Persistence of palatability-induced polydipsia

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Rats were given either a 2% sucrose solution or a 0.2% saccharin solution as their sole fluid for 18 days when food was freely available and for 38 days when food was restricted. There were no long-term trends in the consumption of either solution, although consumption during the first solution day was usually higher than during other days. More of each solution than water was ingested, especially when food was restricted. The results emphasize the role of palatability in the regulation of food intake. However, they do not support the view that palatability is important only when food is restricted.

Conventional wisdom and introductory texts perpetuate the notion that the regulation of food intake during food deprivation depends mainly on factors related to blood-sugar level and hence on the calorific value of the food. The notion is buttressed by the well-known ability of fistulated rats to maintain normal food intake by delivering food directly to the stomach (Epstein & Teitelbaum, 1962), a finding that seems to rule out palatability as a source of control. However, as Jacobs & Sharma (1969) have noted, studies suggesting that regulation of food intake occurs on the basis of calorific value were carried out under ad lib feeding conditions. These authors review their studies in which caloricity and palatability were varied independently for both dogs and rats and conclude that, when the animals were deprived of food, palatability seemed to be the regulating factor. Other results also implicate palatability, including those of Gilbert & Sherman (1970), whose results also implicate palatability in regulation by nondeprived rats. The question remains as to whether the effectiveness of palatability depends upon its usual correlation with caloricity. Jacobs (1964) found that palatability was the important factor in the acceptance of various solutions by neonate rats. The possibility remains open, however, that the inherited dependence upon taste is restricted to a critical period shortly after birth and that subsequent control by taste depends upon the reliable pairing of taste and calories. If such pairing is necessary for continued dependence on taste, it might be expected that the palatability of saccharin solutions would decrease with chronic consumption when compared with the palatability of sucrose solutions.

The only previous comparison of the chronic intake of sugar and saccharin solutions was made by Valenstein (1967), who found that food-satiated rats preferred 3% and higher concentrations of glucose in water to a 0.25% saccharin solution, but that during 30 days of food restriction the saccharin solution was preferred to the 3% glucose solution. In a comment on the Jacobs and Sharma paper, Valenstein noted that this surprising result does not always occur but that when it does occur the preference for saccharin may cause avoidable starvation. It is possible that the attractiveness of the saccharin solution in Valenstein's study depended in part on the concurrent availability of the glucose solution, some of which was consumed each day. The effect of the predictive sweet taste of glucose for calories could have generalized to the saccharin solution. Other relevant studies have investigated the chronic consumption of saccharin solution alone. Neither Strouthes (1970) nor Valenstein (1966) found a decline in the 24-h intake of the most palatable solutions used. Strouthes investigated consumption over periods of more than 300 days, throughout which food and water were freely available. However, he did not use a solution within the range 0.1%-0.3% concentration of saccharin, and, thus, his animals drank relatively little. Valenstein noted the intake of a 0.25% saccharin solution and a 0.28% sodium saccharin solution during 36 days of food restriction when each solution was presented singly. Intake of the former solution rose throughout the period; intake of the latter solution reached an asymptote after 6 days. These results are difficult to interpret because the intake of a third group, which had only water, generally increased during the first 26 days of food restriction and only thereafter remained stable.

In the present study, the 24-h intake of a 2.0% sucrose solution and a 0.2% saccharin solution was determined when each was presented alone for many days, both when food was freely available and when it was restricted. The concentrations were chosen as being close to maximum palatability for the rat, as estimated by the single-bottle test (Gilbert & Sherman, 1970). It was expected that, at these concentrations, more sucrose than saccharin solution would be consumed. A difference between trends of consumption of the two solutions could implicate caloricity as a basic regulating factor. Lack of difference in trend could be considered as further evidence for the importance of palatability in the control of food consumption.

SUBJECTS AND APPARATUS

Twelve male black-hooded rats were used. For the first 110 days of the study, the rats were housed individually in a room that was darkened between 7 p.m. and 7 a.m. each night and whose relative humidity and temperature were kept at 50% ± 10% and 22° ± 2° C, respectively. The cages measured 170 x 240 x 170 mm high, and each was provided with one or two 100-ml Richter drinking tubes. On Day 111, the laboratory premises were changed, and the rats were transported 1 mile in their cages in a heated vehicle to a new room whose humidity and temperature were maintained at 40% ± 5% and 21° ± 1° C, respectively. The same light-dark cycle was maintained. Rockland rat diet cubes were used throughout the study; they were left on the floors of the cages as necessary. The animals had been obtained from Woodlyn Farms, Guelph, Ontario, when they were approximately 120 days old. Day 1 of the study began at 3 p.m., December 3, 1970, 4 days after their arrival in the laboratory. Subsequently, body weights and liquid intake were recorded, and further food and liquid allocated, between 2 and 3 p.m. each day. Richter tubes were replenished at other times when necessary to avoid their becoming empty.

