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A behavioral analysis of the ingestion of glucose, maltose and maltooligosaccharide by rats

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Abstract

Glucose, maltose, and Polycose are stimuli that differ in their effectiveness in stimulating ingestion in the rat. To understand better how variation in glucose chain length affects the ingestion of these compounds, we compared the effect of six concentrations of glucose, maltose, and maltooligosaccharide (MOS) on the microstructure of the licking behavior of the rat. At the three lowest concentrations the order of effectiveness in stimulating ingestion was MOS > maltose > glucose. At the three highest concentrations, there were no differences among the three compounds in volume ingested. As measured by initial rate of licking, the orosensory stimulating effectiveness of the three compounds were ordered as MOS > maltose > glucose. The magnitude of the negative feedback signals were very similar for MOS and maltose and greater than glucose at all but the highest two concentrations of glucose, suggesting that glucose chain length, not caloric density, is responsible for the differences in the magnitude of negative feedback. With the three lowest concentrations, the ordering of the compounds in their ability to stimulate intake depended on orosensory stimulating ability.

Keywords: Glucose; Maltose; Maltooligosaccharide; Licking behavior; Microstructure of ingestion; Negative feedback; Orosensory stimulation

1. Introduction

It is well documented that the monosaccharide glucose and the disaccharide maltose, both of which taste sweet to humans, are capable of stimulating ingestion in nonfood-deprived rats. More recently, investigators have shown that glucose polymers of variable chain lengths, such as Polycose [8], and maltooligosaccharide [7], are also very effective in-stimulating intake in nonfood-deprived rats. The ingestion of the polysaccharide starches is especially interesting, because they are ingested preferentially to sucrose, maltose, and glucose [9], and do not taste particularly sweet or palatable to humans [6]. The reasons that the number of glucose units in the chain affect ingestion differentially are not known, but differences in both taste and postingestive effects have been implicated.

A study of the ingestion of glucose, maltose, sucrose, and Polycose by rats [9] reported no differences in intake between Polycose and maltose at each of six concentrations (1, 2, 4, 8, 16, and 32%) tested. However, their rats ingested more of both of these carbohydrates than glucose when they were tested with the three lowest concentrations. This difference in intake was accounted for, at least in part, by the orosensory properties of the solutions, because both Polycose and maltose elicited many more licks during the first 3 min of the tests than did glucose. Postingestive factors must also have played a role because, although the intakes of 1 and 2% maltose and Polycose were the same, maltose elicited many more licks (~250) during the first 3 min of the tests than did Polycose. Postingestive stimulation occurring later in the test must have been greater for maltose than Polycose to have kept the total intakes the same.

In this study, we sought to extend these analyses of the effects of varying length glucose polymers [G1 (glucose), G2 (maltose), and G1–G30 or higher (Polycose) to maltooligosaccharide]. Maltooligosaccharide (MOS) is a mixture of glucose polymers, almost exclusively (96%) oligosaccharides, distributed roughly equally between polymers of three to six glucose molecules. The remaining 4% are glucose chains seven to nine units in length. Thus, while similar to Polycose in its complexity, it is simpler in that it contains no glucose (G1) or maltose (G2) or any polymers longer than nine glucose units. By exploring the similarities and differences in the licking behavior of rats ingesting glucose, maltose, and MOS, we hoped to obtain a more thorough under-

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standing of the control of ingestion of simple glucose-derived carbohydrates, and to supplement the work of Sclafani et al. [10]. We would also liked to have used maltotrios (G3 alone) but it is too expensive to use in intake studies.

We used the microstructural analysis of licking behavior [5] to describe how the three carbohydrates differed in their effects on ingestive behavior. This type of analysis has been applied to the licking behavior of rats ingesting sucrose and maltose [5] and Polycose [2]. It has not yet been applied to glucose, a commonly used test solution, or to maltooligosaccharide, which also is a very effective stimulant of ingestion [7,10,11]. We used six concentrations of MOS, maltose, and glucose spanning the range from 1 to 32% in equal log steps. The effects of concentration of glucose and maltose on some features of the ingestive behavior of rats are well known, but the effect of variation of the concentration of MOS on ingestive behavior is not. We felt that by examining the orosensory and postingestional effects of these three substances on licking behavior, we would be able to understand better how starches differ in their control of intake from the simpler mono- and diglycerides, glucose, and maltose.

2. Materials and methods

2.1. Subjects

The subjects were 30 male albino rats of the Sprague–Dawley strain bred in the animal colony of the Department of Psychology at the University of Illinois at Chicago where the data were collected. They ranged in weight from 385 to 423 g at the beginning of the experiment. They were divided into three groups of 10 each, with one group tested on MOS, another on maltose, and the third on glucose. Room temperature was 21 ± 1°C, and the room lights were on from 0600 to 1700 h daily. The rats were maintained on ad lib food (Purina lab chow) and water throughout the experiment except for two preliminary training trials and during the 30-min test sessions when only the test solution was available.

2.2. Training and testing

To train the rats to drink from the drinking tubes in the test cages they were water deprived at 1700 h and tested with water in the drinking tubes at 1000 h the following day. Two days of this training were sufficient to train all the rats to approach the drinking tube and drink promptly. Following this adaptation period, the rats were returned to an ad lib food and water schedule.

