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Taste reception of binary sugar mixtures: Psychophysical comparison of two models

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The taste reception of binary sugar mixtures may be described by (1) the single-site model, in which the sugars compete for reception at the same receptor sites, or (2) the separate-sites model, in which the sugars are transduced at independent receptor sites and then integrated in a common effector system. These models make different predictions about the sweetness of the mixture relative to the sweetness of its components. Two experiments, one using sucrose and fructose and the other using glucose and fructose, provide support for the separate-sites model, although its exact formulation has yet to be resolved. The separate-sites model can account for the phenomenon of supplemental action ("synergism") sometimes observed in binary sugar mixtures.

In the taste reception of a binary sugar mixture, do the sugars compete for reception at the same receptor sites, or is there a different type of receptor site for each sugar? This is an important question for both the physiology and psychophysics of taste, and of some relevance to food scientists, since binary sugar mixtures (e.g., high-fructose corn syrup) are now of considerable commercial importance (McBride, 1986b). This article reports a psychophysical investigation.

Beidler (1954) proposed the following equation to account for the *neural* response to a taste stimulus:

$$R/R_{max} = CK/(1+CK), \qquad (1)$$

where R is neural response, R_{max} the maximum (saturated) neural response, C the (molar) stimulus concentration, and K the association (binding) constant of the stimulus. Equation 1 provides, however, a good description not only of the neural taste response in animals (e.g., see De Graaf & Frijters, 1986; Maes, 1985), but also of the *psychophysical* taste response in humans (Beidler, 1987; McBride, 1987a, 1987b).

For human taste, the sugars sucrose, fructose, and glucose have been found to have approximately the same R_{max}, but differing K values of 5.3, 3.3, and 1.6, respectively (McBride, 1987b). Figure 1 shows the psychophysical functions for sucrose and fructose as calculated from Equation 1, with percentage weight per volume (% w/v) as the stimulus unit. Both functions are consistent with previous work in which other scaling methods were used (De Graaf, Frijters, & van Trijp, 1987; McBride, 1983a, 1983b, 1986a, 1987a, 1987b; Schutz & Pilgrim, 1957).

Mixtures: Single-Site Model

By assuming that the two sugars in a binary mixture compete for absorption at the same receptor sites, and by further assuming that R_{max} is constant for sugars and their mixtures, the sweetness of the mixture may be given as (Beidler, 1962, 1987)

$$R_{AB}/R_{max} = (C_A K_A + C_B K_B)/(1 + C_A K_A + C_B K_B), \qquad (2)$$

where R_{AB} is the taste response to a mixture of sugars A and B, R_{max} is the maximum (saturated) taste response, K_A and K_B are, respectively, the association constants of sugars A and B, and C_A and C_B are molar concentrations. The predicted curve for an equal-parts mixture is given in Figure 1. The abscissa values represent total weight per volume; thus, at the 10.0% mark, the sucrose concentration is 10 g/100 ml, the fructose concentration is 10 g/100 ml, and the mixture consists of (5.0 g sucrose + 5.0 g fructose)/100 ml.

The model has met with mixed success, being supported by some neurophysiological studies (e.g., Jakinovich & Oakley, 1976) but not by others (Jakinovich, 1982). At the psychophysical level, the limited evidence is also equivocal: Beidler (1987) claimed support for the model with sucrose–glucose mixtures, whereas De Graaf and Frijters (1986) found it to underestimate the sweetness of glucose–fructose mixtures (G/F) at high concentration.

Mixtures: Separate-Sites Model

Jakinovich (1982) found the single-site model unable to account for the neurophysiological response of the gerbil to sucrose–saccharin mixtures. He proposed the alternative formulation

$$R_{AB} = R_A + R_B - (R_A \cdot R_B/R_{max}), \qquad (3)$$

where R_{AB} is the response to the mixture of A and B, R_{max} is maximum response, and R_A and R_B are, respectively, the responses to components A and B. The mixture curve predicted by Equation 3 is given in Figure 1, with values for R_A and R_B obtained from Equation 1. This model represents the "interaction of two substances with two independent receptor sites through a common effector sys-

