly so in Experiment 2). We also considered whether explicit beliefs about the energy content of sweet foods mediated the effects of PI demand on optimal sweetness (observed in Experiment 1). Therefore, in Experiment 2 we included a condition in which participants were informed that the five desserts were equated for energy content. However, we still observed an effect of sweetness on meal size. This might be because the information was not attended to or was forgotten, or that it failed to compete with established (learned) and/or engrained (innate) disposition towards sweetness signaling greater energy or satiety. Indeed, in both experiments, increased PI demand reduced optimal sweetness preference, demonstrating that this effect is replicable and somewhat resistant to interference (i.e., inclusion of a condition in Experiment 2 wherein participants were informed that the five desserts were equated for energy content did not abolish the effect). Further research is needed to determine how the composition and complexity of the modern diet impacts these effects (see Martin 2016).

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Table 1. Ingredients and macronutrient composition of the novel desserts. Separate values are provided for each level of sweetness (0% Truvia, 2% Truvia, 4% Truvia, 16% Truvia, & 16% Truvia + 0.2% sucralose). Values are provided per 100g and energy densities are rounded to one decimal place.

	Sweetness level				
Ingredient	**1** (0% Truvia)	**2** (2% Truvia)	**3** (4% Truvia)	**4** (16% Truvia)	**5** (16% Truvia + 0.2% sucralose)
Instant ClearJel® (3.9 kcal / g)	9 g	9 g	9 g	9 g	9 g
Skimmed milk powder (3.6 kcal / g)	4 g	4 g	4 g	4 g	4 g
Caster sugar (4.0 kcal / g)	10 g	10 g	10 g	10 g	10 g
Maltodextrin glucidex® 19 (3.8 kcal / g)	10 g	10 g	10 g	10 g	10 g
Hot water (0.0 kcal / g)	67 ml	65 ml	59 ml	51 ml	50.8 ml
Truvia® (0.0 kcal / g)	0 g	2 g	8 g	16 g	16 g
Sucralose (3.9 kcal / g)	0 g	0 g	0 g	0 g	0.2 g

Figure legends

Figure 1. Perceived sweetness ratings (*M* ± *SE*) for the five novel desserts in Experiment 1 (N = 40). The desserts were equated for energy content but varied in their sweetness level (lowest to highest: 1 - 5). Values are presented separately for ratings obtained when participants were fasted (before lunch) and fed (after lunch). Ratings were collected on a 100-mm VAS scale.

Figure 2. In Experiment 1 (N = 40), participants were asked to rate their expected enjoyment for consuming the five novel desserts (100-mm VAS scale). The dessert (1-5) that received the highest rating was coded as the participants' optimal sweetness level. Data represent the participants' optimal sweetness level when evaluating a small portion consumed in a fasted state (Min PI), a large portion consumed in a fasted state (Med PI), and a large portion consumed in a fed state (Max PI). Note: One participant rated all of the desserts in the Max PI condition with an expected enjoyment score of 'zero' and was excluded from this analysis.

Figure 3. In Experiment 1 (N=40), participants evaluated the expected satiety (A: "If you ate this portion of food right now, how long would it take until you were hungry enough to eat again? Anchors: 30 min -- 4 hours); expected satiation (B: "How full would you feel if you ate this portion of food right now? Anchors: Not at all -- Extremely"); and expected sickliness (C: "How sickly would you feel if you ate this portion of food right now? Anchors: Not at all -- Extremely") of the five novel desserts. The desserts were equated for energy content but varied systematically in sweetness level (lowest to highest: 1 - 5). All ratings were collected on a 100-mm VAS scale. Values (*M* ± *SE*) are provided separately for ratings obtained when participants were fasted (before lunch) and fed (after lunch).

Figure 4. Anticipated dinner meal size (*M* ± *SE* kcal) after imagining eating a 250 g portion of the five novel desserts (sweetness level 1 - 5) in Experiment 1 (N = 40). The desserts were equated for energy content but varied in their sweetness level (lowest to highest: 1 - 5).

Figure 5. In Experiment 2 (N = 40), participants were asked to rate their expected enjoyment for consuming the five novel desserts (100-mm VAS scale). The desserts were equated for energy content but varied in their sweetness level (lowest to highest: 1 - 5). Data represent the optimal sweetness level (*M* ± *SE*) when evaluating a small portion consumed in a fasted state (Min PI), a large portion consumed in a fasted state (Med PI), and a large portion consumed in a fed state (Max PI). Data are shown separately for the 'No Info' (*n* = 20) and 'Equicaloric' (*n* = 20) groups.

Figure 6. In Experiment 2, participants evaluated the expected satiety (A: "If you ate this portion of food right now, how long would it take until you were hungry enough to eat again? Anchors: 30 min -- 4 hours); expected satiation (B: "How full would you feel if you ate this portion of food right now? Anchors: Not at all -- Extremely"); and expected sickliness (C: "How sickly would you feel if you ate this portion of food right now? Anchors: Not at all -- Extremely") of the five novel desserts. The desserts were equated for energy content but varied systematically in sweetness level (lowest to highest: 1 - 5). All ratings were collected on a 100-mm VAS scale. Values (*M* ± *SE*) are provided separately for ratings obtained when participants were fasted (before lunch) and fed (after lunch). The top panel show the data for the 'No Info' (*n* = 20) and the bottom panel show the data for the 'Equicaloric' (*n* = 20) groups.

Figure 7. Anticipated dinner meal size (*M* ± *SE* kcal) after imagining eating a 250 g portion of five novel desserts (sweetness level 1 – 5) in Experiment 2 (N = 40). Data are shown separately for the 'No Info' (*n* = 20) and 'Equicaloric' (*n* = 20) groups.