Chem. Senses 23: 675–682, 1998

The Taste of Polycose in Hamsters

Bradley K. Formaker, Cristin E. Kearns and Marion E. Frank

School of Dental Medicine, The University of Connecticut Health Center, Farmington, CT, USA

Correspondence to be sent to: Bradley K. Formaker, PhD, MC-3705, Department of BioStructure and Function, The University of Connecticut Health Center, 263 Farmington Avenue, Farmington, CT 06030, USA. e-mail: brad@neuron.uchc.edu

Abstract

Hamsters show a preference for Polycose, a mixture of starch-derived glucose polymers, that is as strong as their preference for sucrose. However, in the hamster, taste aversions to Polycose may be less easily acquired than taste aversions to sucrose and the qualitative aspects of Polycose are unknown in this species. In order to examine the taste of Polycose in the hamster, we utilized a taste-aversion protocol with two conditioning trials. Animals were trained to avoid one of three different conditioning stimuli: 50 mM sucrose, 100 mM Polycose and a mixture of 50 mM sucrose with 100 mM Polycose. Control animals were conditioned with deionized water. After the second conditioning trial, generalization testing began for the three conditioning stimuli plus 3 mM citric acid, 300 mM KCl and 30 mM NaCl. The results showed that aversions to Polycose, sucrose or the Polycose/sucrose mixture cross-generalized, demonstrating that Polycose and sucrose share a common taste percept in the hamster. None of the aversions generalized to NaCl, citric acid or KCl. In addition, comparisons among the patterns of taste generalizations indicated that the tastes of Polycose and sucrose also had distinct qualitative components. Finally, although the taste of 100 mM Polycose was more salient than the taste of 50 mM sucrose, the taste of sucrose could still be detected in a mixture with Polycose.

Introduction

Species differences in taste have been documented (Beidler *et al.*, 1955; Tonosaki and Beidler, 1989), as have species similarities (Nowlis *et al.*, 1980; Frank and Nowlis, 1989). For example, aversions to compounds reported to be sweet in humans, such as D-phenylalanine, L-alanine, fructose, sodium saccharin or sodium cyclamate (McBurney and Shick, 1971; Schallenberger and Acree, 1971), all generalize to sucrose in the hamster (Nowlis *et al.*, 1980; Frank and Nowlis, 1989). However, certain polysaccharides, such as Polycose, may have taste qualities that are different from the human perceptions of sweet, sour, salty or bitter (Nissenbaum and Sclafani, 1987). Polycose, a water-soluble powder derived from corn starch, consists of 2% glucose, 7% maltose, 55% maltooligosaccharides (3–10 glucose units) and 36% maltopolysaccharides (>10 glucose units).

Two-bottle preference tests indicate that gerbils, mice, hamsters and bonnet macaques like Polycose as much as, or more than, sucrose (Feigin *et al.*, 1987). While hamsters may prefer Polycose to sucrose, a recent investigation failed to demonstrate a conditioned taste aversion to 3.2% Polycose in hamsters (Rehnberg *et al.*, 1996). Hamsters were able to acquire an aversion to 3.2% glycogen, another preferred polysaccharide, but this aversion did not generalize to Polycose.

Taste aversion studies in the rat indicate that aversions to Polycose do not generalize to sucrose and vice versa (Sclafani, 1987). It was concluded that the rat discriminates the taste of Polycose from the taste of sucrose and that Polycose does not share taste qualities with sucrose in the rat (Sclafani, 1987). However, at similar concentrations humans judge Polycose to be sweet, but not as sweet as sucrose (Feigin *et al.*, 1987). In fact, humans judge 4% sucrose (percentage weight by volume) to be almost 200% sweeter than 4% Polycose. Rodents may make similar distinctions between the tastes of Polycose and sucrose.

With regard to taste preferences, rats prefer binary mixtures of sucrose, saccharin and Polycose to any of these components presented alone (Ackroff *et al.*, 1993). In humans, binary mixtures of sweet-tasting stimuli (i.e. homogenous mixtures) are judged to be sweeter than either component presented alone (Lawless, 1986; McBride, 1988). Rodents have a distinct attraction for sweeteners. In fact, rats will mix a 'cocktail' of glucose and saccharin intraorally if the two solutions are presented side by side (Smith *et al.*, 1976). A rat's preference for a mixture of Polycose and sucrose over either of the components presented alone may derive from an enhanced appetite for the mixture.

