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Rats' preferences for high fructose corn syrup vs. sucrose and sugar mixtures

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Abstract

High fructose corn syrup (HFCS) has replaced sucrose in many food products, which has prompted research comparing these two sweeteners in rodents. The present study examined the relative palatability of HFCS and sucrose for rats, offering 11% carbohydrate solutions to match the content of common beverages for human consumption. The animals initially preferred HFCS to sucrose but after separate experience with each solution they switched to sucrose preference. Approximating the composition of HFCS with a mixture of fructose and glucose (55:45) yielded a solution that was less attractive than sucrose or HFCS. However, HFCS contains a small amount of glucose polymers, which are very attractive to rats. A 55:42:3 mixture of fructose, glucose and glucose polymers (Polycose) was equally preferred to HFCS and was treated similarly to HFCS in comparisons vs. sucrose. Post-oral effects of sucrose, which is 50% fructose and 50% glucose, may be responsible for the shift in preference with experience. This shift, and the relatively small magnitude of differences in preference for HFCS and sucrose, suggest that palatability factors probably do not contribute to any possible difference in weight gain responses to these sweeteners.

Keywords

sugar; sweeteners; Polycose

1. Introduction

The controversy regarding high fructose corn syrup (HFCS) as a contributing factor in the increased incidence of human obesity has been the subject of considerable discussion. HFCS-55, which contains 55% fructose, 42% glucose, and 3% glucose polymers [34] has largely replaced sucrose, a disaccharide containing 50% fructose and 50% glucose, in soft drinks and some other foods. Many studies have demonstrated that fructose is more lipogenic than glucose [30]. A concern sometimes expressed is that the slightly higher fructose content of HFCS compared to sucrose may promote obesity [16]. However, the minor difference in the fractions of fructose and glucose in HFCS and sucrose are not sufficient to generate differences in metabolic and behavioral responses in humans [3,19,20,28,29]. The consensus view is that HFCS and sucrose do not differ in weight

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promoting action in humans [9,18,34]. However, thus far there are no direct comparisons of HFCS and sucrose effects during long-term consumption in humans.

Two recent rat studies, which were conducted to remedy the lack of information on long-term effects, appeared to contradict the idea of equivalence: animals offered prolonged access to a HFCS solution tended to gain more weight than rats given a sucrose solution [4,16]. However, the carbohydrate content of the HFCS and sucrose solutions were not equivalent in these studies, which complicates the interpretation of the findings. The HFCS solutions contained less carbohydrate than did the sucrose solutions which may have influenced the amount of solution consumed.

A second concern expressed about HFCS is that it has a sweeter taste to humans than sucrose, which might promote overconsumption. This idea appears to be based on an interpretation of the greater sweetness of fructose than glucose [5]. However, HFCS and sucrose are reported to be similar in their sweet taste intensity at a 10% carbohydrate concentration [34], and HFCS-55 was specifically formulated to match the sensory properties of sucrose [23]. The relative sweetness or palatability of HFCS and sucrose to rodents has not been investigated, although some authors assume that HFCS, like pure fructose, is sweeter than sucrose to rats [16]. This assumption is questioned, however, by behavioral findings indicating that rats and mice are more attracted to sucrose than fructose at isocaloric concentrations [12,22]. As noted above, HFCS contains not only fructose and glucose, but also a small amount of glucose polymers (polysaccharides) which may influence HFCS palatability to rats because of their sensitive taste for glucose polymers (e.g., Polycose) [25].

The present study determined the preference of rats for HFCS and sucrose in 24-h two-bottle choice tests. In addition, preference tests were conducted with mixtures of fructose and glucose with and without glucose polymers (Polycose) to assess the influence of glucose polymers on HFCS preference. The solutions contained 11% carbohydrate to approximate the concentration of sweetener in common soft drinks as calculated from nutritional labels. Matching the carbohydrate concentration of the solutions ensured that any differences in intake and preference would reflect relative palatability without confounding effects due to difference in energy density. Intakes during 24-h tests are influenced by post-ingestive factor; accordingly, preferences were measured before and after rats were given experience with individual solutions alone. In theory, differences in the relative palatability of HFCS and sucrose may contribute to possible differences in their weight promoting effects in rodents. Palatability differences may be a factor because, at least in extreme cases, they can alter food metabolism via cephalic phase responses [11,14,15,17].

