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Taste-Masking: A Function of Exaggerated Prandial Drinking in Desalivate Mice

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ABSTRACT

Taste thresholds for the bitter compound sucrose octaacetate (SOA) were elevated by desalivation in mice. Thresholds were determined for control and experimental animals both before and after ligation of all salivary ducts. There was a significant increase in SOA thresholds in the desalivate mice, and the pre- to post-operative differences in threshold between the control and experimental groups were significant.

The altered response to SOA by desalivate mice is shown to be due to the assumption of a prandial pattern of drinking as a result of desalivation. This conclusion is based on experiments with wet mash which failed to show any differences in threshold between the same control and desalivate mice that demonstrated a significant difference when tested on fluids and dry pellets.

INTRODUCTION

Vance (1965) demonstrated an elevated rejection threshold to quinine hydrochloride (QHCl) in desalivate rats, and suggested a salivary influence on taste receptors to be responsible for the difference in threshold.

To appreciate the significance of changes in taste aversion after ligation of the salivary ducts, it is important to consider coincident changes in the temporal patterning of feeding and drinking. Preventing saliva from reaching the oral cavity, either by removing the salivary glands (Epstein *et al.*, 1964) or by ligating the salivary ducts (Vance, 1965; Kissileff and Epstein, 1969), results in a modification of nutritive behavior in the rat and has been described as prandial drinking (Teitelbaum and Epstein, 1962). Prandial drinking is characterized by small draughts of water being consumed immediately after a morsel of dry food is taken into the mouth (Kissileff and Epstein, 1969). Vance (1965) proposed that desalivate rats use their drinking water as an exogenous saliva to permit the swallowing of dry food, a view clearly supported by Kissileff (1969b).

The present study demonstrates that desalivate mice also assume a prandial pattern of drinking which is consistent with the descriptions of this behavior in desalivate rats. Small draughts of water are alternated with short feeding episodes, the durations of each of these activities consisting of only a few seconds. It is suggested that the difference in threshold between control and desalivate animals is due to a "masking effect" related to the prandial drinking pattern assumed by the desalivate animal as originally proposed by Lewis and Warren (1969). The masking hypothesis is based on two assumptions: one, that desalivate mice and rats use their drinking water as an exogenous saliva to permit the swallowing of dry food; and two, that the great majority of drinking bouts occur in close temporal association with feeding. Under the conditions, the taste of any compound in the drinking water would be masked by having it compete simultaneously with the taste of food in the mouth which was being softened into a mash to permit swallowing.

This study employed the aversive substance sucrose octaacetate (SOA) and tested the hypotheses of Vance (1965) and Lewis and Warren (1969) by eliminating the differences in nutritive behavior between normal and desalivate mice by the use of a wet mash. The effect of the absence of saliva on rejection thresholds could then be assessed without the interference that may be contributed by behavioral differences.

MATERIALS AND METHODS

Threshold determinations were made by employing paired 25 ml burettes in a modified 24-hour choice test. Over any four-day period,

the burettes would be rotated daily in a LRLR manner, while the test solution was rotated LRLR. The effect of this rotation scheme was the presentation for a 24-hour period of each of the four possible combinations of side and burette for the test solution and the water it was paired with. By this means, the biasing of threshold data by side or burette preference was avoided. The test solution was presented in an ascending series by increasing the concentration every two days by about one-third of a log molar step. For example, the sequence of SOA concentrations used was $6 \times 10^{-7}M$, $1.5 \times 10^{-6}M$, $3 \times 10^{-6}M$, $6 \times 10^{-6}M$, etc. Rejection was defined as that concentration of SOA at which its intake constituted less than 30% of the total fluid consumption over a 48-hour period. Lab Blox food pellets were available *ad libitum*.

Special cages with two food cups attached were employed for the wet mash experiments. The food cups were located at the end of short runways attached to one wall of the cage. The cups were filled each day with mash prepared by mixing food pellets, which were ground to a powder, with water (or SOA solution) in the ratio of 35 grams of dry food for every 65 ml of solution. The concentration of test solution used to make the test mash was increased every two days, and the position of the test mash was alternated with the control mash daily. The mouse then had a two-cup, 24-hour choice situation essentially identical in method to the tests with burettes. The amount of mash consumed from each cup was determined by weighing the cup when filled and again after the 24-hour feeding period. Rejection was defined as that concentration of SOA at which the SOA mash constituted less than 30% by weight of the total mash consumption for the 24-hour period.

All animals were tested for frequency and duration of feeding and drinking episodes on burettes both before and after desalivation. Data was recorded for a 30-minute test period which was preceded by 16-20 hours of food and water deprivation. Drinking was monitored both for duration and frequency by means of an Esterline-Angus event recorder, while feeding episodes were observed and noted on the drinking record.

Desalivation was performed by ligating all six salivary ducts with silk thread (size 000) through a 2 cm incision in the throat. A suturing needle was used to pass the thread beneath the ducts to minimize damage to surrounding tissues.