PROCEDURE

A summary of the main experimental manipulations occurs as an incidental feature of Fig. 1. Food and water were freely available during Days 1-13. At the end of Day 13, the animals were ranked according to their median water intake during the previous 9 days and divided into two groups, the sucrose group and the saccharin group, each group having three animals from the half that drank most (range of medians, 50-56 ml) and three animals from the half that drank least (range, 39-49 ml). The range of individual body weights during the same 9 days was 299-348 g. The Spearman rank correlation coefficient between the daily water-intake medians and the daily body-weight medians is −0.10 ($p > .10$).

During Days 14-28, food continued to be freely available, but, instead of water, the sucrose group received a 2% saccharin solution and the saccharin

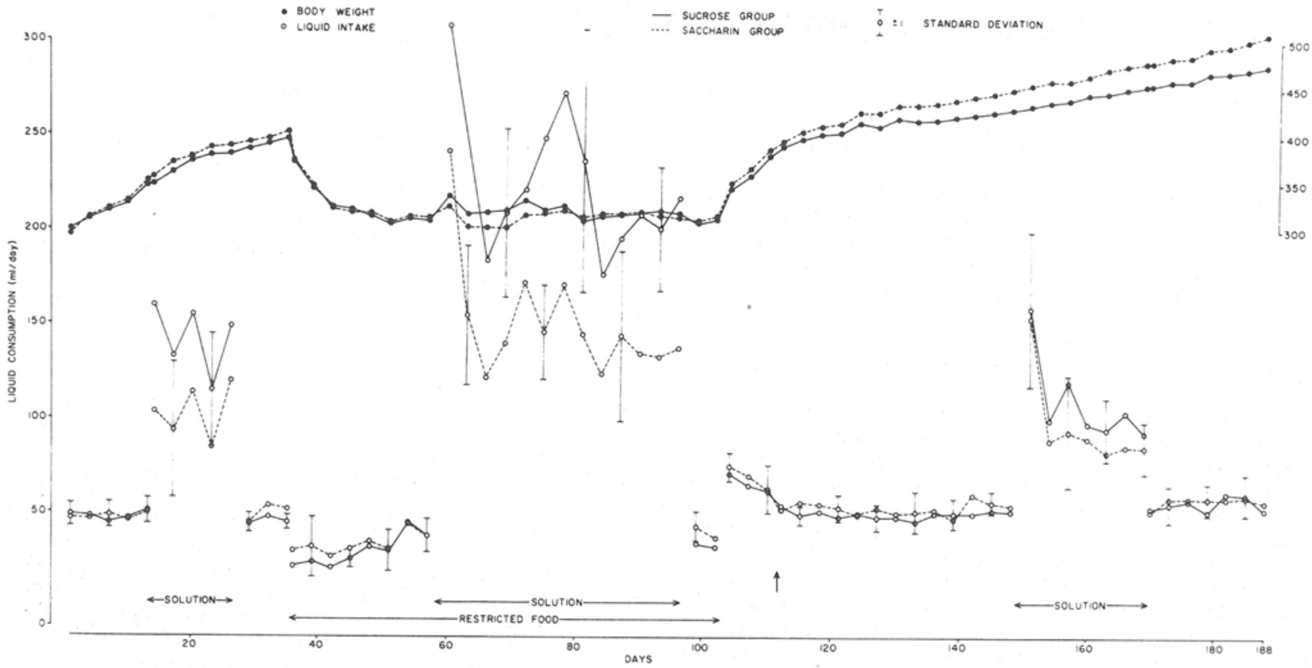

Fig. 1. Mean daily liquid intake and body weight of the two groups of six animals for various days throughout the study, selected in the manner described in the text. Food and water were freely available except during the days for which "solution" or "restricted food" are indicated above the abscissa. Details of these procedures are given in the text. The vertical arrow indicates when there was a change in the location of the experiment.

group received a 0.2% saccharin solution. The solutions were prepared by dissolving 20 g or 2 g of sucrose or sodium saccharin, respectively, in 1,000 ml of tap water, at least 12 h before use. Water was restored at the beginning of Day 29.

