Study of a Lifetime of Sucrose Intake by the Fischer-344 Rat[a]

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INTRODUCTION

There is a growing amount of information on the effect of aging on taste (see Murphy[1]), but the literature on longitudinal studies with animal models is nonexistent. The Committee on Animal Models for Research on Aging (Institute of Laboratory Animal Resources) strongly recommends the use of the Fischer-344 rat for studies of aging because the median life span is only 27 months, a span allowing for detailed observations from weaning until death. We initiated a longitudinal program to study how sucrose was tasted and ingested by the Fischer-344 rat as a function of the aging process. Sucrose was selected as the tastant for the following reasons:

1. Many papers have been published on the ingestion of sucrose by the rat. Sucrose, which is chemically pure, is convenient because solutions of it are easily prepared and because the rat drinks sucrose solutions in large quantities.
2. One of the more controversial issues in the literature on taste and aging involves the decrease in sensitivity to sucrose as a function of age. Balogh and Lelkes,[2] Cooper *et al.*,[3] Dye and Koziatek,[4] Hermel *et al.*,[5] Hinchcliffe,[6] Moore *et al.*,[7] and Richter and Campbell[8] have all shown some decrease in sucrose sensitivity as a function of age. Byrd and Gertman,[9] Hyde and Feller,[10] Osepian,[11] Schiffman,[12] and Weiffenbach *et al.*[13] failed to show a loss of sucrose sensitivity.
3. From electrophysiological evidence, a small, but significant, age-related change occurs with sucrose (see McBride and Mistretta[14]).
4. There have been reports that specifically implicate excessive intakes of sucrose (as compared to other carbohydrates) as a factor in decreased longevity in rats (see Reiser and Hallfrisch[15]).
5. Recent studies on the rat by Travers *et al.*,[16] Nejad,[17] and Krimm *et al.*[18] have indicated that the taste receptors on the palate rather than those on the tongue are most important in mediating the sweet taste of sucrose. Little is known about changes in the palate as a function of age in either humans or animals.

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6. Sucrose has a sweet taste to the human, and most investigators allow one to infer the same for the rat. The sweet tooth of the rat is in many ways similar to that of man. Understanding more about sucrose ingestion across the life span of the rat may help us to understand why sweet-tasting foods are so abused by humans with eating disorders.

This longitudinal study was designed to examine changes in taste and ingestion patterns of sucrose in the Fischer-344 rat from 30 days of age until death. Because each rat received only one concentration of sucrose during its lifetime, we were able to note the effects of long-term experience with a particular sucrose concentration on ingestion and taste of the sweetened solutions.

METHODS

Subjects

Ninety-six weanling Fischer-344 male rats served as subjects. The rats were housed individually in the special cages described below. The animal room was lighted from 7 A.M. to 7 P.M. daily, and the temperature and humidity were closely controlled. The room was isolated from all traffic except for that during the daily maintenance period.

Apparatus

Special individual Hoeltge rat cages were modified to hold a 4-ounce jar containing powdered Purina Chow and to accommodate two half-pint fluid containers. Because food and fluid consumption were to be measured daily, these containers were all mounted on the front of the cage so that both rat and experimenter could easily reach them. An electronic balance was used for all weight measurements. The output of this electronic balance was connected to a microprocessor such that the consumption data could be stored for subsequent analysis. Body weights of the rats were recorded once a week.

Procedure

The 96 rats were divided into six groups of 16 each. These six groups were designated as the 1.0 M sucrose, the 0.5 M sucrose, the 0.25 M sucrose, the 0.125 M sucrose, the 0.0625 M sucrose, and the water control groups. All rats had access to food and water at all times. For 4 days each week, the rats in the six groups received their specific concentration of sucrose solution in the second fluid container. For the other 3 days of the week, the second bottle contained only water. Hence, the rats received food, sucrose, and water for 4 days each week and only food and water for the other 3 days. Daily intakes were measured for each of the 4 days, and one food and one water measurement were taken for the 3-day weekend period. These home-cage measurements allowed for a study of the effects of long-term sucrose experience on sucrose intake throughout the rat's lifetime. As a consequence of the large contribution of postingestional feedback on sucrose ingestion in these daily 24-hr tests, however, these data did little to

measure the effects of these various long-term sucrose exposures on the taste of sucrose to the rat.

In previous work, we have shown that inferences about the taste of sucrose to the rat can be made from 24-hr, two-bottle tests if detailed measurements are made from the pattern of sucrose ingestion. Two measures from ingestion patterns have been shown to correlate quite well with integrated neural responses recorded from the greater superficial petrosal nerve (see Smith[19]). These measures are 1) the rate of licking during a sucrose drinking bout and 2) the proportion of sucrose bouts ingested in the daylight hours. In order to attempt such measures of taste in this present longitudinal study, six rats from each group described above were moved from home cages into special test cages for a 1-week study of their detailed pattern of consumption. These 1-week studies were done with the same rats approximately every 6 months. The rats were given their same respective sucrose solutions each day while in these special cages. The ingestion period lasted for 23 hr each day, allowing 1 hr for weighing and replenishing the containers and for cage cleaning.