2. Experiment 1A

The first experiment examined preferences for sugar solutions in male rats. After an initial two-bottle test with 11% HFCS vs. 11% sucrose, the animals were given separate exposure to each sugar solution vs. water and then retested for their HFCS vs. sucrose preference. Then each sugar solution was offered vs. an 55:45 mixture of fructose and glucose.

2.1 Methods

2.1.1 Subjects—Male Sprague-Dawley rats bred in the laboratory from Charles River (Wilmington MA) stock were studied. The animals were 80 days old and weighed 454–555 g (mean 517 g) at the start of testing. They were singly housed in wire mesh cages in a vivarium maintained on a 12:12 light:dark cycle (lights on at 0800 h) at 21 degrees C. The animals were given ad libitum access to pelleted chow (Lab Chow 5001, PMI Nutrition International, Brentwood, MO) and to fluids as specified. The experimental protocols were

approved by the Brooklyn College Institutional Animal Care and Use Committee, certifying that all subjects and procedures were in compliance with the National Institute of Health Guide for Care and Use of Laboratory Animals.

2.1.2 Test solutions—All solutions were prepared to contain 11% carbohydrate w/v. For accurate preparation, the solutions were made once using volumetric flasks, and the weights of syrup or sugars and water were determined so that the solutions could subsequently be prepared by weighing all components. HFCS was obtained from Nature's Flavors (Orange, CA). It contains 76 g carbohydrate per 100 g syrup, so the solution was made with 144.7 g syrup ($*0.76 = 110$ g of carbohydrate) per liter of solution. The other solutions were prepared with sucrose (110 g/l; Domino Foods, Yonkers, NY) and with a mixture of fructose (60.5 g/l) and glucose (49.5 g/l; both from Honeyville Food Products, Rancho Cucamonga, CA) designed to parallel the major components of HFCS (55% fructose and 45% glucose, FG).

2.1.3 Procedure—Prior to the introduction of carbohydrate solutions, the rats were maintained on chow and water only. The solutions were presented in glass bottles with rubber stoppers and stainless steel spouts. The bottles were secured side by side to the front of the cage with stainless steel springs, and the spouts protruded into the cages about 5 cm apart. Each two-bottle test lasted two days; the left-right positions of the bottles were shifted from the first to the second test day. Test 1 was HFCS vs. sucrose. In Test 2, the animals were exposed to HFCS vs. water, and sucrose vs. water, with the order of carbohydrates counterbalanced so that half the rats received HFCS first. The purpose of this testing vs. water was to provide unambiguous experience with the oral and post-oral stimulation from each sweet solution. After a day of water only, Test 3 was a return to HFCS vs. sucrose. In the last two tests, sucrose (Test 4) and HFCS (Test 5) were offered vs. the FG mixture; there were 2 water-only days between these tests. Fluid intakes were measured daily by weighing the bottles to the nearest 0.1 g, and averaged across the two days of each test. Intakes within tests were compared with paired t-tests. Tests 1 and 3 were compared with 2-way repeated measures analysis of variance (anova) and simple main effects. Total intakes in the tests were compared with 1-way repeated measures anova and Newman-Keuls tests.

2.2 Results and discussion

The intakes in the first three tests are shown in the upper panel of Figure 1. In Test 1, the rats preferred HFCS to sucrose (67%, $p < 0.05$). When next given each solution vs. water in Test 2, they consumed over 100 g/day of solution and almost no water; solution intakes did not differ. When their solution preference was retested in Test 3, the rats now preferred sucrose over HFCS (64%, $p < 0.05$). An interaction of test and solution ($F(1,9) = 20.9$, $p < 0.01$) showed that the change from Test 1 to Test 3 reflected an increase in sucrose intake ($p < 0.0001$) with no change in HFCS intake. This suggests that the preference was modified by the separate experience with each solution, which could include small differences in post-oral effects, e.g., differences in osmolarity, fructose content (see below).

The final tests, shown in the upper panel of Figure 2, examined the rats' response to the FG mixture of 55:45 fructose:glucose. They clearly preferred both sucrose (80%, $p < 0.001$) and HFCS (76%, $p < 0.005$) to this mixture. Thus the simple mixture of the two monosaccharides did not mimic the attractiveness of the HFCS solution.

Total intakes changed across tests ($F(5,45) = 36.4$, $p < 0.0001$), increasing from the first test to the comparisons with water, then increasing again to stable values in the last 3 tests. Total intake increased by 77% from the first to the second HFCS vs. sucrose test, due entirely to nearly tripled sucrose intake.