From this point on the test solutions were different concentrations of glucose (Sigma), maltose (Sigma) or maltooligosaccharide (M138, Pfanstiehl Laboratories, Waukegan, IL). Six different concentrations of each were used: 1, 2, 4, 8, 16, and 32% (w/v). Each concentration was offered for 2 consecutive days in the order of increasing concentration. The data analyzed were those obtained on the second of the two tests, to allow for some degree of familiarity to each novel concentration.

2.3. Data recording

All testing was done in wire mesh cages measuring 24 cm wide × 20 cm high × 29 cm deep. A stainless steel drinking tube inserted in a 60-mL calibrated tube was mounted 6 cm above the floor centered on the front of the cage. It was connected to an amplifier (DiLog Instruments), which passed <60 nanoamps through the animal each time its tongue made contact with the tube. This current was amplified and fed to a PC computer that stored the onset time of each tongue contact to the nearest msec in a data array in memory. At the end of the test session, these data were transferred to a data file for later analysis.

2.4. Data analysis

We measured the rate at which the rats ingested the solutions during the tests by calculating the number of licks in 3-min intervals on each test. These individual animal curves were fit to the linear function $y = a + bt$. This function was chosen because it is the simplest one that can provide an initial rate of licking estimate (a) and a rate of decline in the rate of licking (b). These two variables have been shown to be useful in analyzing two of the variables that control meal size, the initial stimulating effectiveness of the test solution, and the magnitude of negative feedback. Different functions fit our data better in many individual cases, but a linear function provided a reasonable good fit in most instances. Thus, this function provided a common metric by which the value of the initial rate and decline in the rate of licking

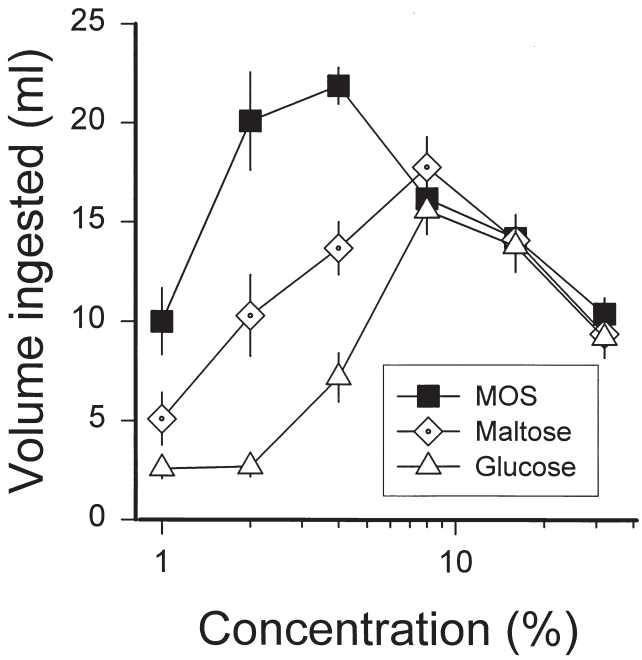

Fig. 1. Mean volume ingested (±1 SE) of the three carbohydrates as a function of concentration.

Table 1
Mean meal duration and SEs for the test solutions in minutes

	1%	2%	4%	8%	16%	32%
MOS	18.4	25.0	23.7	17.0	17.0	14.8
SE	2.4	0.9	0.9	2.2	1.2	1.5
Maltose	18.5	17.2	18.6	18.6	12.8	11.9
SE	1.8	2.6	1.5	1.6	1.3	1.3
Glucose	23.8	17.1	19.5	20.7	17.8	23.3
SE	1.3	2.4	2.7	1.2	2.0	1.1

could be compared across the six concentrations of the three carbohydrates. An average rate of licking curve for each concentration of the three carbohydrates was obtained by averaging the individual animal curves.

We analyzed the licking behavior of the rats at the microstructural level [5]. The licking behavior of rats ingesting liquid diets is characterized by bouts of licking at a high constant rate ($\sim$6 s^{-1}) separated by pauses of varying duration [5]. We measured the size of these bouts, or clusters of bursts (SC, size of cluster) by counting the number of licks that occurred before a pause of 500 ms [5]. To describe the microstructure of licking at different times during the tests we calculated the average SC and their number during the first minute of the test, and over the first and second halves of each test separately. The duration of the meal was obtaining by finding the time of the last lick in the first cluster that was followed by a pause of 3 min or more. Because the first lick in the test was assigned a time of 0, the time of the last lick in that cluster defined the end of the meal, and its time of the duration of the meal.

Statistical tests of significance were done using Systat 6.0 for Windows (SPSS, Chicago, IL) software. Curve fitting was done with Table Curve 2D for Windows (SPSS, Chicago, IL), and graphics were done with the Sigma Plot 2.0 for Windows (SPSS, Chicago, IL) software programs.