The test cages were identical to the home cages except that an infrared beam was placed in front of each of the three ingestion ports (one for each of the two fluid containers and one for the food container). When the rat licked on one of the fluid tubes, or entered the food bin, the beam was broken and a signal was sent to a microcomputer to be stored for subsequent analysis. During the 23-hr period, data were sent to the computer every 6 sec. This stream of data allowed 13,800 data points for each food or fluid container to be recorded by the end of the period. For each rat, the 13,800 data points were plotted in a daily strip chart, and the number of ingestion bouts, the bout duration, the number of licks per bout, and the amounts of time between bouts were recorded in a table. From these data, the mean rate of licking during each bout and the proportion of daytime drinking could be calculated.

RESULTS

The concentration of sucrose available over the lifetime of the rat had no effect on longevity. In the three panels of FIGURE 1, the number of surviving rats in each group is shown from week 75 through week 129. Fifty percent of the rats had died from the 1.0 M sucrose group by the 106th week of the study, from the 0.5 M sucrose group by the 97th week, from the 0.25 M sucrose group by the 105th week, from the 0.125 M sucrose group by the 109th week, from the 0.0625 M sucrose group by the 110th week, and from the water control group by the 104th week. The differences in longevity among the six groups were not statistically significant at any time during the study. The overall LD_{50} for the 96 rats was about 111 weeks or about 27 months. The first rat to die was in the 1.0 M sucrose group, and death occurred at 43 weeks of age. The longest surviving rat lived 133 weeks and was in the 0.25 M sucrose group.

For analysis, the data were divided into blocks of 15 weeks. Ninety-two of the rats survived into the sixth time block (76–90 weeks), but deaths began to occur rapidly in the seventh time block. The initial analysis was performed on the first six time blocks (first 90 weeks) for the six groups of rats. The eight dependent variables analyzed were as follows:

1. Mean weekly body weight.
2. Mean amount of sucrose solution ingested during the 4-day test period.

3. Mean amount of sucrose solute ingested during the 4-day test period.
4. Mean amount of Purina Chow ingested during the 4-day test period.
5. Mean weekly caloric intake.
6. Mean amount of water consumed during the 4-day test period.
7. Mean amount of food consumed during the 3-day weekend period.
8. Mean amount of water consumed during the 3-day weekend period.

A six (the six sucrose groups) by six (the means of the first six 15-week blocks) repeated sampling of the analysis of variance was run for each of the eight dependent variables. This was followed by the appropriate statistical comparisons using

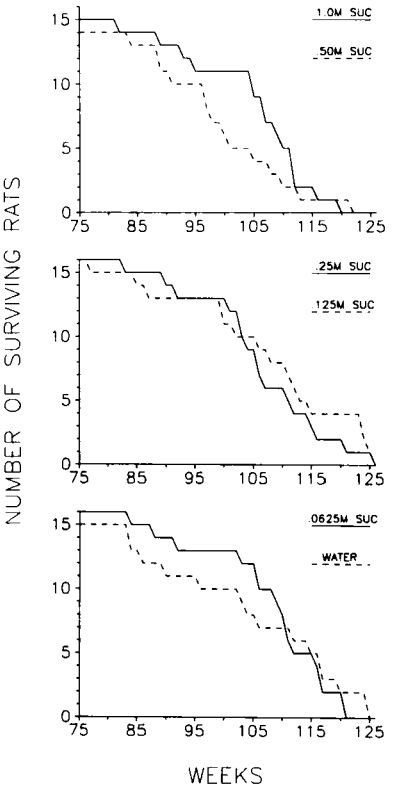

FIGURE 1. The number of surviving rats from each of the six groups is plotted as a function of the final weeks of the experiment. The 1.0 M and 0.5 M sucrose groups are seen in the top panel, the 0.25 M and 0.125 M sucrose groups are seen in the middle panel, and the 0.0625 M sucrose group and the water control group are seen in the bottom panel.

the Tukey test (all Tukey tests were done at the 5% level of significance). The results of these analyses will be given for each of the dependent variables in the following sections.

Body Weight

The mean body weights for the six groups over the six time periods are presented in FIGURE 2. It can be seen that body weight increased over the lifetime of the rats in an orderly manner for each group. The time variable was significant (F = 1281.6; df = 5, 430; and $p < .001$), the group variable was significant (F =