Sixteen F₁ progeny of C₅₇B1/6 and CFW mice were tested to rejection on sucrose octaacetate (SOA) by means of burettes. Drinking and feeding patterns were then assessed for all animals in a 30-minute test period following 16-20 hours of food and water deprivation. Nine of the 16 mice were desalivated, and upon their recovery, all animals were again tested to rejection on SOA as in the pre-operative test. Following this post-operative threshold test, nutritive behavior was again monitored in a 30-minute test as before to detect and record differences due to desalivation. In each case, the assessment of feed-

ing and drinking behavior was carried out immediately after testing for SOA rejection thresholds to elucidate any behavioral differences that may have existed between the mice on the pre-operative and post-operative threshold determinations with burettes. Lastly, a third and final threshold determination for SOA was performed, this time comparing the control and desalivate groups by means of a wet mash.

RESULTS

As can be seen in Table I, in only the second of the three threshold determinations on SOA is there a significant difference in consumption. This marked increase in fluid consumption by desalivate mice is paralleled by a modification of nutritive behavior as indicated in Table II. Although desalivate mice show a marked alteration in drinking when eating dry lab pellets, the differences in nutritive behavior between desalivates and controls disappear in mice eating wet mash. In the wet mash experiment no differences could be detected in amount of mash consumed or SOA thresholds between the two groups.

Table II is consistent with what would be expected if desalivate mice responded to dry food as has been described for desalivate rats.

The most important of these measures in terms of the masking hypothesis, however, are those concerned with the temporal relationship of feeding and drinking. It can be seen that 70% of all drinking bouts by desalivate mice occurred within five seconds of the end of a feeding episode, whereas in the controls and the experimental group (before desalivation) no drinking bouts occurred this close to a feeding episode.

DISCUSSION

Desalivation in mice brings about essentially the same changes in nutritive behavior (prandial drinking) as has been described for desalivate rats (Kissileff 1969a). In each case, a desalivated animal shows a marked increase in water consumption when it is eating dry food (Epstein *et al.*, 1964). This is due to the desalivate animal's using its drinking water as an exogenous saliva to facilitate the swallowing of dry food (Vance, 1965; Kissileff, 1969b). The present study supports this view in that the great majority of drinking bouts follow immediately the taking of dry food into the mouth.

Desalivate mice on dry food show an increased rejection threshold to SOA. These results are similar to those reported by Vance (1965)

Table I. Comparison of SOA rejection levels in normal and desalivate F₂ mice.

	Experimental condition	N	Mean fluid and mash consumption	Mean rejection level	t	p
Preoperative (solutions)	Control	7	6.26 ml	$1.46 \times 10^{-5} M$	0.426	.69
	Desalivate	9	5.91 ml	$1.67 \times 10^{-6} M$		
Postoperative (solutions)	Control	7	5.49 ml	$5.60 \times 10^{-6} M$	2.27	.04
	Desalivate	9	10.80 ml	$5.50 \times 10^{-5} M$		
Postoperative (wet mash)	Control	6	11.34 g	$1.15 \times 10^{-4} M$	0.390	.71
	Desalivate	8	10.91 g	$9.76 \times 10^{-5} M$		

Table II. Results of 30-minute tests for prandial drinking on F₂ mice before (Test-1) and after (Test-2) desalivation.

Experimental condition	N	Total feeding bouts	Total drinking bouts	Mean duration of individual bouts (in seconds)		Number of drinking bouts preceded by feeding within		
				Feeding	Drinking	5 sec.	10 sec.	30 sec.
Control (Test-1)	7	53	57	42.8	12.7	0/57	1/57	2/57
Control (Test-2)	7	34	56	31.6	8.7	0/56	2/56	7/56
Desalivate (Test-1)	8	66	77	43.3	16.9	0/77	2/77	10/77
Desalivate (Test-2)	8	275	285	14.8	3.6	199/285	208/285	236/285

with rats tested on quinine hydrochloride. Whereas Vance suggests that a salivary influence on taste receptors is responsible for the alteration in threshold, the present study leads the author to postulate a "masking effect" as the basis of the elevated thresholds. The masking is a result of the modification in drinking behavior which occurs as a consequence of desalivation.

The masking hypothesis derives further support from a consideration of the magnitude of the differences in threshold between desalivate and normal animals. In the present study, the analysis of drinking in desalivate mice indicated that about 25% of their drinking bouts were not immediately preceded by feeding (Table II). This would allow the desalivate animal to encounter the test substance without the masking effect being operative. If it is the masking that occurs in the other 75% of the drinking bouts which causes the difference in threshold between normal and desalivate mice, then the masking hypothesis would predict an even greater difference in threshold if the desalivate mouse were completely prandial in its drinking. Kissileff (1969a) has reported in his analysis of feeding and drinking in desalivate rats that virtually 100% of their drinking follows within seconds the taking in of a morsel of dry food. Whereas the study shows that the rejection thresholds between normal and desalivate mice on SOA differ by a factor of 10, Vance's data with desalivate rats on QHCl show a difference in threshold of approximately 80 times between his control and desalivate animals. In the light of the threshold data on SOA mash reported above, this difference in magnitude is most likely due to the more complete masking that would occur in prandially drinking rats.

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