3. Results

3.1. Volume and duration

Volume ingested during the 30-min tests was nonmontonically related to the concentration of each of the three carbohydrates. The inverted "U"-shaped function, typical of the relationship found between intake and concentration of carbohydrates, is clearly apparent for each carbohydrate in Fig. 1. There was a significant quadratic component in the volume by concentration relationship for each carbohy-

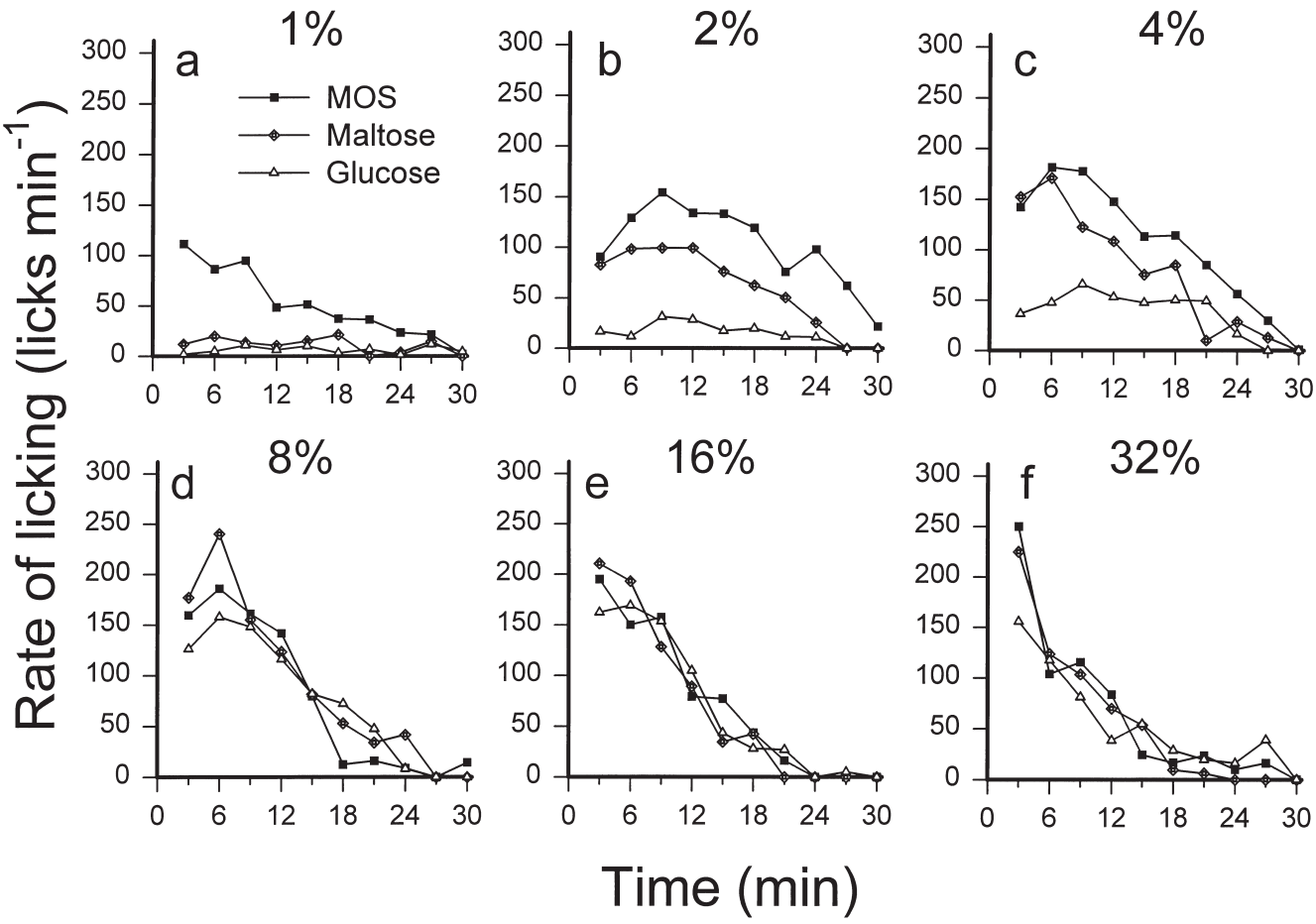

Fig. 2. (a–f) Rate of licking calculated at three minute intervals for the tests with three carbohydrates at the six concentrations.

drate; the smallest F-ratio occurred with glucose, $F(1, 9) = 52, p < 0.001$. There was an overall significant difference in intake among the three carbohydrates, $F(2, 27) = 13.0, p < 0.001$. There was also a significant interaction between concentration and type of carbohydrate, $F(10, 135) = 16.6, p < 0.001$. The interaction occurred in part because, while there was a large and significant difference in intake among the three carbohydrates at the three lowest concentrations, $F(2, 27) = 26.9$, $p < 0.001$), there was no difference among them at the three highest concentrations, $F(2, 27) = 0.3$).

There was a small decline in the duration of the meals as concentrations increased with MOS, $F(1, 9) = 14.7$, $p = 0.004$, and maltose, $F(1, 9) = 8.7, p = 0.016$, but not with glucose, $F(1, 0) = 0.0, p < 0.001$ (Table 1). The type of carbohydrate also affected the duration of the meals, $F(2, 27) = 4.0$, $p = 0.029$, because the meals were slightly longer with 2% MOS than with the other two carbohydrates, $F(2, 27) = 5.5$, $p = 0.010$, and because the duration of the 32% glucose meals were significantly longer than those of the other two carbohydrates at this concentration, $F(2, 27) = 20.4, p < 0.001$. These effects of type and concentration of the carbohydrates were too small, however, to account for the large differences in intake. We, therefore, examined in more detail how these two variables influenced the rat's ingestive behavior.