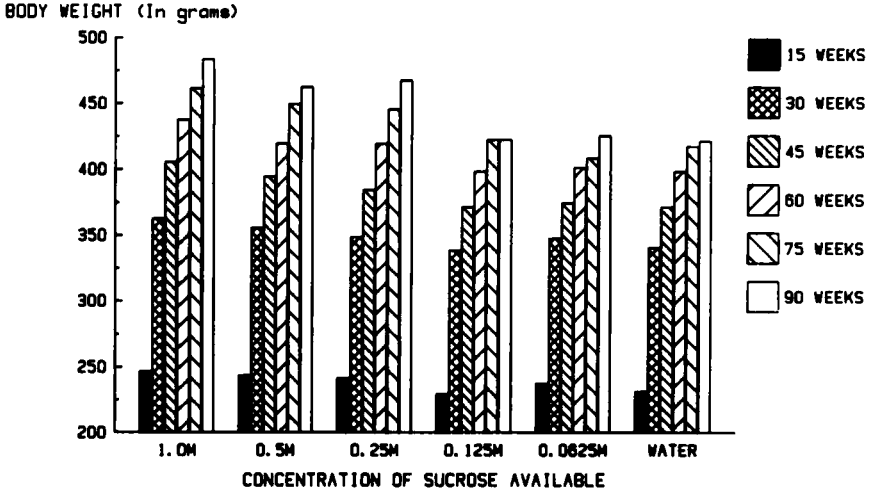

FIGURE 2. The body weights of the rats are plotted across the six groups and over the six time periods up to week 90 of the experiment.

8.44; df = 5, 86; and $p < .001$), and the interaction of time by group was significant ($F = 2.86$; df = 25, 430; and $p < .001$). Tukey comparisons made across the variable for time allowed for the following conclusions: There was a significant increase in body weight for the three highest sucrose concentration groups in all of the six time periods. For the two lower concentration groups and for the water group, the increase in weight was significant until the 75th week, after which time weight stabilized. Tukey comparisons made across the variable for the groups

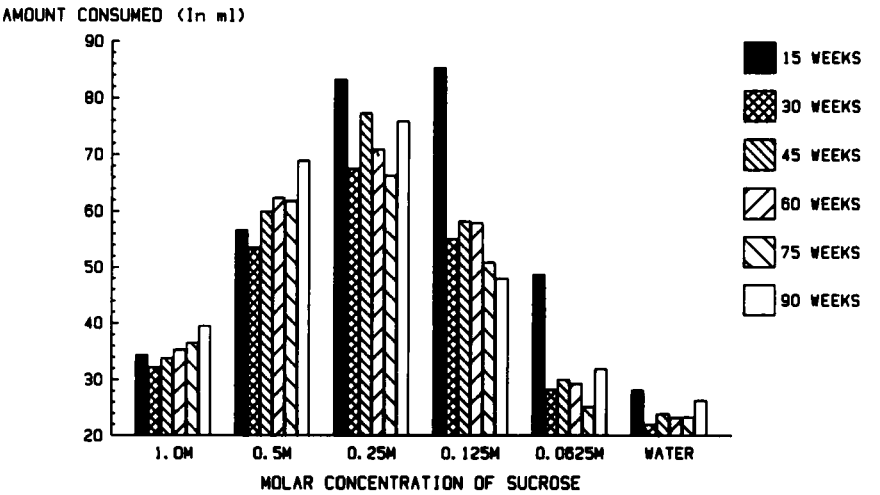

FIGURE 3. The amounts of sucrose consumed by the rats are plotted across the six groups and over the six time periods up to week 90 of the experiment.

allowed for these conclusions: There was no significant difference in body weights across the six groups during the first time period. This difference was significant during the second time period and remained significant over the third, fourth, fifth, and sixth time periods.

Sucrose Solution Intake

The mean sucrose solution intakes for the six groups over the six time periods are presented in FIGURE 3. The time variable was significant ($F = 27.40$; df = 5, 430; and $p < .001$), the group variable was significant ($F = 106.14$; df = 5, 86; and $p < .001$), and the interaction of time by group was significant ($F = 9.03$; df = 25, 430; and $p < .001$). Tukey comparisons made across the variable for time allowed for the following conclusions: In the two higher concentration groups, there was a significant increase in sugar solution intake as the rats grew older. Within the 0.25 M sucrose group, there was little change in sucrose intake with age. At the two lower concentration groups, there was a significant decrease in sucrose solution intake as the rats aged. Tukey comparisons made across the variable for the groups allowed for these conclusions: The typical 24-hr preference–aversion function for sucrose drinking by rats was confirmed by our results. For each of the time periods, the difference across the six groups was significant. Percentage changes in sucrose intake from week 15 to week 90 are illustrated in FIGURE 4 for the five sucrose groups. Water intake in the group that never received sucrose decreased by only 7% from week 15 to week 90.

Sucrose Solute Intake

The mean sucrose solute intakes for the six groups over the six time periods are presented in FIGURE 5. It can be seen that the sucrose solute consumed decreased as the concentration of sucrose decreased. The time variable was significant ($F = 11.71$; df = 5, 430; and $p < .001$), the group variable was significant ($F = 611.93$, df = 5, 86; and $p < .001$); and the interaction of time by group was significant ($F = 6.53$; df = 25, 430; and $p < .001$). Tukey comparisons made across the variable for time allowed for the following conclusions: As with the sucrose solution intakes, the solute intake increased in the 1.0 M and the 0.5 M sucrose groups as the rats grew older. There was no change with age in the 0.25 M group, and there was a significant decrease in intake in the two lower concentra-

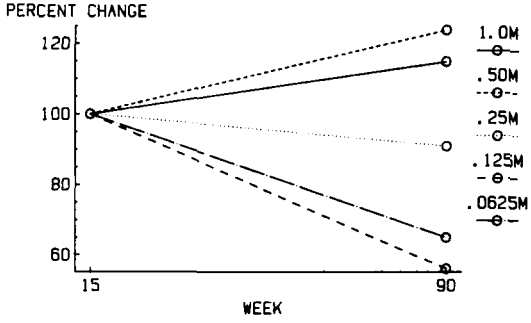

FIGURE 4. The percentage changes in sucrose intake from week 15 to week 90 are plotted for each of the sucrose-consuming groups.