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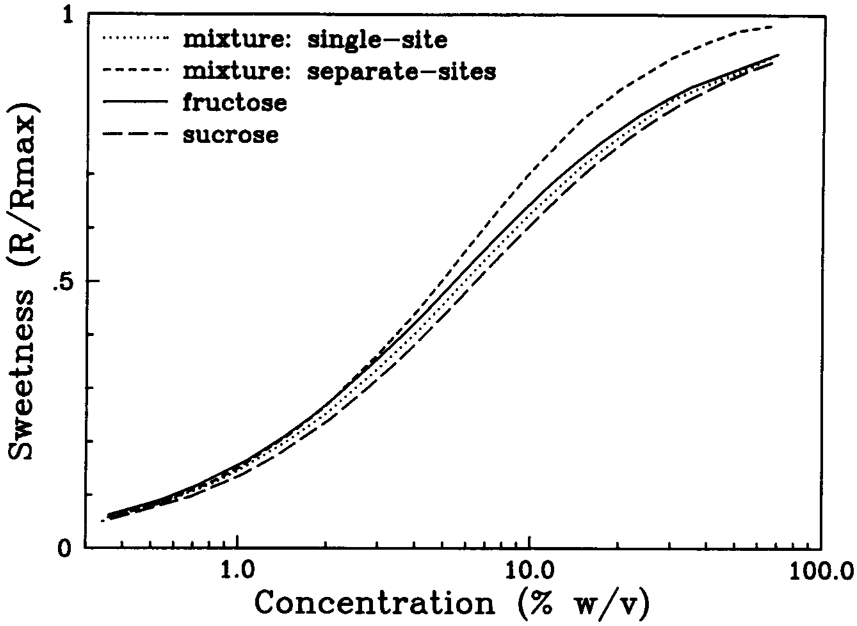

Figure 1. Psychophysical functions for sucrose, fructose, and an equal-parts (by weight) mixture of the two as specified by the single-site and separate-sites reception models (% w/v = percentage weight per volume).

tem which limits the maximum response" (Jakinovich, 1982, p. 50). Support for this model was inferred in a recent psychophysical study on sugar mixtures (McBride, 1986b), but a critical, quantitative check was not practicable.

Model Predictions

As Figure 1 shows, at low concentration (around 1.0%) the two predicted mixture curves lie almost one upon the other. The curves diverge, however, with increasing concentration: The single-site model predicts that the sweetness of the mixture will always lie between the sweetnesses of equivalent concentrations of each sugar alone, whereas the separate-sites model predicts a faster growth of sweetness against concentration, with the sweetness of the mixture exceeding that of sucrose alone above 2.2%.

This predicted disparity permits a simple empirical check. If the single-site model is correct, then, irrespective of the concentration level, the sweetness of the sucrose-fructose mixture (S/F) will lie between the sweetnesses of equivalent concentrations of sucrose alone (S) and fructose alone (F); that is, F > S/F > S. On the other hand, if the separate-sites model is correct, the relative sweetness of the mixture will vary with concentration level. Below 2.2%, the predicted ordering is F > S/F > S; above 2.2%, the prediction is S/F > F > S.

Figure 2 shows a similar picture for fructose, glucose, and an equal-parts mixture of each. Here the disparity between the mixture models is not as pronounced as in Figure 1, but it follows the same trend: For the single-site model, F > G/F > G at all concentration levels; for the separate-sites model, F > G/F > G below 11.0%, but G/F > F > G above 11.0%.

The choice of stimulus unit warrants brief comment. Weight per volume, rather than molarity, was used in the following sweetness comparisons, because stimuli of equivalent concentration are then also of equivalent viscosity. This is not necessarily the case in molarities: 1.0 M sucrose (34.2%) is more viscous than 1.0 M fructose (18.0%), which might confound the sweetness comparison.

EXPERIMENT 1

Method

Subjects. Five women and 5 men, employees of the CSIRO Food Research Laboratory, served as subjects. All participated voluntarily, and most had had experience in sensory testing.

Stimuli. All stimuli consisted of reagent-grade sugar(s) dissolved in distilled water. There were three types of stimuli: sucrose alone, D-fructose alone, and an equal-parts (by weight) mixture of the two. Each of these was made up at five concentration levels: 1.0%, 3.2%, 10.0%, 17.8%, and 31.6% (½ log unit steps except for 17.8%, which is spaced at ¼ log unit).