3.2. Rate of licking

The average rate of licking declined with time in all the tests except those with the low concentrations of glucose (Fig. 2). The Davis and Levine model [3] predicts that these curves should be exponential in shape. This appears to be true of the curves generated by the higher concentrations, but it is not true of the curves generated by the lower ones. Thus, to use a common metric to quantify the differences among these curves, we fit them all by the least squares method to the simplest function that we felt would be able to capture the essential characteristics of most of them, i.e., the linear function y = a + bt. The fits to this function provided, for each test, an estimate of the initial rate of licking, a, and the rate of decline of the rate of licking, b. An evaluation of the accuracy of the linear function (y = a + bt) in describing the individual rate of licking curves was obtained from the coefficient of determination (r^2). The averages of these coefficients across the 10 animals tested at each concentration of each carbohydrate are shown in Table 2. Although some of these coefficients are not as large as one would like, they do indicate that there was a definite linear component in the curves generated by all but the weakest concentrations of glucose.

The magnitude of the estimates of the initial rate of licking at time zero increased substantially with concentration. Among the lower three concentrations, they were greatest for MOS, next for maltose and least for glucose (Fig. 3a). The magnitudes of the estimates of the slopes were also a function of concentration, increasing in absolute magnitude over the four lowest concentrations (Fig. 3b). The magnitudes of these

Table 2
Coefficient of determination (r^2) means and SEs for the linear fits to rate of licking functions

	1%	2%	4%	8%	16%	32%
MOS	0.39	0.28	0.54	0.60	0.67	0.58
SE	0.07	0.08	0.90	0.08	0.04	0.03
Maltose	0.30	0.38	0.55	0.62	0.63	0.55
SE	0.10	0.08	0.09	0.08	0.05	0.05
Glucose	0.08	0.19	0.30	0.64	0.69	0.47
SE	0.02	0.05	0.07	0.07	0.03	0.08

two parameters were closely related. The Pearson correlation coefficient between them were: $r = -0.83$ for MOS, $r = -0.98$ for maltose, and, $r = -0.99$ for glucose. Calculated over all 18 estimates of a and b as a group the correlation coefficient was -0.95. High initial rates of licking were closely associated with rapid rates of decline in the rate of licking with each of the three carbohydrates.

3.3. Microstructure of licking

3.3.1. Entire concentration range

To determine how the type and concentration of the carbohydrates affected the microstructure of licking we measured the size and number of the clusters (SC) in each test with each animal. Over the entire concentration range cluster size increased significantly with concentration, $F(5, 135) = 12.7, p < 0.001$, but was unaffected by the type of carbohydrate, $F(2, 27) = 1.8, p = 0.181$. There was no interaction between these two variables, $F(10, 135) = 1.1, p = 0.353$ (Fig. 4a). In each case there was a significant linear component in the trends across the concentration range, $F(1, 9) = 7.8, p = 0.021$; $F(1, 9) = 13.3, p = 0.005$; $F(1, 9) = 25.4$, $p = 0.001$, MOS, maltose, and glucose respectively. The number of clusters, on the other hand, was affected by both the type of carbohydrate, $F(2, 27) = 6.4, p = 0.005$, and its concentration, $F(5, 135) = 13.6, p < 0.001$ (Fig. 4b). In addition, there was a significant interaction between these variables, $F(10, 135) = 8.9, p < 0.001$. The nature of the interaction is complex but can be readily seen in Fig. 4b.

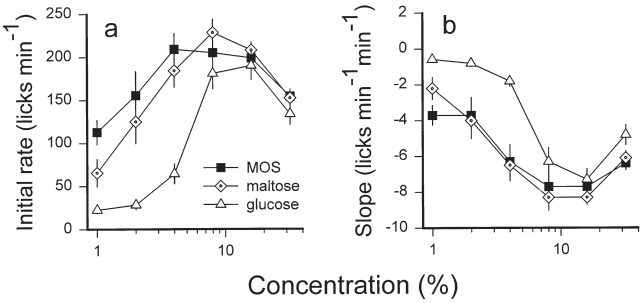

Fig. 3. The means (±1 standard error of estimate) of the estimates of the initial rate of licking (a) and of the slope of the function y = a + bt fit to the rates of licking rate curves in Fig. 3a–f.

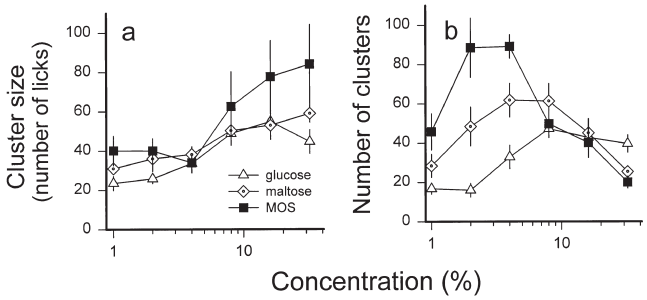

Fig. 4. The mean (±1 SE) cluster size (a), and number of clusters (b) for each carbohydrate as a function of concentration.