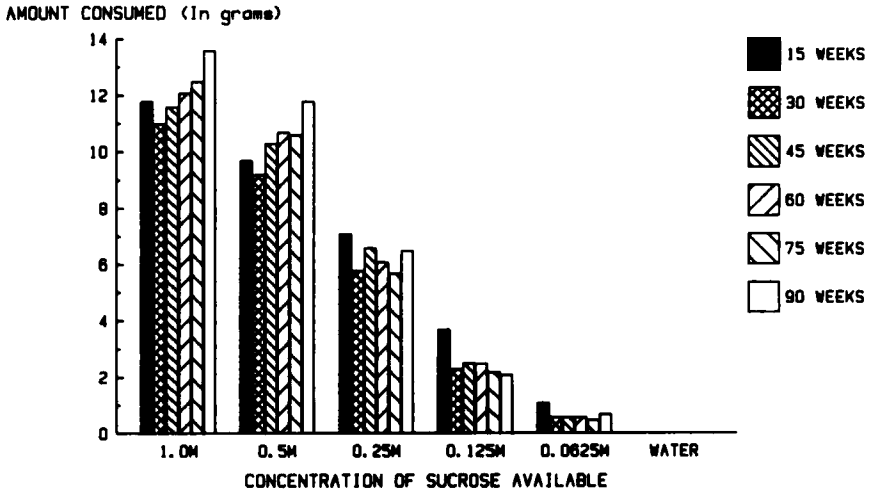

FIGURE 5. The amounts of sucrose solute consumed by the rats are plotted across the six groups and over the six time periods up to week 90 of the experiment.

tion groups. There was a significant decrement in sucrose solute intake during the second time period for the three highest sucrose groups. Tukey comparisons made across the variable for the groups allowed for these conclusions: All of the sucrose groups were different from each other at each of the six time periods.

Purina Chow Intake

The mean amounts of powdered Purina Chow ingested during the 4-day test period by the six groups over the six time periods are presented in FIGURE 6. It can be seen that the amount of food consumed increased as the concentration of available sucrose decreased. The time variable was significant ($F = 20.19$; df = 5, 430; and $p < .001$), the group variable was significant ($F = 117.89$; df = 5, 86; and $p < .001$), but the interaction of time by group was not significant ($F = 1.78$; df = 25, 430; and $p > .05$). Tukey comparisons made across the variable for time allowed for the following conclusions: With the exception of the 0.25 M sucrose group, there was no significant change in food intake with age. For all of the groups except the 0.25 M sucrose group, however, there was a significant temporary decrement in food intake during the second time period. This was when the rats were from 19 to 34 weeks of age. As was noted above, the rats also showed a drop in sucrose solute intake during this time period. Tukey comparisons made across the variable for the groups allowed for these conclusions: At all of the time periods, the 1.0 M, the 0.5 M, and the 0.25 M groups were statistically different from each other. The amount of food consumed by the lower two sucrose concentration groups and the amount of food consumed by the water group were not different from each other.

It is interesting to note that Purina Chow intake for the 3-day weekend period, when no sucrose was available, was quite similar to the intakes described above when sucrose was present. Even the decrement in chow intake during the 16–30-week period was also present during the weekend periods.

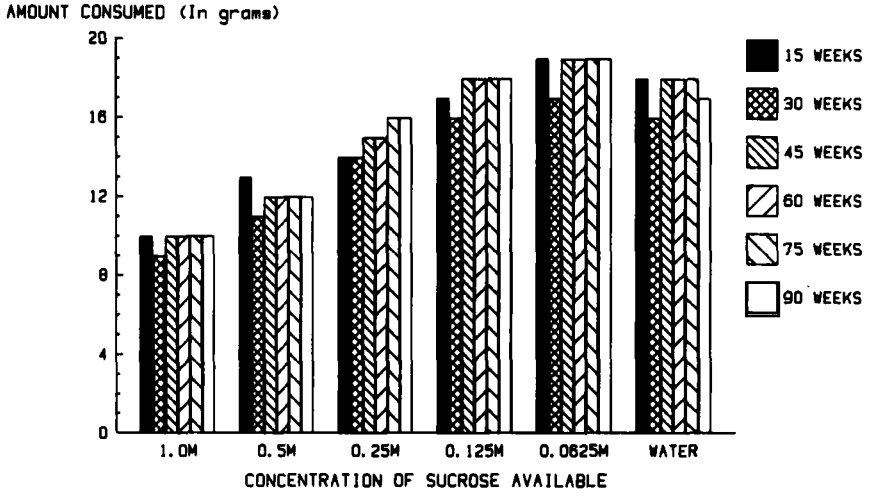

FIGURE 6. The amounts of powdered Purina Chow consumed by the rats are plotted across the six groups and over the six time periods up to week 90 of the experiment.