3. Experiment 1B

Female rats are often more responsive to sweet solutions than males [32,33]. Therefore the test sequence was replicated in female rats, to determine if they showed the same pattern of responses to the 11% carbohydrate solutions as male rats.

To explore the lack of attraction to the FG mixture, an alternate FGP solution that included the small fraction of glucose polymers (P) that occurs in HFCS was created and compared to HFCS in a final test.

3.1 Methods

Twelve female rats of the same provenance and housing were 140 days old at the start of testing and weighed 258–345 g (mean 306 g). They received the same series of tests as the males, with the minor difference that 2 water-only days, rather than 1, preceded Test 3. In addition, after Test 5 there were 3 water-only days before a final Test 6 with HFCS vs. a mixture that approximated the carbohydrate composition of HFCS (55% fructose, 42% glucose, and 3% glucose polymers). The FGP was prepared with fructose (60.5 g/l), glucose (46.2 g/l) and Polycose (3.3 g/l, Ross Laboratories, Columbus, OH).

3.2 Results and discussion

The intakes in the first three tests are shown in the lower panel of Figure 1. In Test 1, the rats preferred HFCS to sucrose only weakly (58%, $p = 0.10$). When next given each solution vs. water in Test 2, they consumed about 125 g/day of the sweeteners and almost no water; intakes of HFCS and sucrose did not differ. When their sweetener preference was retested in Test 3, the rats now weakly preferred sucrose over HFCS (60%, $p = 0.09$). An interaction of test and solution ($F(1,11) = 35.0$, $p < 0.0001$) showed that the change from Test 1 to Test 3 reflected an increase in sucrose intake ($p < 0.01$) with no change in HFCS intake. These results are similar to those of the males except that the preferences were weaker and not statistically significant.

The next tests, shown in the lower panel of Figure 2, examined the rats' response to the FG mixture. They clearly preferred both sucrose (Test 4: 79%, $p < 0.001$) and HFCS (Test 5: 84%, $p < 0.005$) to the FG mixture. However, in the final test of HFCS vs. FGP, which more closely approximates HFCS composition, preference for HFCS was reduced to 57% and intakes of HFCS and FGP did not significantly differ (Test 6, Figure 2). Thus HFCS was effectively simulated by adding glucose polymers to the fructose+glucose mixture.

Total intakes differed across tests ($F(6,66) = 12.0$, $p < 0.001$). Intakes were lowest in Test 1, highest in Test 4, and declined in the last two tests, which did not include sucrose. Total intakes increased by 21% from the first to the second HFCS vs. sucrose test, with sucrose intake doubling and HFCS intake declining slightly. The females' peak intakes were markedly greater than those of the males in Experiment 1 when expressed as a function of body size: 49 g solution per 100 g body weight for the females, and only 30 g per 100 g for the males.

4. Experiment 2

The results of the tests involving the HFCS and FGP solutions were intriguing, suggesting that the small amount of glucose polymer might be important in rats' attraction to HFCS. However, because the animals were experienced with carbohydrate solutions prior to the FGP test, it was not clear whether this preference would also occur in naïve animals. To explore the mixtures further, Experiment 2 began with tests of HFCS vs. mixtures, rather than vs. sucrose as in Experiment 1.

4.1 Methods

Ten male rats of the same provenance and housing were 110 days old and weighed 542–630 g (mean 580 g) at the start of testing. They were first given the pairs of solutions that had been used in tests 5 and 6 in Experiment 1B: HFCS vs. FG and then vs. FGP. Following 3 water-only days, the FGP mixture was pitted against sucrose, using the same sequence as in Tests 1–3 of Experiment 1 to determine if solution preference would reverse as with HFCS testing.

4.2 Results and discussion

The upper panel of Figure 3 shows that in the first test, the rats clearly preferred HFCS to FG (76%, $p < 0.001$). However, they were indifferent when offered HFCS vs. FGP (46%, $p = 0.68$) in Test 2. These results are quite consistent with those of Experiment 1B.