3.3.2. Low concentrations

With the three lowest concentrations the licking behavior of the rats was sensitive to the size of the carbohydrate as well as to its concentration because there were very large differences in intake among the three types, a difference that was not present on the tests with the three highest concentrations (Fig. 1). These differences among the carbohydrates at the low end of the concentration range were caused by differences in the number of clusters, which increased with both the number of glucose units of the polymers in the test solutions, $F(2, 27) = 18.1, p < 0.001$, and with the concentration of the solution, $F(2, 54) = 16.2, p < 0.001$ (Fig. 4b). Cluster size, on the other hand, was not affected by either the type of the carbohydrate, $F(2, 27) = 2.1, p = 0.142$, or its concentration, $F(2, 54) = 0.6$ (Fig. 4a). Thus, among the three lowest concentrations the increase in intake with concentration and the greater intakes associated with the longer chain carbohydrate was due entirely to variation in the number of clusters with no significant contribution from variation in their size.

3.3.3. High concentrations

With the three highest concentrations there were no differences in volume ingested among the three types of carbohydrates, $F(2, 27) = 0.3$, but intake decreased significantly, $F(2, 54) = 70.6, p < 0.001$, with increasing concentration (Fig. 1). This decrease in intake occurred because of a reduction in the number of clusters, $F(2, 54) = 26.6, p < 0.001$ (Fig. 4b). Once again, although there was a trend for SC to increase with MOS concentration, an overall ANOVA of SC showed no significant variation with concentration over this range, $F(2, 54) = 1.6, p = 0.218$ (Fig. 4a).

3.3.4. First minute of licking

To determine how the type and concentration of the carbohydrates affected the microstructure of licking at the beginning of the tests we calculated the average number of licks, average SC, and number of clusters that occurred during the first minute of each test with each rat. There was an overall statistically significant effect of type of carbohydrate on the number of licks, $F(2, 27) = 6.3, p < 0.001$, a significant effect of concentration, $F(5, 135) = 14.9, p < 0.001$, and a significant interaction between the type of carbohydrate and concentration, $F(10, 135) = 2.7, p = 0.005$ (Fig. 5a). The

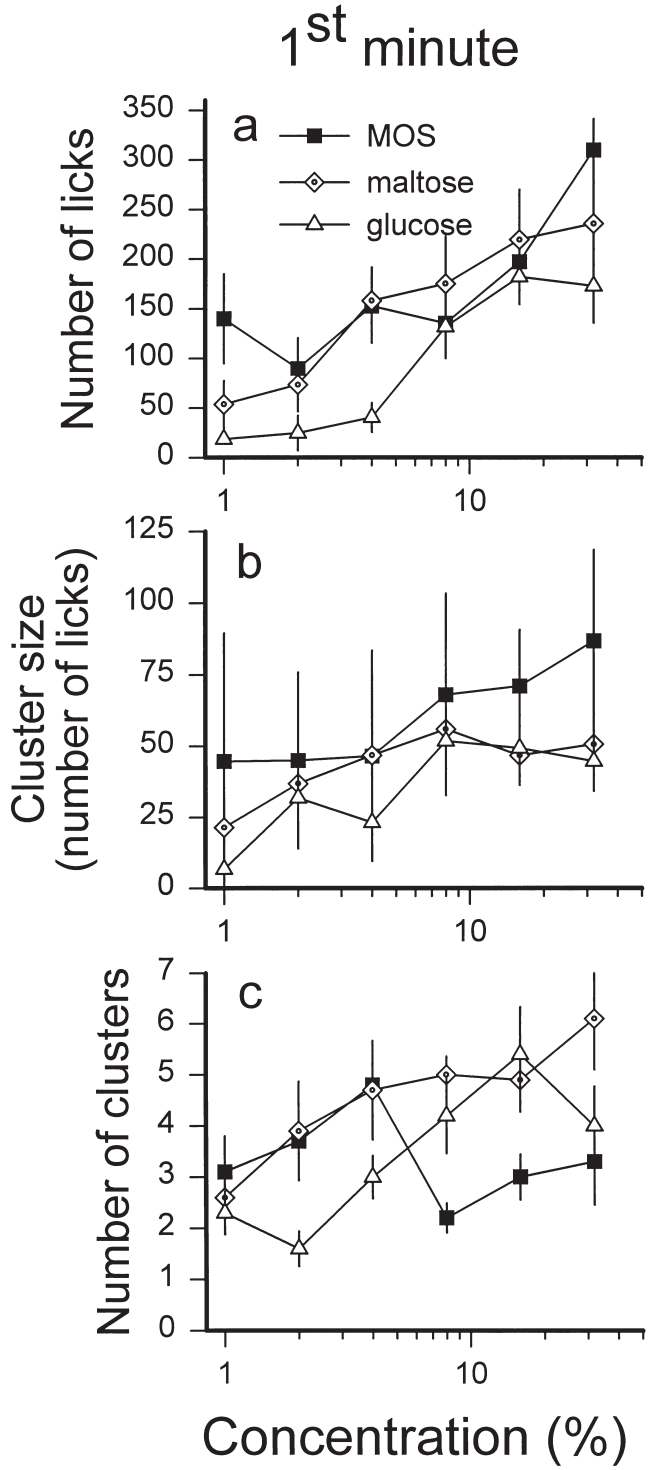

Fig. 5. The mean (±1 SE) of the number of licks (a), size of clusters (b), and number of clusters (c) during the first minute of testing for each carbohydrate as a function of concentration.

interaction occurred because while the number of licks increased significantly with maltose, $F(5, 45) = 11.0, p < 0.001$, and glucose concentration, $F(5, 45) = 17.2, p < 0.001$, it did not with MOS, $F(5, 45) = 0.6$ (Fig. 5a).