Weekly Caloric Intake

The mean caloric intakes (this includes calories from food for the entire week and calories from available sucrose during the 4-day testing period) by the six groups over the six time periods are presented in FIGURE 7. It can be seen that in general there is a decrease in caloric intake across the groups as the concentration of the available sucrose is lower. The time variable was significant ($F = 37.28$;

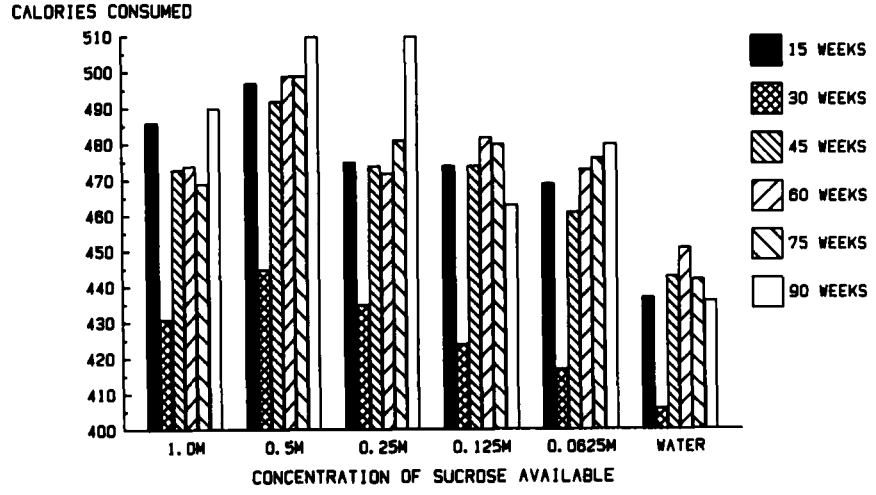

FIGURE 7. The mean weekly caloric intakes of the rats are plotted across the six groups and over the six time periods up to week 90 of the experiment.

df = 5, 430; and $p < .001$), the group variable was significant ($F = 8.29$; df = 5, 86; and $p < .001$), but the interaction of time by group was not significant ($F = 1.03$; df = 25, 430; and $p > .05$). Tukey comparisons made across the variable for time allowed for the following conclusion: There were reductions in both weekly food and sucrose intakes during the second time period; these reductions are reflected in the reduction in caloric intake seen in FIGURE 7. Tukey comparisons made across the groups variable allowed for this conclusion: Caloric intake for the two higher sucrose concentration groups was significantly different from that for the water control groups.

Water Intakes

When sucrose of nearly any concentration is available, rats consume almost no water. The analysis of variance for water when sucrose was available yielded the following results: The time variable was significant ($F = 15.17$; df = 5, 430; and $p < .001$), the group variable was significant ($F = 833.54$; df = 5, 86; and $p < .001$), and the interaction of time by group was significant ($F = 4.13$; df = 25, 430; and $p < .001$). The Tukey test across the variable for time suggests there is no pattern of change in water intake as a function of the age of the rats. The Tukey comparison across the groups revealed that most of this variance was accounted for by the difference between the water control group and all of the sucrose groups.

The weekend water intake was quite variable, but no meaningful trends appeared across either time or the groups.

Relations between the Dependent Variables

Correlation coefficients were calculated between each of the dependent variables for each of the six time periods. These coefficients are presented in TABLE 1. Any correlation coefficient greater than .17 was statistically significant. It can be seen from the table that body weight is either not correlated or correlated negatively with food intake (with the exception of time 1 with weekend food intake). Body weight is positively correlated with sugar solute intake. Food intake during the sucrose access periods is highly correlated with weekend food intake and shows high negative correlation with sugar intake. Food intake is significantly correlated with water intake both during the week and on the weekend. Sucrose solute intake is significantly negatively correlated with water intake. It is interesting to note that the correlation between body weight and sucrose solute intake grew larger as the rats aged. A similar trend is seen in the negative increase in correlation magnitude between body weight and water intake during the sucrose testing days.