From Day 36 onwards, food was restricted by giving each animal 10-15 g per day until its weight at feeding time was less than 85% of its mean weight during Days 31-35. Subsequently, from approximately Day 48 until the end of food deprivation on Day 104, each rat was fed an amount equal to its feeding-time weight subtracted from its 85% weight or 5 g, whichever was larger.

Sucrose or saccharin solution was available instead of water from Day 60 until Day 98, and again from Day 151 until Day 169. Food restriction was discontinued and food was freely available from Day 104 until the end of the study on Day 188.

RESULTS

Figure 1 gives mean body weight and mean liquid intake for each group for every third day, beginning with Day 1 and beginning again whenever the experimental conditions were changed. The standard deviation is given for one liquid intake mean in four. The standard deviations of body weight distributions within groups were always between 4% and 8% of the respective means. Figure 1 is provided to give an overall picture of the results. The analysis that follows is based largely on the data given in Fig. 2, which shows individual means of liquid intake, with standard deviations, for the six sessions (five in one case) that preceded and followed a change in procedure.

Water Intake

Considering the stability of the water intake baseline first: 10 of the 12 rats were drinking more per day during Days 170-175 (overall mean = 56 ml) than during Days 8-13 (overall mean = 49 ml), and another was drinking at the same rate. Assuming a binomial distribution of increases and decreases, the probability of occurrence of this set of events is 0.006, suggesting either that the effect of the various procedures was to increase water intake or that water consumption increased with age and/or weight. In the absence of a control group that was not deprived and did not receive the solutions, a positive correlation between body weight and water intake at the beginning of the study, and other supporting data, it may be better to assume the first alternative, especially in view of a similar finding by Gilbert & Sherman (1970). Local comparisons of water intake before and after the solution was given and before and after food restriction do not reveal significant differences.

The immediate effect of food restriction was to reduce water intake by more than 40% in each case, except that of Rat S_8 (20%), which was drinking unusually large amounts of water during Days 29-34, and that of Rat S_4 (22%), which had the lowest water consumption during the same period. The overall average water intake per day just before food restriction was 49 ml. Just after the beginning of deprivation, it was 28 ml, a decrease by 43%. However, when body weights had stabilized at about 85% of free-feeding weights (Days 54-59), the average daily intake had risen to 39 ml, a change of 20% from intake under free-feeding conditions.

The immediate effect of removing the restriction on food intake was to increase average water intake from 37 ml to 67 ml per day. However, with continued unlimited feeding, water intake subsequently declined to an average of 54 ml per day (Days 145-150) when the postdeprivation large daily increases in body weight had ceased to occur.

Solution Intake

All 12 rats drank much more sweet solution than they did water, whether food was restricted or not. Table 1 shows that the minimum increase was 50%, in the case of one rat in the saccharin group when food was freely available, and the maximum increase was 550%, in the case of one rat in the sucrose group when under food restriction. On the average, more sucrose solution was consumed than was saccharin solution, although it