The increasing number of licks with concentration dur-

ing the first minute of the tests with maltose and glucose occurred because of a significant increase in both cluster size, $F(5, 90) = 6.7, p < 0.001$ (Fig. 5b), and the number of clusters, $F(5, 90) = 7.3, p < 0.001$ (Fig. 5c).

3.3.5. Decline in rate of licking

In the majority of the tests there was a decrease in the rate of licking over time (Fig. 2). This could have occurred because of reduction in the size or number of clusters or

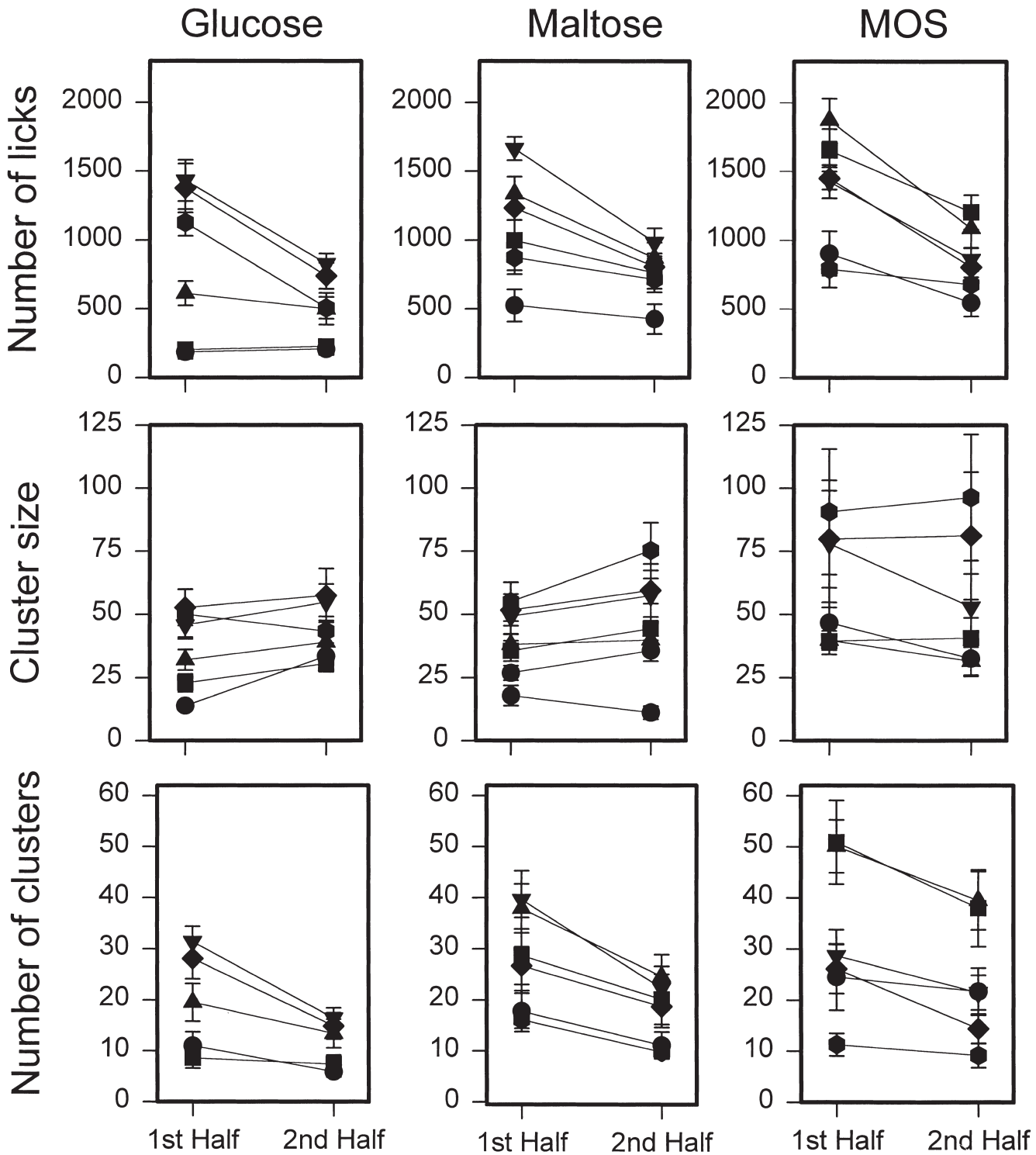

Fig. 6. The mean (±1 SE) of licks, mean SC, and number of clusters in the first and second halves of the tests for the three carbohydrates. Concentrations are represented by the following symbols: circle —1%, square—2%, triangle up—4%, triangle down—8%, diamond—16%, and hexagon—32%.