Data Analysis in Special Cages

Six rats from each group were selected for testing in the special cages. The first test was run between weeks 20 and 26; the second test, between weeks 62 and 66; and the third test, between weeks 96 and 100. Further tests were attempted during weeks 102–106 and weeks 110–114, but the data from these latter tests were not included in the analysis because there were only one or two rats per

TABLE 1. The Intercorrelations among the Eight Dependent Variables Analyzed for the First 90 Weeks of the Study

		FD4	FD3	ST4	SL4	WA4	WA3	CA7
Body weight	1	−.12	.25	.24	.02	−.13	.36	.35
	2	−.11	.09	.30	.02	−.15	.26	.69
	3	−.30	−.30	.45	.09	−.21	−.07	.55
	4	−.36	−.28	.47	.10	−.21	−.17	.34
	5	−.43	−.33	.54	.33	−.29	−.02	.26
	6	−.22	−.02	.55	.31	−.34	−.11	.53
FD4	1		.84	−.84	.03	.44	.63	−.12
	2		.92	−.94	−.26	.44	.68	−.01
	3		.94	−.92	−.27	.40	.65	.16
	4		.95	−.91	−.31	.33	.14	.22
	5		.86	−.89	−.33	.33	.18	.29
	6		.89	−.78	−.23	.28	.27	.27
FD3	1			−.69	−.05	.46	.27	.27
	2			−.83	−.31	.50	.72	.09
	3			−.86	−.38	.50	.71	.08
	4			−.88	−.41	.47	.69	.17
	5			−.78	−.36	.33	.14	.34
	6			−.59	−.15	.32	.30	.50
ST4	1				.13	−.61	.08	.40
	2				.38	−.56	−.51	.42
	3				.41	−.56	−.62	.39
	4				.44	−.51	−.68	.26
	5				.50	−.54	−.17	.22
	6				.51	−.51	−.08	.36
SL4	1					−.49	−.10	.23
	2					−.50	.15	.34
	3					−.49	.09	.32
	4					−.53	−.05	.25
	5					−.53	.22	.30
	6					−.46	.25	.41
WA4	1						.27	−.31
	2						.30	−.36
	3						.35	−.39
	4						.35	−.32
	5						.18	−.38
	6						.16	−.27
WA3	1							.23
	2							.26
	3							.06
	4							−.04
	5							−.05
	6							.20

NOTE: The eight dependent variables are as follows: weekly body weight, food during the 4-day test (FD4), food during the 3-day weekend (FD3), sucrose solute (ST4), sucrose solution (SL4), water during the 4-day test (WA4), water during the 3-day weekend (WA3), and weekly caloric intake (CA7).

group surviving at that time. An example of a typical strip chart record for one rat from the 0.25 M sucrose group on one day during the third test is seen in FIGURE 8. The horizontal axis is shown as 13,800 6-sec time bins (23 hr). Sucrose drinking is shown in the top panel, water drinking in the middle panel, and food ingestion in the bottom panel. The *y* axis (counts) for the top and middle panels is expressed as the absolute number of licks per 6-sec bin. The *y* axis for food shows the number of seconds from each 6-sec bin in which the rat's head had broken the infrared beam. The horizontal bars in each panel signify the 12-hr lights-off period.

It can be seen that there was little water drinking. The rat ate the powdered Purina Chow and drank the sucrose in discrete "bouts." For these studies, we defined a bout in the following way: A bout started when there were at least three counts per bin. It stopped when there were 50 consecutive bins without at least three counts per bin. A table showing quantification of these strip charts was printed daily for subsequent data analysis. For example, from the record shown

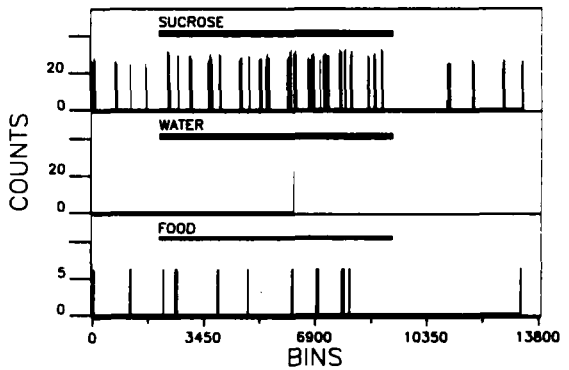

FIGURE 8. A computer-derived record of sucrose and water drinking and the record of eating powdered Purina Chow can be seen above. The counts show the actual number of licks on the sipper tubes for each 6-sec time bin. The counts for the food chart (bottom panel) indicate how many seconds during each 6-sec time bin during which the rat's head broke the photo beam. There are 13,800 6-sec time bins in a daily 23-hr run. The horizontal lines in each panel indicate when the room lights were off.

here, this rat had 29 sucrose bouts that lasted an average of 5.9 min, he made an average of 734 licks per bout, and his average interbout interval was 39.8 min. Twenty-one of the sucrose bouts were at night, and eight were during the daylight hours. The rat had 11 feeding bouts, 3 of which were during daylight hours. These bouts averaged 4.8 min in duration.