Conditioned taste aversion procedures have been used many times to assess the qualitative characteristics of taste perception in the rat and hamster (Nachman, 1963; Nowlis, 1974; Nowlis *et al.*, 1980; Frank and Nowlis, 1989; Formaker and Hill, 1990; Hill *et al.*, 1990). Generalization

of a specific aversion to other novel stimuli is an index of qualitative similarity among the taste stimuli. Behavioral investigations of heterogeneous mixtures (i.e. mixtures of unique taste qualities) suggest that rodents are able to identify and respond to the components of heterogeneous taste mixtures as if they were presented separately (Nowlis and Frank, 1981; Frank, 1989; Smith, 1989). Hamsters conditioned to avoid a taste mixture composed of a 'novel' taste stimulus (NaCl) and a 'familiar' taste stimulus (sucrose) learned to avoid the novel stimulus as well as the mixture, but not the familiar stimulus (Nowlis and Frank, 1981). Thus, the taste of the novel stimulus was not altered by mixing it with the familiar stimulus and the two stimuli were perceptually separable to the hamster.

The present study was conducted in the hamster to examine the qualitative aspects of Polycose, and the binary mixture of Polycose with sucrose, relative to sucrose alone. We wanted to determine if Polycose and sucrose shared any qualitative taste similarities with each other in the hamster. We utilized the known characteristics of binary taste mixtures, described previously (Frank, 1989; Nowlis and Frank, 1981; Smith, 1989), to determine if these two stimuli shared common taste percepts. We predicted that if Polycose and sucrose were completely unique with regard to taste quality, then an aversion to either stimulus alone should show less generalization to the mixture than an aversion to the mixture shows to each component (Frank, 1989). However, if Polycose and sucrose were similar with regard to taste quality, then an aversion to either stimulus alone or the mixture should cross-generalize.

Materials and methods

Subjects

Behavioral taste generalizations were examined in 36 adult male golden hamsters (*Mesocricetus auratus*). Hamsters were obtained from Charles-River Laboratories and were individually housed in the vivarium at the University of Connecticut Health Center. The vivarium temperature was maintained at 22°C and vivarium lights cycled on a 12 h reverse day/night cycle (lights *off* at 7:00 a.m.). Throughout the experiment animals had ad-libitum access to Agway rodent laboratory chow. All conditioning and testing was conducted in the home cage.

Water deprivation schedule

Two weeks prior to conditioning, hamsters were placed on a restricted water schedule and were maintained on that schedule for the duration of the experiment. Each hamster was given 1 h of fluid access in the home cage twice a day, Monday through Friday, from 10:30 to 11:30 a.m. and again from 4:30 to 5:30 p.m. Ad-libitum deionized water was available during the weekend from 4:30 p.m. on Friday until 5:30 p.m. on Sunday, when water was removed. All conditioning and testing occurred during the morning drinking sessions and rehydration with deionized water occurred during the afternoon.

Table 1 Experimental procedure for the 1 h a.m. drinking session[a] (see text for details)

Week	a.m. drinking session
One	
Monday–Thursday	distilled water access
Friday	conditioning
Two	
Monday–Thursday	distilled water access
Friday	conditioning repeated
Three and four	
Tuesday, Thursday	distilled water access
Monday, Wednesday, Friday	generalization testing (test cycle one)
Five	
Monday–Saturday	generalization testing repeated (test cycle two)

[a]The p.m. drinking session consisted of 1 h access to deionized water.

Conditioning procedure

Conditioning took place during the morning drinking session on two consecutive Fridays. Each animal was given one-bottle access to its respective conditioning stimulus (CS) for 1 h. Immediately following the 1 h CS drinking session, each animal was injected with apomorphine hydrochloride (30 mg/kg, i.p.). The following week, animals were maintained on the restricted water regimen with deionized water and reconditioned to the same CS. Thus, all animals received two conditioning trials before generalization testing. Table 1 outlines the experimental procedure.

Taste stimuli

Because the average molecular weight of Polycose is 1000, a 10% Polycose solution is, on average, equivalent to 100 mM. Since all other taste stimuli are reported in mM concentrations, we will refer to 10% Polycose as 100 mM Polycose throughout the manuscript. Hamsters were randomly assigned to experimental groups (n = 6) according to CS. Conditioning stimuli consisted of 100 mM Polycose, 50 mM sucrose and a mixture of 100 mM Polycose with 50 mM sucrose. The concentration of each component in the mixture equaled its concentration presented alone. Controls (n = 12) were conditioned against deionized water. Test stimuli consisted of the three conditioning stimuli plus 3 mM citric acid, 300 mM KCl and 30 mM NaCl. One test solution was available per hamster, per test session. The concentration of Polycose used was a half-log step increment from the concentration used by Rehnberg *et al.* (1996). Sucrose concentration was chosen based on equal, steady-state chorda tympani (CT) response magnitudes with 100 mM Polycose (data not shown). We used the

steady-state CT response because temporally it is closer to the effects of the unconditioned stimulus than the transient response. Note that perceptual gustatory responses represent a synthesis of neural information and the CT only transmits a portion of the overall, ascending, peripheral gustatory information. At present we do not have neural data on the greater superficial petrosal or glossopharyngeal nerve response to Polycose in the hamster. The concentrations of NaCl, citric acid and KCl were chosen based on previous behavioral work in the hamster (Frank and Nowlis, 1989). All stimuli except Polycose (Ross Laboratories) were reagent grade, dissolved in deionized water and presented at room temperature.