both. To decide among these alternatives, we divided each meal in half temporally and compared the average number of licks, cluster size, and the number of the clusters in the first half with those in the second. These summary statistics for the two halves of the tests and for the six concentrations of the three carbohydrates are shown in Fig. 6. Overall with each carbohydrate there were significantly fewer licks in the second than in the first half of the tests [MOS, $F(1, 9) = 63.8$, $p < 0.001$; maltose, $F(1, 9) = 63.6$, $p < 0.001$; and glucose, $F(1, 9) = 21.3$, $p = 0.001$]. This decrease occurred because of a significant reduction in the number of clusters from the first to the second half of the tests, $F(1, 9) = 6.0$, $p = 0.036$, $F(1, 9) = 37.7$, $p < 0.001$, $F(1, 9) = 23.9$, $p = 0.001$, MOS, maltose, and glucose, respectively. The size of the clusters, on the other hand, were not significantly different in the two halves of the tests [MOS, $F(1, 9) = 0.9$; maltose, $F(1, 9) = 3.7$, $p = 0.089$; and glucose, $F(1, 9) = 3.0$, $p = 0.123$].

4. Discussion

4.1. Macrostructure of ingestion

The dependence of intake on both glucose chain length and concentration is similar to that reported by Sclafani and Clyne [9]. They reported increasing intake with concentration when 1, 2, and 4% solutions were used, and decreasing intake as the concentration increased further from 8 to 32%. They also reported that with the three lowest concentrations, significantly more maltose than glucose was ingested, and that with the three highest there was no difference in intake between the two. Our results with these two carbohydrates closely resemble theirs.

However, our results differ from theirs, in the comparison of maltose to the more complex carbohydrate, MOS in our case, Polycose in theirs. They reported no differences in intake between maltose and Polycose at any concentration. Our rats, on the other hand, ingested about twice as much MOS as maltose when tested with the 1, 2, and 4% solutions. Although both MOS and Polycose are mixtures of glucose polymers, MOS consists virtually exclusively of glucose polymers in the three to six chain length, while Polycose, in addition to containing glucose and maltose contains many polymers more than six glucose units long. The small presence of glucose and maltose in Polycose might have been expected to enhance its ability to stimulate ingestion relative to MOS rather than reduce it. This, however, was not the case. Perhaps the presence of the longer chain polymers in Polycose reduced its effectiveness relative to MOS in stimulating intake.

Our results provide strong support for Sclafani's claim that rats must be responding to the orosensory properties of multiunit glucose polymers because, unlike Polycose, MOS contains only glucose polymers greater than two units. The fact that MOS stimulated more intake at the low concentrations than did glucose or maltose indicates clearly that the three to six chain glucose polymers in MOS can stimulate ingestive behavior independently of the mono- or disaccharides. Therefore, MOS either elicits the same sensory qualities as glucose and maltose, only more intensely, or it has its own unique orosensory qualities, or both.

4.2. Rate of ingestion

Two important features of the rat's ingestive behavior that determine how much will be ingested are the initial rate of ingestion and the rate of decay of the rate of ingestion during the test. The initial impact of the solution on the animals ingestive behavior assessed by estimates of the initial rate of licking from linear fits on the one hand, and by counting the number of licks during the first minute of the tests on the other, were similar. Both measures increased with concentration over the 1 to 8% range, and showed no further increase from 16 to 32%. They were ordered similarly over the 1 to 2% range, with the values for MOS being greater than maltose, and those for maltose being greater than glucose. The main discrepancy occurred with the highest concentration (32%) where the estimates obtained from the linear fits were smaller than those at 16%, whereas the number of licks in the first minute were the same (maltose and glucose) or greater (MOS) than at 16%.

This discrepancy can be accounted for by the fact that the linear function provides a good estimate of the y-intercept for the curves generated by the 16% solutions (Fig. 2e) but does not for the curves generated by the 32% solutions (Fig. 2f). With the 32% concentration there is a clear exponential trend with each type of carbohydrate, which, when extrapolated to the y-intercept, gives much greater estimates than does a linear function. In fact, an exponential function provides estimates of the y-intercept that are about 50 to 60% greater than those provided by the linear fits. However, the linear function was used throughout in the interests of using a common metric across carbohydrates and concentration.

Our measurement of the orosensory properties of glucose and maltose at stimulating licking are in close agreement with those of Sclafani and Clyne [9] as far as the shapes of the curves and the relationship between them are concerned. We found, as they did, that the number of licks during the first part of the meal was an increasing monotonic function of concentration, and that at every concentration maltose was significantly more effective in stimulating licking than was glucose. On the other hand, we found that with the 1 and 2% concentrations MOS stimulated significantly more licking during the first minute of the test than did maltose. They found that maltose was much more effective in stimulating licking during the first 3 min of the tests than was Polycose. This greater ability of MOS over maltose to stimulate ingestion at the beginning of the meal is at least partially responsible for the ability of the 1 and 2% solutions of MOS to stimulate more intake than maltose at these concentrations. Whatever the explanation for the differences between maltose and MOS in our study, and maltose and Polycose in

theirs, our results indicate that the longer the glucose chain within the tested range (G6–G3 > G2 > G1), the more effective it is in stimulating intake of the low concentrations.