Solutions were made up at least 24 h before testing and stored at 5° C for no longer than 4 days before use. Each stimulus was 30 ml of solution in a small glass tumbler, served at room temperature (21° C).

Procedure. One concentration level was assessed at each of five testing sessions. Order of assessment of the concentration levels was randomized. At a single session, each subject tasted 12 pairs of coded solutions (4 pairs each of F vs. S, S/F vs. S, and S/F vs. F). The tasting order of the 12 pairs was randomized, and tasting order within pairs was counterbalanced.

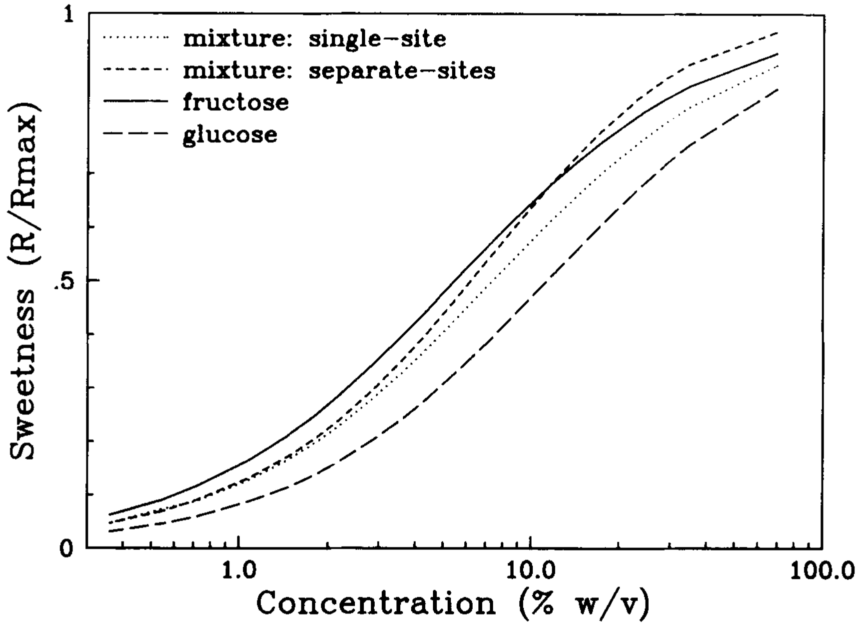

Figure 2. Psychophysical functions for glucose, fructose, and an equal-parts (by weight) mixture of the two as specified by the single-site and separate-sites reception models (% w/v = percentage weight per volume).

Subjects were required to "sip and spit" the solutions within each pair, then to choose the sweeter solution. "No difference" responses were not permitted. Rinsing with distilled water during a 20-sec break was mandatory between pairs.

Results

There were 40 responses to every pair; response frequencies are given in Table 1. In all but 2 of the 15 pairs in Table 1, the response split was significantly different ($p < .05$) from that expected by chance (i.e., $p = .5$, binomial test).

Data were analyzed by the Friedman rank analysis of variance (e.g., see Conover, 1971). For the F versus S comparison, there was no significant change in the response split with concentration level [$\chi^2(4, N{=}200) = 4.24$, $p = .37$]. However, the change in response split with concentration level was significant for both the S/F versus S comparison [$\chi^2(4, N{=}200) = 15.28$, $p = .004$] and the S/F versus F comparison [$\chi^2(4, N{=}200) = 10.88$, $p = .03$].

Table 1
Numbers of "Sweeter" Responses in Experiment 1

Concentration	Sugar Pair: F vs. S		S/F vs. S		S/F vs. F	
1.0%	38	2	27	13	8	32
3.2%	36	4	38	2	19	21*
10.0%	31	9	38	2	31	9
17.8%	33	7	39	1	26	14
31.6%	30	10	35	5	24	16*

Note—Except for the pair marked with an asterisk, all response splits are significantly different ($p < .05$) from chance occurrence.