Testing procedure

Generalization testing began the first week after the second conditioning trial and consisted of two test cycles spread over 3 weeks (see Table 1). Test solutions were presented in a counterbalanced order using a Latin-square design. During the first test cycle animals were given access to the six test stimuli on Monday, Wednesday and Friday. Because there were six test stimuli and three test days, the first test cycle took 2 weeks to complete. The second test cycle occurred during the third week, Monday through Saturday. Therefore, all animals underwent generalization testing twice over a period of 3 weeks.

Data analyses

In order to determine if absolute differences in test solution intake between the conditioning groups and the control group were significant, we analyzed solution intake with a three-way, mixed-factors ANOVA (conditioning group by test solution by test cycle). Conditioning group was the between subjects measure while test solution and test cycle were within subjects measures. A-priori predictions regarding reductions in test solution intakes between the control group and each conditioning group were individually examined with planned comparisons. The Studentized Newman–Keuls (SNK) test was used to examine the significance of any post-hoc comparisons.

In order to compare qualitative taste characteristics among the three conditioning stimuli, relative suppression scores were also calculated and analyzed with a three-way mixed factors ANOVA. Relative suppression scores were computed as follows:

$$1 - (\text{individual test solution intake}/\text{mean control test solution intake})$$

Thus, a relative suppression score of 1 indicates complete rejection of the test stimulus. A score of 0 indicates that the conditioning group and the control group drank equal amounts of the test solution. Scores less than 0 indicate that the conditioning group drank more test solution than the control group.

Results

Figure 1 illustrates the absolute intakes to all test stimuli for all conditioning groups in both test sessions. In the ANOVA comparing absolute solution intakes, the conditioning group main effect was significant [$F(3,26) = 5.37$, $P < 0.01$]. Control hamsters consumed significantly more total solution during testing than any of the other groups (SNK, $P < 0.05$), which did not differ from each other. Overall, total fluid intake significantly increased from the first test cycle to the second [$F(1,26) = 77.91$, $P < 0.01$]. A simple main effects analysis of the significant test cycle by conditioning group interaction [$F(3,26) = 6.67$, $P < 0.01$] revealed that the three conditioning groups drank significantly more total fluid during the second test cycle than the first; control animals did not differ in total fluid intake between test cycles. Thus, the overall suppressive effects of conditioning were less evident during the second test cycle than the first (Figure 1).

A significant test stimulus main effect indicated that the six test solutions were differentially consumed during testing [$F(5,130) = 25.57$, $P < 0.001$]. The significant conditioning group by test stimulus interaction [$F(15, 130) = 3.77$, $P < 0.001$] further indicated that solution intake varied as a function of conditioning group. The three-way interaction involving conditioning group, test solution and test cycle was not significant [$F(15,130) = 0.59$, $P > 0.88$]; this indicates that the pattern of solution intake across conditioning groups was not significantly altered by test cycle. Because test cycle did not alter the pattern of solution intake across the conditioning groups, the following comparisons of test solution intake were calculated based on mean intakes averaged over the two test cycles. Sucrose-conditioned animals consumed significantly less sucrose than controls [means = 1.62 versus 3.78 ml; $F(1,26) = 15.66$, $P < 0.001$]; less Polycose than controls [1.86 versus 2.89 ml; $F(1,26) = 11.25$, $P < 0.01$]; and less mixture than controls [1.40 versus 2.45 ml; $F(1,26) = 7.02$, $P < 0.05$]. Therefore, the sucrose aversion generalized to Polycose and the mixture. Polycose-conditioned animals consumed less Polycose (0.80 ml) than controls [$F(1,26) = 46.30$, $P < 0.001$]; less sucrose (2.27 ml) than controls [$F(1,26) = 7.66$, $P < 0.05$]; and less mixture (0.63 ml) than controls [$F(1,26) = 20.93$, $P < 0.001$]. Hence, the Polycose aversion generalized to sucrose and the mixture. Finally, mixture-conditioned animals consumed less sucrose (2.12 ml) than controls [$F(1,26) = 9.26$, $P < 0.01$]; less Polycose (0.70 ml) than controls [$F(1,26) = 50.85$, $P < 0.001$]; and less mixture (0.60 ml) than controls [$F(1,26) = 21.71$, $P < 0.001$]. Thus, the mixture aversion generalized to sucrose and Polycose. Comparisons between control and conditioning groups were not significant for any of the remaining stimuli.