The remaining tests, shown in the lower panel of Figure 3, involved sucrose and the FGP mixture. At first FGP was marginally preferred to sucrose (62%, $p = 0.067$). Each solution was overwhelmingly preferred to water, and FGP intake was slightly greater than that of sucrose ($p = 0.09$). In the final test, there was no longer any hint of a difference in FGP and sucrose intakes (47% FGP, $p = 0.37$). An interaction of test and solution ($F(1,9) = 8.74$, $p < 0.05$) showed that the change from Test 3 to Test 5 reflected an increase in sucrose intake ($p < 0.01$) with no change in FGP intake. Total intakes differed across tests ($F(5,45) = 36.4$, $p < 0.0001$), with increased intake when sucrose was introduced in Test 3. The total solution intake in the final FGP vs. sucrose test was higher than all other tests.

5. Discussion

The primary findings of this study are: 1) naïve rats preferred HFCS to sucrose, but following separate experience with the two sweeteners, they switched their preference to sucrose, and 2) the palatability of HFCS is enhanced for rats by its small fraction of glucose polymers. Rats significantly preferred an 11% HFCS solution to an 11% mixture of fructose and glucose (55:45 ratio) but not to an 11% fructose+glucose+Polycose (55:42:3 ratio) mixture that approximates the carbohydrate composition of HFCS-55.

In initial preference tests, naïve rats drank more HFCS than sucrose with the preference being more pronounced in male than female rats. However, when given HFCS or sucrose versus water, both sexes showed near-total preferences for both sweeteners and consumed equivalent amounts. Yet when retested for their sweetener preference, they now preferred sucrose to HFCS, with the difference again being more pronounced in males than females. The males' greater attraction to the HFCS with its glucose polymer content is consistent with their greater preference for dilute Polycose over dilute sucrose: male rats preferred 1% Polycose to 1% sucrose, whereas females were indifferent [24].

While taste factors alone may have been responsible for the preference shift, it is also likely that post-oral effects were involved. The osmolarity of the sucrose solution was about half that of the HFCS solution, which may have reduced gastrointestinal distention and/or enhanced gastric emptying and absorption. It is also possible that continued exposure to sucrose induced greater production of enzymes (e.g., sucrase) that facilitated its digestion and absorption. In addition, digestion of sucrose yields a higher glucose fraction (50%) than that of HFCS solution (45% including the glucose polymers) which may enhance the relative palatability of sucrose solution. Prior work shows that glucose has a more potent post-oral flavor conditioning action than does fructose [2]. It is important to note that the shift in sweetener preference from Test 1 to 3 resulted primarily from a selective increase in sucrose intake. HFCS intake did not significantly change from the first to third test,

suggesting that the absolute palatability of the solution did not change but that the preference shift was due to a selective increase in the attractiveness of the sucrose solution.

Tests conducted with the fructose-glucose mixtures with and without glucose polymers provide insights into the attractiveness of the HFCS to rats. Clearly it is not the fructose component alone of HFCS that determines its palatability, since the rats significantly preferred HFCS to the FG mixture containing the same amount of fructose. Replacing a small amount of glucose with Polycose (3.3 g/l) was sufficient to negate the preference for the HFCS over the sugar mixture, as well as to convert the preference for sucrose over FG to a slight preference for FGP over sucrose (Fig. 2A vs. 3B). The powerful effects of substituting a small amount of Polycose for glucose in the fructose-glucose mixture demonstrate the rat's impressive ability to detect a weak polysaccharide stimulus (0.33%) even in the presence of sugars at higher concentrations. This is further indicated by the earlier finding that rats significantly preferred a 9.7% sucrose + 0.3% Polycose solution to a 10% sucrose solution [26]. Other studies revealed that the preference threshold for Polycose is much lower than that for sucrose (0.01 vs. 0.09%) in saccharide vs. water tests [25], that rats taste Polycose as qualitatively different from sucrose and other sugars as indicated by conditioned taste aversion tests [21], and that Polycose taste is not mediated by the T1R2 or T1R3 sweet receptors in mice [31,35]. Another finding relevant to the present results is that rats prefer a mixture of Polycose and sucrose (1:1) to Polycose-only as well as sucrose-only solutions of the same total concentration (2–32%) [1]. In 23 h/day preference tests, rats consume much more of a 1% sucrose + 1% maltodextrin mixture than of either 2% sucrose or 2% maltodextrin [27]. Thus, the combination of the Polycose taste and sweet taste is particularly attractive to rats and can explain their preference for HFCS over sucrose and over the FG mixture. The significant preference rats displayed for sucrose over FG suggests that these solutions are not equally sweet to rats, which is consistent with reports that rats and other rodents are more attracted to sucrose than fructose and glucose at isocaloric concentrations [6,12,22].