From such records, we could calculate the two measures that correspond so well with electrophysiological measurements of taste. They are 1) the rate of licking within a bout and 2) the proportion of daytime drinking bouts. The relative responses of these two measures are compared with Nejad's electrophysiological recordings from the GSP nerve[17] and are illustrated in FIGURE 9 (see Smith[19]). Plots similar to that in FIGURE 9 were made from the data of the present experiment at week 20, week 62, and week 97. At these three age levels, the rats do not differ in sucrose ingestion in terms of the number of bouts, the bout length, the number of licks per bout, or the interbout interval. The rate of drinking (ml/min) is

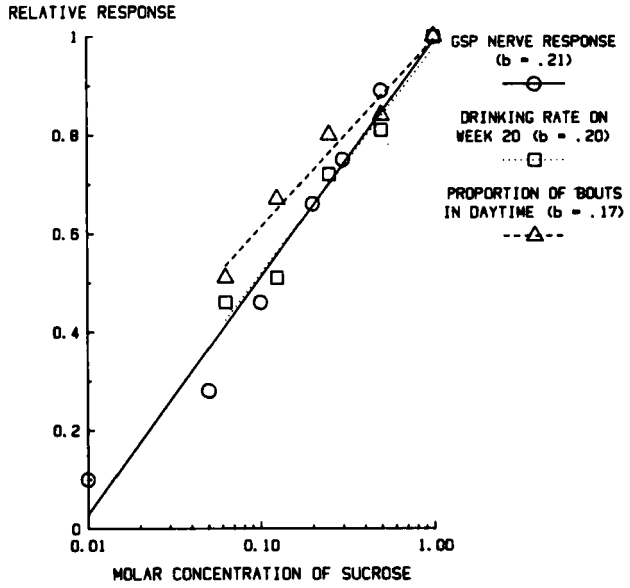

FIGURE 9. A comparison of electrophysiological response from the greater superficial petrosal nerve (solid line) and two behavioral measures of the taste of sucrose across two log units of concentration. The electrophysiological data were plotted from data reported by Nejad.[17] Straight lines were fitted with a semilog plot, and the slope (b) for each curve is reported.

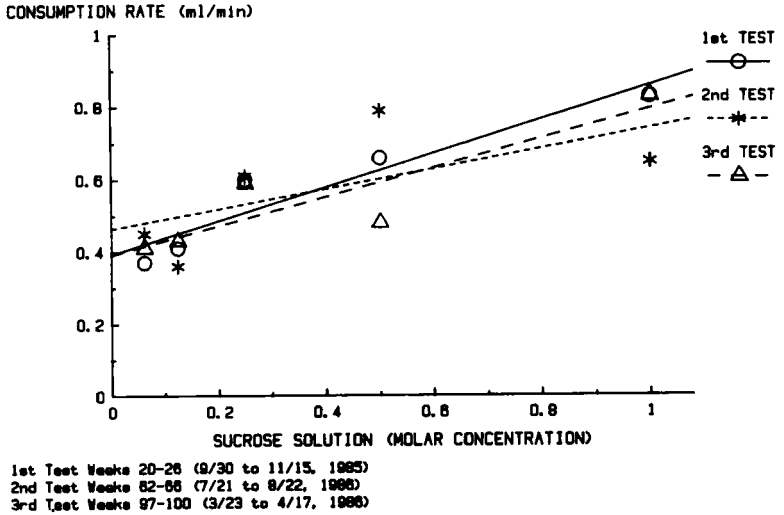

FIGURE 10. The consumption rate as a function of sucrose concentration is plotted for three testing periods during the longitudinal study.

plotted for the three different testing period times in FIGURE 10. Here one can see the general trend of lick rate increases as a function of concentration (not unlike the electrophysiological data described above) for all three test periods. A similar function can be seen in FIGURE 11, where the percentage of daytime sucrose drinking bouts is plotted as a function of sucrose concentration. The correlation between the rate of drinking within a bout and the proportion of daytime bouts for these three test periods is .79. The variability within these three test periods is high, so the differences between the three test periods are not significant on either measure. We can conclude that up to the time when the rats are 24 months old, age seems to have no effect on taste as measured in this manner.

We have made a detailed study of the ingestive responses of all of the surviving rats from week 90 until week 127, when the last rat died. The mean food and

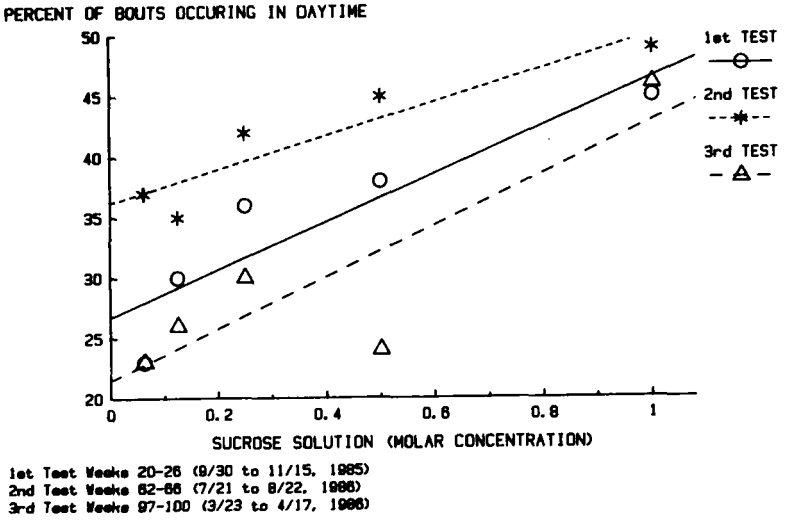

FIGURE 11. The proportion of sucrose bouts that occur in the daytime is plotted as a function of sucrose concentration for three testing periods during the longitudinal study.

sucrose ingestion of these surviving rats are plotted in FIGURE 12 for the last eight daily periods of sucrose ingestion before death. It can be seen that there is a gradual decrease in food intake in most of the groups. Sucrose intake stays relatively steady right up to day of death.