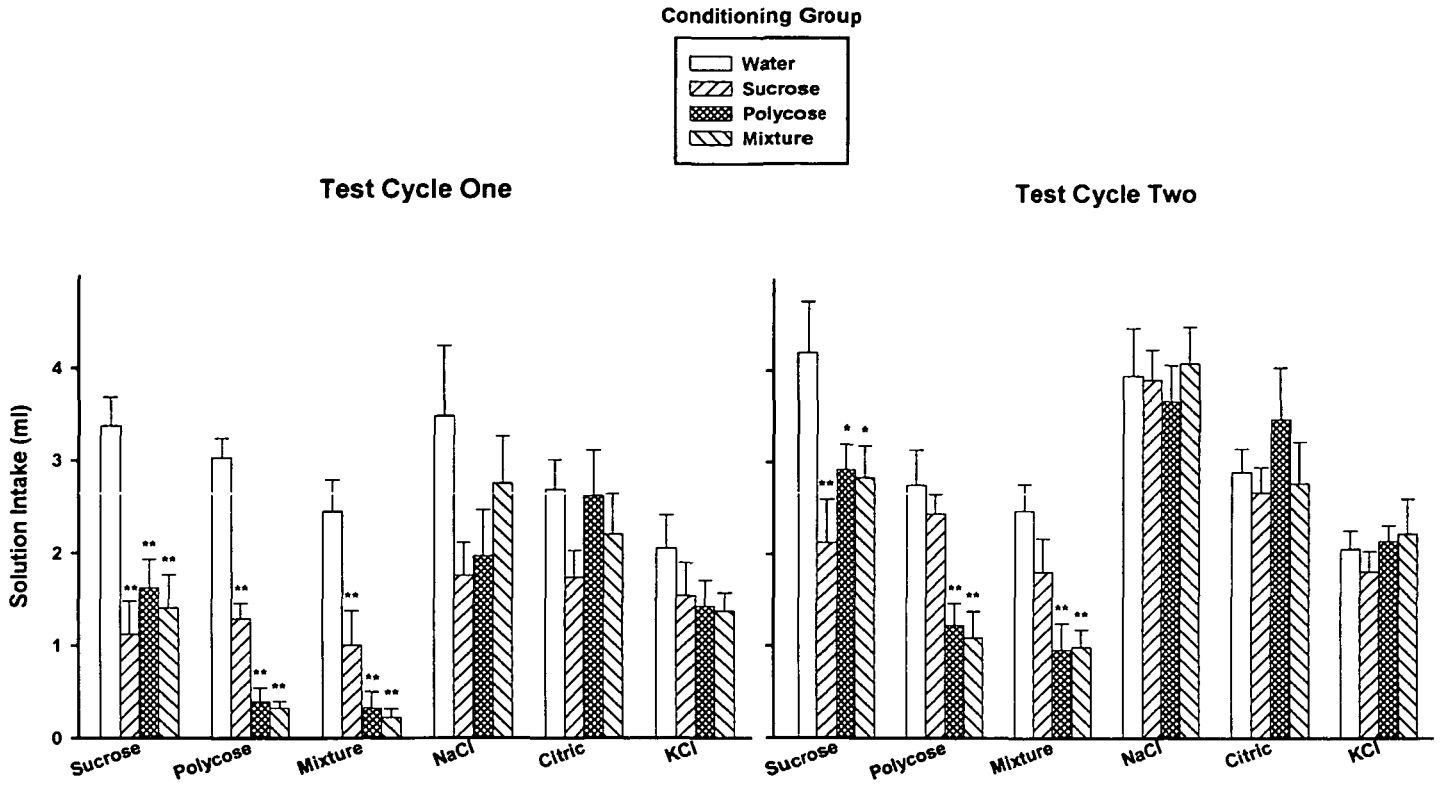

Figure 1 Test solution intakes for all groups. The pattern of intake for each test stimulus across CS groups is represented as a four-bar cluster. Intake values are means ± SE; $^{**}P < 0.01$; $^{*}P < 0.05$ versus controls.

The raw intake analysis demonstrates that each conditioning group reliably suppressed its intake of various test solutions compared with controls. However, in order to compare the qualitative perceptual taste characteristics among the three conditioning stimuli, we re-analyzed the data as relative suppression scores. The non-carbohydrate stimuli (NaCl, citric acid and KCl) were eliminated from the relative suppression analysis; these three stimuli were not conditioned and there were no significant effects on their intake.