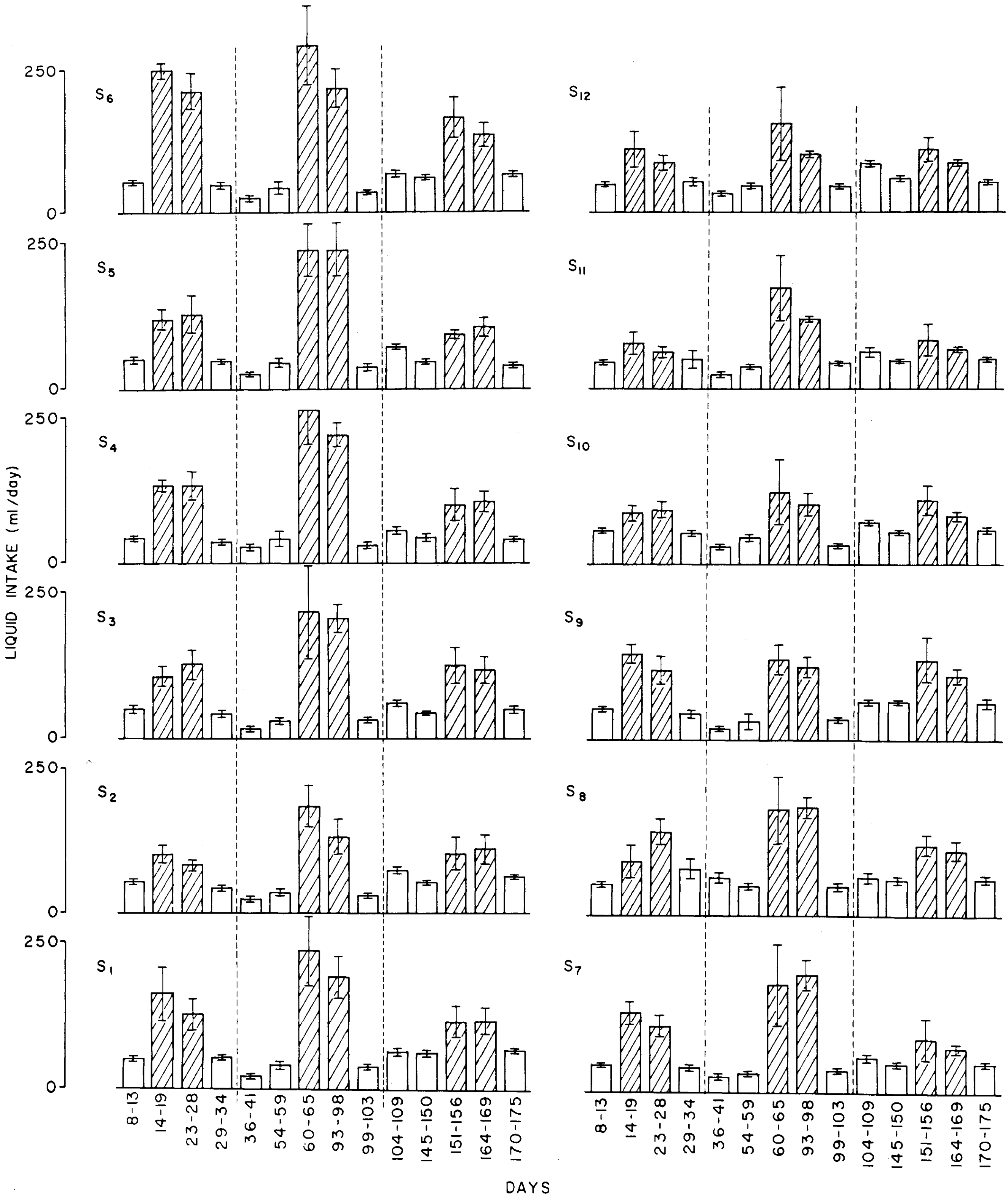

Fig. 2. Individual daily liquid intake by the 12 rats used in this study for the days indicated. The hatched bars represent sucrose solution intake at the beginning and end of each solution phase for Rats $S_{1\text{-}6}$ and saccharin intake for the same periods for Rats $S_{7\text{-}12}$. The open bars represent water intake. Food was restricted during the periods that fall between the pairs of vertical dashed lines.

should be noted that there was appreciable overlap between intakes of the two kinds of solution under similar conditions of food availability.

More of each kind of solution was consumed when food was restricted

Table 1
Ratio of Sweet Solution Intake to Water Intake Before, During, and After Food Restriction

Group	Before		During		After	
Sucrose	3.0	(1.9-2.5)	5.9	(4.7-6.5)	2.2	(1.8-2.6)
Saccharin	2.0	(1.5-2.9)	3.7	(2.9-5.9)	1.8	(1.5-1.9)

Note—Each ratio is the overall mean intake of sweet solution by one group during days at the beginning and end of one solution phase divided by the overall mean water intake by that group just before and just after that phase. Thus each mean is based on data from 11 or 12 days. Ranges of individual ratios are given in parentheses.

than when it was not, both absolutely and in relation to the respective baseline water intake. On the average, the sucrose rats drank 71% more solution when food was restricted; the equivalent increase for the saccharin rats was 47%. Again, considerable overlap in group ranges may be noted: 35%-112% in the case of the sucrose group and 3%-101% in the case of the saccharin group. Comparing these percentage increases using a Mann-Whitney U test, the probability of occurrence of the difference between groups is estimated to be 0.09.