The importance of the glucose polymer content of HFCS to the sensory evaluation of sweeteners for humans is not known. People rate glucose polymers such as Polycose as bland tasting. Interesting recent data from exercise studies suggests that humans are responsive to oral stimulation with dilute glucose polymer solutions, as expressed by enhancement of motor output following mouth rinses without swallowing [7,10,13]. These effects are observed even when flavor differences from control solutions are minimized, suggesting that humans may sense and respond to the glucose polymers even when they are not ingested and when the solutions are not distinguishable from carbohydrate-free stimuli [8]. As reviewed elsewhere, these findings suggest that the human taste response to glucose polymers requires further study [13].

In view of the relatively small differences in HFCS vs. sucrose preferences observed in the present study and the experience-induced change in preferences, palatability factors are unlikely to account for any differential metabolic or weight gain responses to HFCS and sucrose in rats. In one recent study [16], in which female rats were offered HFCS-55 or sucrose solutions (24 h/day) for 8 weeks, only the HFCS rats gained significantly more weight than control rats, although the weight gain difference between the HFCS and sucrose rats was small and not significant. Interestingly, the HFCS rats consumed less energy as sweetener than did the sucrose rats, although the groups did not differ in total energy intakes. The interpretation of these data is complicated, however, by the fact that the carbohydrate content of the HFCS and sucrose solutions differed. The solutions were prepared with 13% w/v HFCS or sucrose, but this does not account for the different carbohydrate contents of crystalline sucrose and liquid HFCS, which is only 76% carbohydrate by weight. Consequently, the HFCS solution contained only 9.9%

carbohydrate compared to the sucrose solution's 13% carbohydrate. The lower caloric density and perhaps reduced palatability of the HFCS relative to the sucrose solution may account for why the HFCS rats consumed less sweetener than the sucrose rats, although it does not explain why the HFCS gained slightly more weight than the sucrose rats.

In another recent study [4], female rats given 12 h/day access to HFCS or sucrose and chow gained identical amounts of weight over a 7 month period. In contrast to these results, male rats given 12 h/day access to HFCS gained more weight than did male rats given 12 h/day access to sucrose for 2 months. The sweetener solutions were prepared as 10% w/v sucrose and 8% v/v HFCS, which contains 8.9% carbohydrate on a w/v basis; no rationale was given for the different concentrations used. Thus, in both studies reporting some evidence for enhanced weight gain in rats fed HFCS instead of sucrose solutions, the HFCS solution had a lower caloric density than did the sucrose solution. While it seems unlikely that this could account for the reported body weight differences, studies comparing the effects of different sweeteners should ensure that the amounts of carbohydrate are matched to avoid potential confounds due to differences in energy density. Also, sweetener preferences should be evaluated to account for differences in palatability.

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Figure 1. Mean (+SEM) intakes of 11% HFCS (HFCS-55), 11% sucrose, and water in Tests 1–3 of Experiment 1A (male rats, upper panel) and 1B (female rats, lower panel). Percentages above bars indicate percent preference for the solution relative to total intake. Asterisks indicate significant differences in intake of the solutions within tests.

Figure 2. Mean (+SEM) intakes of 11% HFCS, 11% sucrose, 11% FG, and 11% FGP solutions in Tests 4 and 5 of Experiment 1A (male rats, upper panel) and in Tests 4–6 in Experiment 1B (female rats, lower panel). The FG solution consisted of 6.05% fructose and 4.95% glucose whereas the FGP solution consisted of 6.05% fructose, 4.62% glucose, and 0.33% Polycose. Percentages above bars indicate percent preference for the solution relative to total intake. Asterisks indicate significant differences in intake of the solutions within tests.

Figure 3.

Mean (+SEM) intakes of sugar solutions in Experiment 2 with male rats. Tests 1 and 2 with 11% HFCS, 11% FG, and 11% FGP are shown in the upper panel. Tests 3–5 with 11% sucrose, 11% FGP and water are shown in the lower panel. The FG solution consisted of 6.05% fructose and 4.95% glucose whereas the FGP solution consisted of 6.05% fructose, 4.62% glucose, and 0.33% Polycose. Percentages above bars indicate percent preference for the solution relative to total intake. Asterisks indicate significant differences in intake of the solutions within tests.