Figure 2 (first three sets of three bars only) illustrates the mean relative suppression scores, averaged across both test cycles, to the three conditioning stimuli, for each of the three conditioning groups described previously. Since all interaction effects involving test cycle were *not* significant, group comparisons were made for each test stimulus based on the averaged relative suppression value for the two test cycles. The conditioning group main effect was not significant in the suppression score analysis [$F(2,15) = 2.68$, $P > 0.10$], indicating that total relative fluid consumption was similar between conditioning groups. A significant test cycle main effect [$F(1,15) = 87.27$, $P < 0.001$] indicated that relative suppression scores decreased from test cycle one to test cycle two, reflecting extinction of the taste aversions. Post-hoc analysis of the significant test stimulus main effect [$F(2,30) = 5.16$, $P < 0.05$] demonstrated that the overall mean suppression to sucrose (0.48) was significantly less than suppression to Polycose (0.60) or the mixture (0.64; SNK, $P < 0.05$). Polycose and mixture suppression scores did not differ from one another. Thus, relative to controls, more sucrose was consumed on average than either Polycose or the mixture. Finally, the significant conditioning group by test stimulus interaction [$F(4,30) = 6.99$, $P < 0.001$] indicated that the pattern of solution suppression varied as a function of conditioning group. This result suggests qualitative taste differences among the conditioning stimuli. Contrast analysis comparing the combined effects of the Polycose- and mixture-conditioned groups versus the sucrose group alone showed no differences between the three groups at sucrose (Figure 2). However, significant group differences were evident for the Polycose [$F(1,15) = 26.54$, $P < 0.001$] and mixture stimuli [$F(1,15) = 6.60$, $P < 0.05$]. Thus, all three conditioning groups showed similar relative suppression ratios to sucrose, but differed in their suppression to Polycose and the mixture. Contrast analyses within each conditioning group demonstrated that when sucrose was the CS, sucrose suppression was greater than Polycose suppression [Figure 2; $F(1,15) = 9.43$, $P < 0.01$] but not greater than mixture suppression [$F(1,15) = 3.04$, $P < 0.096$]. When Polycose was the CS, Polycose suppression was greater than sucrose suppression [$F(1,15) = 15.56$, $P < 0.01$] but not mixture suppression. Finally, when the CS was the

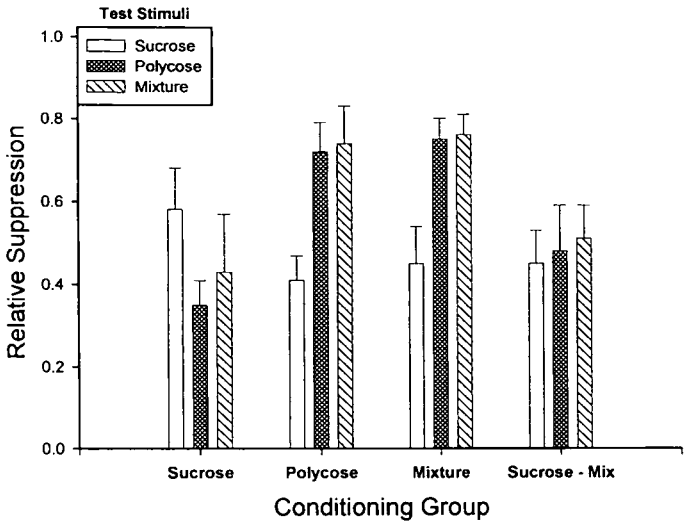

Figure 2 Relative suppression scores for all conditioning groups to the three conditioning stimuli. The pattern of suppression across three test stimuli for each of the four conditioning groups is represented as a three-bar cluster. Values are means ± SE. See text for within and between group statistical comparisons.

mixture, mixture suppression was greater than sucrose suppression [$F(1,15) = 10.68$, $P < 0.01$] but not Polycose suppression.

Because generalization responses in Polycose- and mixture-conditioned animals were virtually indistinguishable (Figures 1 and 2) it appeared that 100 mM Polycose might have overshadowed the perception of 50 mM sucrose in the mixture. In order to determine whether 50 mM sucrose was perceptible in a mixture with 100 mM Polycose we conditioned an additional group of six animals using the same protocol described earlier with the following exception. Animals in this new group were conditioned to avoid sucrose alone during the first conditioning trial and conditioned to avoid the mixture during the second conditioning trial. At issue was whether prior conditioning to sucrose would block subsequent conditioning to Polycose in the mixture.

Blocking occurs when prior conditioning to one component of a mixture interferes with subsequent learning about the second component in the mixture (Kamin, 1969). Blocking has been demonstrated previously in taste aversion paradigms (Revusky, 1971; Gillan and Domjan, 1977). We hypothesized that if 100 mM Polycose totally masked the perception of 50 mM sucrose in the mixture, then prior conditioning to sucrose should have no interfering effect on subsequent Polycose conditioning when the mixture is the CS.

Figure 2 (fourth set of three bars) illustrates the suppression scores of the sucrose first, mixture second (S-M) conditioning group. S-M suppression scores did not differ significantly from sucrose group suppression scores. Furthermore, addition of the S-M group to the relative suppression analysis did not alter any of the significance values reported previously.