There was a very high negative correlation (−0.95) between the effectiveness of a test solution to stimulate ingestion and the magnitude of the negative feedback signal generated by the accumulation of ingested fluid in the gastrointestinal tract. This also can be seen in the curves displayed in panels a and b of Fig. 3, which are essentially mirror images of each other. This suggests that the magnitude of the negative feedback signals may be related to the effectiveness of test solution to stimulate intake at the start of a test, which, in turn, determines the early rate of flow to the gastrointestinal tract. Solutions that stimulate an initial high rate of ingestion cause a rapid rate of flow into the gastrointestinal tract, which may limit further intake. One might have expected the molar concentration of the solutions to play a major role in controlling the magnitude of the negative feedback signal, but it did not. At any given % concentration there were many fewer molecules in MOS than maltose solutions, yet the magnitudes of the estimates of the slopes of the rate of licking function for the 1, 2, and 4% solutions were virtually identical. Furthermore, at 16 and 32% there was little or no difference in the slopes either between these two concentrations or among all the three carbohydrates, yet there was a twofold difference in the number of unhydrolized molecules between glucose and maltose, and a many fold difference between these and MOS.

4.3. Microstructure of ingestion

Cluster size, when averaged over the entire meal, increased linearly with concentration for all three carbohydrates (Fig. 4a), but the number of clusters showed a nonmonotonic relationship that very closely mirrored the relationship between volume ingested and concentration of the test solutions (compare Fig. 1 with Fig. 4b). The correlation between volume ingested and the number of clusters calculated over the three carbohydrates and six concentrations was 0.74 ($p < 0.001$). A very similar relationship between cluster size and number on the one hand and volume ingested on the other has been reported to occur with Polycose [2] and sucrose [4,5]. Therefore, for the three carbohydrates studied, variation in meal size is determined primarily by how many clusters there were, not how large they were. That is, cluster size is correlated with solution concentration, and the number of clusters is correlated with intake.

Our finding that cluster size increased linearly with the concentration of maltose confirms a previous report. The findings of a linear relationship between cluster size and concentration of glucose and MOS are new, and supports what appears to be a general rule that the tendency to sustain a burst of licking, once begun, increases with the concentration of carbohydrates. This relationship has been reported to occur with sucrose [2,5] and Polycose [2], and to occur with increasing concentrations of saccharin in a saccharin + 0.2 M glucose solution [1].

There were fewer licks in the second half of the tests than in the first, a difference that was accounted for entirely by fewer, not smaller clusters in the second than in the first half. Therefore, because cluster size remained essentially the same in the two halves of the tests, stimulation derived from the accumulation of fluid in the gastrointestinal tract did not interact or interfere with the orosensory control of cluster size acting at the beginning of the test. This control apparently is maintained undiminished throughout the test. Negative feedback provided by these carbohydrates appears to decrease the probability of initiating a new bout of licking during a pause rather than altering the probability of maintaining a bout of licking once initiated. This can be seen also in the fact that during the first minute of the test when negative feedback is absent or minimal, both SC and NC increase with concentration, but when averaged over the last half of the test, SC remains constant while NC decreases with concentration.

This conclusion must be tempered, however, by the recent report [12] that when duration of test meals of a wide range of sucrose solutions was divided into thirds and the size of burst of licking (number of licks before a pause of 1 s) was averaged within each third there was a significant decrease in the size of the bursts across the three intervals. Their finer resolution (thirds rather than halves) may have detected an effect our resolution did not, or the difference may depend on the different bout criterion (our 0.5-s vs. their 1-s criterion) used in the two studies. We do not believe, however, that it is due to the difference in type of carbohydrate used because this is the only discrepancy between their findings and those we report here.

Sclafani and coworkers have inferred that Polycose elicits a different quality of taste than glucose or sucrose in the rat. They have suggested that there is a second carbohydrate taste receptor in the rat that is stimulated by Polycose. There is some electrophysiological evidence to support such a hypothesis [14]. Spector and coworkers reported results that convincingly demonstrate that while maltose and sucrose taste very similar to each other, they also have qualitative differences in their taste [12–15]. These differences can be abolished by selectively sectioning the chorda tympani branch and the greater superficial petrosal branch of the facial nerve that innervate the taste buds of anterior tongue and palate. Our results show the rats lick faster and consume more maltose than glucose and more MOS than maltose. We do not know whether the nonglucose taste quality of MOS and maltose is the same. However, for the sake of parsimony, we shall assume that there are only two carbohydrate taste qualities: a glucose taste quality and a glucose polymer taste quality. Maltose clearly tastes similar to glucose, but has an additional taste component, so we conclude that maltose elicits a taste that is partially glucose-like and partially glucose–polymer-like. The MOS may then elicit very little glucose like taste and be primarily glucose–polymer-like in taste quality. Therefore, given the assertion that the glucose–polymer taste quality (a.k.a., malty) is highly motivating to the rat, it follows that MOS drives the highest lick rates and the largest cluster sizes, and that maltose is intermediate to MOS and glucose.

Acknowledgments

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