In the F versus S comparison, fructose was sweeter than sucrose at all concentration levels, consistent with their psychophysical functions in Figure 1. The S/F versus S comparison also shows the mixture to be sweeter than sucrose at all concentration levels, although the difference is not as pronounced at the bottom (1.0%) concentration level. For the S/F versus F comparison, however, there is a clear reversal in relative sweetness with increase in concentration. At 1.0%, fructose is significantly sweeter than the mixture; at 3.2%, the sweetnesses are nearly equivalent; and at 10.0%, the mixture is significantly sweeter than the fructose. At the top concentration, the mixture is chosen as sweeter more often than the fructose, but the difference is not statistically significant.

Overall, there was a significant effect of order of tasting, with the first solution tasted being identified as sweeter in 344 of the 600 pairs ($p < .05$).

EXPERIMENT 2

Method

Experiment 2 was conducted 8 weeks after Experiment 1. Five men and 5 women participated, 8 of whom had served in Experiment 1; the other 2 were drawn from the same pool. The stimuli in this experiment were D-fructose, D-glucose, and an equal-parts (by weight) mixture of the two. In all other respects, Experiment 2 was identical to Experiment 1.

Results

Table 2 contains the response frequencies; all but one of the response splits were significantly different ($p < .05$) from chance.

Table 2
Numbers of "Sweeter" Responses in Experiment 2

	Sugar Pair					
Concentration	F vs. G		G/F vs. G		G/F vs. F	
1.0%	40	0	33	7	3	37
3.2%	40	0	39	1	2	38
10.0%	40	0	40	0	8	32
17.8%	39	1	38	2	11	29
31.6%	33	7	38	2	18	22*

Note—Except for the pair marked with an asterisk, all response splits are significantly different ($p < .05$) from chance occurrence.

In the F versus G comparison, fructose was markedly sweeter at all concentration levels, consistent with the curves for the single sugars in Figure 1. Accordingly, there was no significant shift in response split with concentration [$\chi^2(4, N{=}200) = 4.08, p = .40$]. Similarly, in the G/F versus G comparison, the mixture was clearly sweeter than the glucose alone at all concentration levels, and there was no shift in response split with concentration [$\chi^2(4, N{=}200) = 1.84, p = .77$]. For the G/F versus F comparison, however, there was an obvious shift in the response split with concentration [$\chi^2(4, N{=}200) = 13.52, p = .009$]. At 1.0% and 3.2%, fructose was markedly sweeter than the glucose–fructose mixture; at 10.0%, fructose was sweeter but the difference had diminished slightly; at 17.8%, the difference had diminished still further; and at 31.6%, the sweetnesses of the glucose–fructose mixture and the fructose alone appeared to be almost equivalent.

No systematic effect of order of tasting was observed; the first solution tasted was chosen as sweeter in 307 of the 600 pairs.

DISCUSSION

Which Model?

In Experiments 1 and 2, the critical comparisons are S/F versus F and G/F versus F, respectively. Data from the other comparisons are consistent with either model. In Experiment 1, data from the S/F versus F comparison are compatible with the separate-sites model but difficult to reconcile with the single-site model. The shift in relative sweetness in Table 1 is exactly as predicted by the separate-sites model in Figure 1, and consistent with the indications of a previous study (see McBride, 1986b, Figure 7). Similarly, in Experiment 2 the data from the G/F versus F comparison are more consistent with the separate-sites model than with the single-site model, although the agreement between model and data in this case is not as impressive.

These results support those other lines of work that have claimed multiple receptor sites for sweetness (Bartoshuk, 1987; Beidler & Tonosaki, 1984; Faurion, Saito, & MacLeod, 1980; Jakinovich, 1982; Schiffman, Cahn, & Lindley, 1981). A separate-sites model could also explain why, in psychophysical investigations of sugar mixtures with the equiratio model (De Graaf et al., 1987; Frijters, De Graaf, & Koolen, 1984; Frijters & Oude Ophuis, 1983), the sweetness of a mixture is often found to be disproportionately closer to that of an equimolar concentration of the sweeter component alone.