In addition to the conditioning analysis reported above, we also examined the one-bottle, non-conditioned ingestion preferences of the control group under water restriction conditions. We compared control test solution intakes with control afternoon water intake (Table 2). Control water intake was averaged over the two consecutive Thursdays immediately prior to conditioning. A significant main effect of solution indicated that control animals did not consume all solutions in equal volumes [$F(6,66) = 7.60$, $P < 0.01$]. Subsequent SNK tests revealed that control hamsters drank significantly less 100 mM Polycose ($P < 0.05$) and less Polycose/sucrose mixture ($P < 0.01$) than distilled water. Control hamsters also drank significantly less 3 mM citric acid ($P < 0.05$) and less 300 mM KCl ($P < 0.01$) than water. Control animals consumed similar volumes of water, 50 mM sucrose and 30 mM NaCl. Thus, under water restricted conditions hamsters consume less Polycose than water in a single-bottle, 1 h test.

Discussion

Hamsters conditioned to avoid Polycose, sucrose, or a mixture of Polycose and sucrose, cross-generalized these stimuli to each other. Regardless of conditioning group, intakes of Polycose, sucrose and the mixture were significantly suppressed relative to controls.

Behavioral responses to test stimuli depend upon their similarity or dissimilarity to the CS. Greater taste similarity between a CS and a test stimulus is reflected as greater similarity in the aversion magnitudes between the two stimuli (Tapper and Halpern, 1968). Conversely, the more dissimilar a test stimulus is from a CS, the greater the discrepancy in aversion magnitudes between the stimuli. The current results imply that the three conditioning stimuli share common perceptual taste characteristics in the hamster. Under the current conditions NaCl, citric acid and KCl were perceived as different from the conditioning stimuli. These results are similar to work in the rat and hamster indicating that aversions to sucrose, NaCl, citric acid or KCl do not cross-generalize to one another (Frank and Nowlis, 1989; Formaker and Hill, 1990; Hill *et al.*, 1990).

The amount of associative strength acquired by a CS is reflected in the magnitude of the avoidance behavior (Rescorla and Cunningham, 1978). For any CS, greater conditioning means greater associative strength between the CS and the unconditioned stimulus (UCS). We compared the amount of associative strength of the three conditioning stimuli with a one-way ANOVA The CS group effect was not significant [$F(2,15) = 1.48$, $P > 0.25$]. Therefore, there were no reliable differences in relative CS suppression among the

Table 2 Mean test solution intake[a] (ml) in control animals (n = 12) for each test cycle, and the mean (± SE) of the two test cycles

Test cycle	Stimulus						
	Water	Sucrose	Polycose	Mixture	NaCl	Citric Acid	KCl
One	3.68	3.37	***3.03***	***2.44***	3.48	***2.68***	***2.05***
Two	4.21	4.19	***2.75***	***2.47***	3.95	***2.89***	***2.05***
Mean (SE)	3.95 (0.20)	3.78 (0.41)	***2.89*** (0.23)	2.45 (0.29)	3.71 (0.60)	***2.79*** (0.24)	2.05 (0.25)

[a]Significant differences from water intakes are in bold italics ($P < 0.05$).

three original conditioning groups (sucrose: 0.58 ± 0.10, Polycose: 0.72 ± 0.07; mixture: 0.76 ± 0.05) and all three conditioning stimuli were effective in their ability to sustain a taste aversion.

The present work agrees with previous results in the rat (Nissenbaum and Sclafani, 1987). However, absolute differences in test solution intake between control and conditioning groups were not reported; all intake data were first converted to percent suppression scores and these scores were then analyzed for between-group differences. The percent suppression score for 100 mM sucrose was ~30% in rats conditioned to avoid 25 mM Polycose (Nissenbaum and Sclafani, 1987). In the current study, the percent suppression score for 50 mM sucrose was ~40% in hamsters conditioned to avoid 100 mM Polycose. Thus, hamsters and rats conditioned to avoid Polycose suppress their intake of sucrose relative to controls.

In contrast to a previous study by Rehnberg *et al.* (1996), we were successful in establishing an aversion to Polycose in the hamster. However, we increased the concentration of Polycose from 32 to 100 mM and used two conditioning trials instead of one. Hence, direct comparisons between the two studies are not possible. Given that hamsters in the Rehnberg *et al.* (1996) study were able to acquire an aversion to 32 mM glycogen, another polysaccharide, in one conditioning trial and that glycogen preference scores were similar to 100 mM Polycose scores, it is possible that we could have established an aversion to 100 mM Polycose with a single conditioning trial. However, we used two trials in an effort to insure an aversion to Polycose.

Figure 2 illustrates that the pattern of aversion generalizations to Polycose was virtually indistinguishable from generalizations to the mixture of sucrose with Polycose. The fact that mixture-conditioned animals were no different behaviorally than Polycose-conditioned animals suggests that when 100 mM Polycose is mixed with 50 mM sucrose, Polycose is the more salient component of the mixture. Less salient stimuli are not as effective as more salient stimuli in acquiring associative strength with the UCS and therefore result in weaker taste aversions. Hence, the more salient component of a binary mixture acquires more associative strength with the UCS.