DISCUSSION

In typical preference tests, rats are kept in home cages for 24 hr and given a choice between two bottles—one containing water and one containing a sucrose solution. The rats in these tests prefer the sugar (see, for example, Collier and Bolles[20]). As the concentration of the sucrose is increased from day to day, the absolute intake increases for concentrations up to about 0.25 M. A decrease in intake of the solution is shown for higher concentrations, resulting in what has

been described in the literature as the preference–aversion function. The amount of solute (and calories), however, has been shown to increase with increases in sucrose concentration up to about 1.0 M. Food intake has been shown to systematically decrease when the concentration of sucrose available increases. The decrease in calories from the food was not enough to compensate for the increase in calories from the sucrose. Hence total caloric intake would increase.

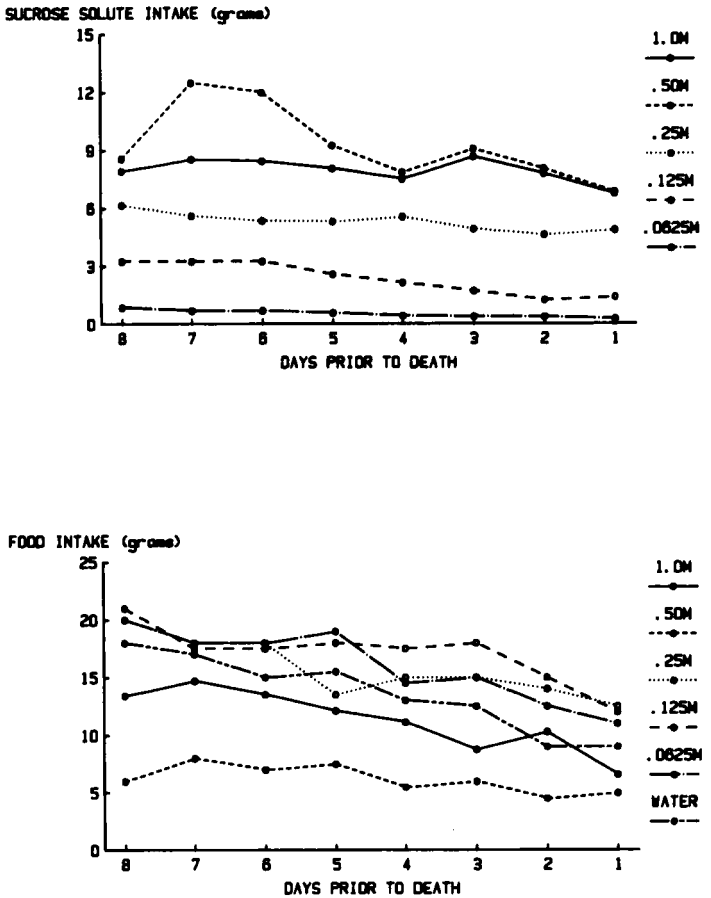

FIGURE 12. The mean sucrose intake (upper panel) and the mean food intake (lower panel) are plotted for the 8 days before death for all of the rats that survived beyond week 90 of the study.

In the present longitudinal study, this 24-hr, two-bottle preference test was continuously conducted for six groups. The rats in each group were exposed to only one concentration of sucrose for their lifetimes. The basic relations between sucrose, water, and food ingestions described by Collier and Bolles[20] held true for

the lifelong tests described in the present longitudinal study. What we looked for were any *changes* that occurred across the life span of the rats.

Rats in the 1.0 M and the 0.5 M sucrose groups gradually increased the amount of the sugar solution ingested between the 15th and 90th week of the study. Hence, they also increased the absolute amount of the sugar solute. In contrast, rats in the 0.0625 M and 0.125 M sucrose groups decreased their intake as they grew older. Food intake did not change much except in the 0.25 M sucrose group, where there was a gradual increase as the rats approached the 90th week.

The body weights of the rats in the 1.0 M, 0.5 M, and 0.25 M groups continued to increase into the sixth time period (weeks 75–90). The body weights of the remaining rats leveled off during the fifth and sixth time periods. In spite of the increase in body weight, the longevity of the rats did not seem to be affected by the various sucrose concentrations.

When given a break from the presence of sugar on the 3-day weekends, the rats tend to "diet," showing the same systematic relative food intakes across the six groups as they did during the weekly sucrose testing periods. Ingestion of both food and sucrose was significantly reduced when the rats were between 20 and 35 weeks of age. This decrement is not understood at the present time. Taste, as inferred from drinking rate or proportion of daytime drinking bouts, as a function of sucrose concentration, does not appear to change as the rats age, at least up to 24 months. The ingestion behavior of the surviving rats from an age of 90 weeks until death is currently being studied and will be reported later.

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