The effect of chronic intake of sweet solution on amount consumed can be assessed by comparing consumption at the beginning and end of each sweet solution phase. The average consumption of each group during the first 6 days of a phase was always higher than during the last 6 days of a phase. However, individual means are consistently different in only one of these comparisons, that for the saccharin group during its final solution phase. If all 36 differences are compared (3 for each rat), the overall difference appears to be highly significant ($p < .002$, using a Wilcoxon matched-pairs test), but the effect is clearly not strong enough to be general. Furthermore, most of the apparent effect is restricted to the first day of each solution phase. For 22 of the 36 comparisons, consumption during the first day of the phase was higher than during any other day of the phase. If consumption during Days 2-6 of each solution phase is compared with consumption during the last 5 days of each phase, an overall decline in consumption is indicated, but the probability of the difference is greater than 0.08 according to the Wilcoxon test. Moreover, no similar comparison within a group or within a deprivation condition indicates a significant effect of chronic consumption.

DISCUSSION

These results indicate that there is no systematic difference between the patterns of consumption of 2% sucrose solution and 0.2% saccharin solution when either one is the sole available fluid for periods of up to 38 days. Intake during the first day was in many cases higher than it was on subsequent days. Subsequent fluctuations in daily consumption were of a local nature and did not indicate a long-term trend in the case of either solution, whether food was restricted or not. The absence of a manifest difference in chronic intake of sucrose and saccharin solutions can be regarded as further evidence for the importance of palatability in the regulation of food intake and evidence that palatability continues to be effective even though it repeatedly fails to be predictive of calorific value. One possible correlation between palatability and caloricity was not taken account of during the present study. Although the Rockland rat diet cubes that were consumed throughout do not taste sweet to humans, two of the four main ingredients (soya bean meal and barley flour) each contain more than 3% sucrose. It is likely that the overall sugar concentration is very low and that its taste is counteracted by the bitter substances (e.g., citric acid) that are also present. Nevertheless, another study of the same problem could remove this possible source of predictiveness by providing a bland or clearly bitter diet.

Jacobs & Sharma (1969) concluded that palatability is of critical importance only when an animal is deprived of food and that metabolic factors predominate when food is freely available. This conclusion leads to the prediction that the increase in saccharin consumption caused by food deprivation should be relatively greater than the similarly caused increase in sucrose consumption. In the present study, the difference was nonsignificant but in the direction contrary to the prediction. Thus, it might appear that palatability can also be the critical factor under conditions of plenty.

The fact that palatability may predominate in the regulation of ingestion does not exclude the participation of other factors. Palatability may predominate only when taste is not neutral. Blandness, or circumvention of oral-pharyngeal receptors, permits control by other mechanisms such as stomach load, osmolarity, and blood-sugar level. These in turn may be ordered hierarchically so that, in the absence of extreme signals from the more important factor, control is assumed by the less important factor. The important effect of food deprivation on palatability may be to narrow the range of blandness. There is some evidence that food-deprived rats and dogs are more "finicky" (Jacobs & Sharma, 1969), i.e., they react more strongly to taste. This model can account for the apparent discrepancy between the present results and those adduced by Jacobs and Sharma in support of their two-factor model. The solution concentrations used here were chosen as being maximally palatable under the conditions of the study and were possibly outside the rats' blandness range, even when they were satiated. Thus, palatability was the important regulating factor. In the studies in which metabolic factors appeared to predominate, even though taste was possible, the palatabilities of the various substances may have fallen within the respective blandness ranges, thus precluding control by palatability. These ad hoc assumptions would be supported by a demonstration that the addition of a sweetener can upset the caloric regulation of intake of an otherwise bland diet by satiated animals.

REFERENCES

EPSTEIN, A. N., & TEITELBAUM, P. Reulation of food intake in the absence of taste, smell, and other oropharyngeal sensations. Journal of Comparative & Physiological Psychology, 1962, 55, 753-759.

GILBERT, R. M., & SHERMAN, I. P. Palatability-induced polydipsia: Saccharin, sucrose, and water intake in rats, with and without food deprivation. Psychological Reports, 1970, 27, 319-325.

JACOBS, H. L. Observations on the ontogeny of saccharine preference in neonate rats. Psychonomic Science, 1964, 1, 105-106.

JACOBS, H. L., & SHARMA, K. N. Taste versus calories: Sensory and metabolic signals in the control of food intake. Annals of the New York Academy of Sciences, 1969, 157, 1084-1125.

STROUTHES, A. Long-range, two choice saccharin and water consumption in rats. Journal of Comparative & Physiological Psychology, 1970, 73, 123-134.

VALENSTEIN, E. S. The significance of sodium in the preference for saccharin solutions. Psychonomic Science, 1966, 5, 341-342.

VALENSTEIN, E. S. Selection of nutritive and nonnutritive solutions under different conditions of need. Journal of Comparative & Physiological Psychology, 1967, 63, 429-433.