Previous research has demonstrated that animals conditioned to avoid a heterogeneous binary mixture and tested on one of the components alone show little degradation (14%) of the original aversion (Frank, 1989). In contrast, animals conditioned to a single CS and tested with a heterogeneous binary mixture containing that CS show a larger degradation (42%) of the original aversion on average (Frank, 1989). In the current study, we did not see the pattern of degradation seen for heterogeneous taste mixtures (i.e. mixtures of stimuli that do not cross-generalize). We saw minimal degradation (1%) of the mixture aversion when tested with Polycose and no degradation of the Polycose aversion (–4%) when tested with the mixture. However, we saw considerable degradation of the mixture aversion (40%) when tested with sucrose and some degradation of the sucrose aversion (26%) when tested with the mixture. These results suggest, in part, that Polycose was the more salient component of the mixture.

The significant CS group-by-taste stimulus interaction, illustrated in Figure 2 and described in the results, demonstrates that hamsters do not find Polycose and sucrose to be qualitatively identical. Previous research has demonstrated that when two conditioning stimuli were qualitatively similar in taste, the stimulus generalization patterns between the conditioning groups were positively correlated (Smith *et al.*, 1979). Examination of the generalization patterns in Figure 2 shows close concordance (Pearson r = +0.94) between the Polycose- and mixture-conditioned animals, indicating that these two stimuli shared a large degree of qualitative similarity. In contrast, the relationship between the generalization patterns of sucrose- and Polycose-conditioned animals is not as great (r = +0.60). The 42% generalization decrement of the Polycose aversion when tested with sucrose is consistent with the idea that Polycose was more intense than sucrose. However, the 41% degradation of the sucrose aversion when tested with Polycose suggests a qualitative difference between these two stimuli. Animals conditioned to a less intense stimulus and tested on a more intense stimulus show similar or even greater avoidance of the more intense stimulus on subsequent testing (Nowlis, 1974; Formaker and Hill, 1990). If sucrose was less intense than Polycose but had the same taste quality, then the aversion to sucrose should have shown equal or greater suppression to Polycose, not

less (Nowlis, 1974; Spector and Grill, 1988; Frank and Nowlis, 1989; Formaker and Hill, 1990). Thus, while Polycose and sucrose may share a taste percept, the hamster does not find the total perception of these two stimuli to be qualitatively equivalent.

The results of the S-M group indicate that 50 mM sucrose was perceptible in the mixture with 100 mM Polycose. The pattern of aversion generalization in the S-M group was similar to the sucrose group (Figure 2). Prior conditioning to sucrose interfered with subsequent Polycose conditioning. This suggests that sucrose was detectable in the mixture with Polycose. Thus, there must be distinguishing perceptual characteristics between Polycose and sucrose.

Hamsters prefer Polycose to water under water-replete conditions (Rehnberg *et al.*, 1996). Because the preference data from the Rehnberg *et al.* (1996) study were collected with 48 h, two-bottle preference tests, under water-replete conditions, direct comparisons between that study and the current study are not possible. Regardless, results from the current control group indicate that under water-restricted conditions, with a 1 h, one-bottle intake test, hamsters consume less Polycose or solutions containing Polycose than they do water. This suggests that the physiological state of the animal or the length of time over which intake is measured, or both, may play a role in Polycose taste preference. It is possible that the supplemental calories of Polycose may also influence the post-ingestional effects of long-term intake in the hamster (Pfaffmann, 1960).

In summary, sucrose and Polycose share a common taste percept in the hamster because these two stimuli, or mixtures containing these stimuli, cross-generalize with each other. However, the pattern of taste generalizations and the results of the S-M group also indicate that Polycose has other characteristics that make it different from the taste of sucrose.

Acknowledgement

This research was supported by NIH Grant DC-00058 to M.E.F.

References

Ackroff, K., Manza, L. and **Sclafani, A.** (1993) *The rat's preference for sucrose, polycose and their mixtures*. Appetite, 21, 69–80.

Beidler, L.M., Fishman, I.Y. and **Hardiman, C.W.** (1955) *Species differences in taste responses*. Am. J. Physiol., 181, 235–239.

Feigin, M.B., Sclafani, A. and **Sunday, S.R.** (1987) *Species differences in polysaccharide and sugar taste preferences*. Neurosci. Biobehav. Rev., 11, 231–240.

Formaker, B.K. and **Hill, D.L.** (1990) *Alterations in salt taste perception in the developing rat*. Behav. Neurosci., 104, 356–364.