At the same time, data from the equiratio approach raise questions about the separate-sites model as formulated in Equation 3. The separate-sites model predicts that, at high molar concentration, the sweetness of a glucose–fructose mixture will exceed the sweetness of equimolar fructose alone (see Figure 2; this plot does not change when expressed in molar concentration, because fructose and glucose share the same molecular weight). However, in a literature survey of the sweetness of binary mixtures, De Graaf and Frijters (1987) found that the sweetness of a mixture would approach, but never exceed, the sweetness of an equimolar concentration of the more potent component alone. Their finding is confirmed by the data in Table 2: At 31.6%, the sweetness of G/F does not exceed the sweetness of F as predicted by the separate-sites model in Figure 2. Similarly, in Table 1, the response splits for S/F versus F, at the two highest concentrations, do not support the magnitude of the sweetness disparity predicted by Figure 1.

There are a number of possibilities for this failure of prediction. One possibility is that R_{max} may not, in fact, be exactly the same for individual sugars and their mixtures. If the R_{max} for a sucrose–fructose mixture were slightly lower than the R_{max} for the single sugars, then the curve for the separate-sites model would not reach the sweetness level predicted in Figure 2. However, this slight change in the mixture R_{max} would have little effect on the model's prediction at the lower concentrations, which was shown to be especially good in Experiment 1. Precise specification of R_{max} values merits further investigation.

Another possibility is that it may be overly simplistic to speak of a dichotomy of single (dependent) versus multiple (independent) receptor sites. Perhaps receptor sites are partially dependent, with the degree of dependence (overlap) proportional to concentration. In this case, Equation 3 would predict well at low concentrations but would predict greater differences than obtained at higher levels.

Supplemental Action

The separate-sites model can account for the supplemental action observed with sugar mixtures—that is, the greater-than-expected sweetness of a mixture relative to its components (e.g., Cameron, 1947). An example of this effect is evident in Table 1. Note that 10.0% fructose is sweeter than 10.0% sucrose (i.e., F > S); however, when half of the fructose is replaced by the less potent sucrose, the sweetness *increases* rather than decreases (i.e., S/F > F).

This paradoxical effect occurs because the psychophysical functions for sugars are negatively accelerated. The sweetness at 5.0% sucrose is considerably greater than half the sweetness at 10.0% sucrose (see Figure 1). The same applies to fructose. Thus, when the sweetnesses of 5.0% sucrose and 5.0% fructose are combined according to Equation 3, their combination exceeds that of 10.0% fructose alone. Note that this effect is in no way "synergistic"; in fact, Equation 3 specifies the sweetness of the mixture to be *less* than the sum of its components. This intriguing phenomenon explains why, in sweetening power, a sugar mixture can sometimes offer an advantage over a single sugar.

Order Effect

Analysis of the effect of tasting order in Experiment 1 revealed it to be due almost solely to the S/F versus F comparison, in which the first solution tasted was judged to be sweeter in 140 of the 200 pairs presented. Collapsed over concentrations, the sweetness discrepancy in this comparison was small: Of the total 200 pairs tasted, there were 108 responses for S/F and 92 for F. This near equivalence in sweetness may have rendered the bias more noticeable; perhaps an order bias operated in all cases but became inconsequential (or at least indetectable) when the sweetness difference was more clear-cut, as in Experiment 2.

The net effect of an order bias is to desensitize the comparison, and it appears to be an idiosyncratic feature of side-by-side taste evaluations. For example, in a triangle test determination of taste threshold, McBride and Laing (1979) found a significant order bias for the sample tasted *last*.

Psychophysics and Reception Mechanisms

Use of the Beidler equation represents another avenue for taste psychophysics. Traditionally, psychophysical functions have been specified in a purely descriptive manner—slopes, intercepts, exponents—with little mechanistic interpretation. In Equations 1-3, however, the psychophysical parameters relate to physiologically meaningful characteristics of the stimulus—to numbers of effective receptor sites and to binding efficacy. Furthermore, the left-hand sides of Equations 1-3 offer standardized scales for taste measurement, varying from 0 (no taste) to 1 (saturation). These end points are asymptotes, only theoretically attainable, and in this respect the scale bears similarity to certain physical scales (e.g., Kelvin scale of temperature). On the practical side, application of Equations 1 and 3 will allow the technologist to predict the sweetness of single sugars and their binary mixtures from knowledge of their physical concentrations alone.

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