Frank, M.E. (1989) *Processing of mixtures of stimuli with different tastes by primary mammalian taste neurons*. In Laing, D.G., Cain, W.S., McBride, R.L. and Ache, B.W. (eds), Perception of Complex Smells and Tastes. Academic Press, New York, pp. 127–147.

Frank, M.E. and **Nowlis, G.H.** (1989) *Learned aversions and taste qualities in hamsters*. Chem. Senses, 14, 379–394.

Gillan, D.J. and **Domjan, M.** (1977) *Taste-aversion conditioning with expected verses unexpected drug treatment*. J. Exp. Psychol.: Anim. Behav. Proc., 3, 297–309.

Hill, D.L., Formaker, B.K. and **White, K.S.** (1990) *Perceptual characteristics of the amiloride-suppressed sodium chloride taste response in the rat*. Behav. Neurosci., 104, 734–741.

Kamin, L.J. (1969) *Predictability, surprise, attention, and conditioning*. In Campbell, B.A. and Church, R.M. (eds), Punishment and Aversive Behavior. Appleton, New York, pp. 274–296.

Lawless, H.T. (1986) *Sensory interactions in mixtures*. J. Sens. Stud., 1, 259–274.

McBride, R.L. (1988) *Taste reception of binary sugar mixtures: psychophysical comparison of two models*. Percept. Psychophys., 44, 167–171.

McBurney, D.H. and **Shick, T.R.** (1971) *Taste and water taste of twenty-six compounds for man*. Percept. Psychophys., 10, 249–252.

Nachman, M. (1963) *Learned aversions to the taste of lithium chloride and generalizations to other salts*. J. Comp. Physiol. Psychol., 56, 343–349.

Nissenbaum, J.W. and **Sclafani, A.** (1987) *Qualitative differences in polysaccharide and sugar tastes in the rat: a two-carbohydrate taste model*. Neurosci. Biobehav. Rev., 11, 187–196.

Nowlis, G.H. (1974) *Conditioned stimulus intensity and acquired alimentary aversions in the rat*. J. Comp. Physiol. Psychol., 86, 1173–1184.

Nowlis, G.H. and **Frank, M.E.** (1981) *Quality coding in gustatory systems of rats and hamsters*. In Norris, D.M. (ed.), Perception of Behavioral Chemicals. Elsevier/North Holland, Amsterdam, pp. 59–80.

Nowlis, G.H., Frank, M.E. and **Pfaffmann, C.** (1980) *Specificity of acquired aversions to taste qualities in hamsters and rats*. J. Comp. Physiol. Psychol., 94, 932–942.

Pfaffmann, C. (1960) *The pleasures of sensation*. Psychol. Rev., 67, 253–268.

Rehnberg, B.G., MacKinnon, B.I., Hettinger, T.P. and **Frank, M.E.** (1996) *Analysis of polysaccharide taste in hamsters: behavioral and neural studies*. Physiol. Behav., 59, 505–516.

Rescorla, R.A. and **Cunningham, C.L.** (1978) *Within-compound flavor associations*. J. Exp. Psychol., 4, 267–275.

Revusky, S. (1971) *The role of interference in associations over a delay*. In Honig, K.W. and James, P.H.R. (eds), Animal Memory. Academic Press, New York, pp. 155–213.

Sclafani, A. (1987) *Carbohydrate taste, appetite, and obesity: an overview*. Neurosci. Biobehav. Rev., 11, 131–153.

Shallenberger, R.S. and **Acree, T.E.** (1971) *Chemical structure of compounds and their sweet and bitter taste*. In Beidler, L.M. (ed.), Handbook of Sensory Physiology. Springer-Verlag, New York, Vol. IV, pp. 221–277.

Smith, D.V. (1989) *Neural and behavioral mechanisms of taste mixture perception in mammals*. In Laing, D.G., Cain, W.S., McBride, R.L. and Ache, B.W. (eds), Perception of Complex Smells and Tastes. Academic Press, New York, pp. 149–170.

Smith, D.V., Travers, J. and **VanBuskirk, R.** (1979) *Brainstem correlates of gustatory similarity in the hamster*. Br. Res. Bull., 4, 359–372.

Smith, J.C., Williams, D.P. and **Jue, S.H.** (1976) *Rapid oral mixing of glucose and saccharin by rats*. Science, 191, 304–305.

Spector, A.C. and **Grill, H.J.** (1988) *Differences in the taste quality of maltose and sucrose in rats: issues involving the generalization of conditioned taste aversions*. Chem. Senses, 13, 95–113.

Tapper, D.N. and **Halpern, B.P.** (1968) *Taste stimuli: a behavioral categorization*. Science, 161, 708–710.

Tonosaki, K. and **Beidler, L.M.** (1989) *Sugar best single chorda tympani nerve fiber responses to various sugar stimuli in rat and hamster*. Comp. Biochem. Physiol., 94A, 603–605.

Accepted June 18, 1998