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Habituation and Dishabituation of Human Salivary Response

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EPSTEIN, L. H., J. S. RODEFER, L. WISNIEWSKI AND A. R. CAGGIULA. *Habituation and dishabituation of human salivary response.* PHYSIOL BEHAV **51**(5) 945–950, 1992.—Habituation may be relevant for understanding how sensory stimuli influence factors related to ingestive behavior. In the first of three experiments in humans we showed that salivation and hedonic ratings to lemon or lime juice habituated within 10 presentations, and dishabituation of the salivation and hedonic ratings to the original juice were observed after a new juice was presented. Experiment 2 replicated the habituation and decrease in hedonics to lemon juice, and showed both dishabituation and a relative increase in hedonics when chocolate taste, rather than another juice, served as the dishabituating stimulus. In a third experiment we showed a video game, a nontaste stimulus, could serve as a distractor to prevent the development of habituation, as well as a dishabituator after habituation had occurred.

Salivation Habituation Hedonics Dishabituation Distractor

HEDONIC preferences for food depend in part on sensory factors that regulate taste and olfaction (1,2). Repeated presentation of preferred foods results in decreases in food palatability and consumption of these foods (7,11,17–19,28). These changes may be based in part on sensory adaptation or habituation to food related stimuli (3,27), in addition to physiological satiation. In addition, presentation of a new food after satiety usually results in an increase in food palatability and resumption of consumption (17–20), which demonstrates that the satiety is specific to the sensory characteristics of the food.

A neurophysiological basis for the decrement in food palatability and acceptance has been studied in monkeys by E. T. Rolls and colleagues (22–25,37,38). These investigators have demonstrated that the response of neurons in the lateral hypothalamus, substantia innominata, and caudolateral orbitofrontal cortex decrease with repeated presentations of a food stimulus, along with acceptability of that food. These electrophysiological and hedonic changes are specific to that particular food, since neuronal responsiveness recovers with presentation of a new taste, along with acceptability of that new food. The electrophysiological response pattern is localized to specific areas of the brain, since neurons in the nucleus of the solitary tract, the insular gustatory cortex, or the frontal opercular gustatory cortex do not change with repeated presentation of the same food stimulus, even as food acceptance decreases. This suggests that activity in these regions relates to sensory and not to evaluative components of taste. These neurophysiological and behavioral changes in monkeys may be analogous to the observation in humans that perceived intensity of a taste does not decrease with repeated presentation, while food pleasantness and desire to eat do decrease (17).

In the present series of studies we used the habituation model to assess changes in whole mouth parotid salivation (4) as a function of repeated presentation of a strong, preferred taste stimulus. Salivation is a physiological response that is related to hunger, taste, food palatability, and amount of food eaten (12,26,35,36). If the habituation model is to be useful in understanding changes in salivation to repeated presentation of food stimuli, salivation should decrease with repeated presentation of a taste stimulus. In addition, since the response decrement could be a function of neural fatigue or adaptation rather than habituation, it is important to show that the response dishabituates to the habituating stimulus after presentation of a novel stimulus or that presentation of a distractor will influence the rate of habituation to the habituating stimulus (31).

Several studies have assessed salivary change to repeated presentation of taste stimuli. Subjects habituate to repeated presentations of acetic acid and dishabituate when presented with a loud auditory stimulus (32). Likewise, subjects who received a distractor noise between two presentations of lemon juice showed greater salivation to the second lemon juice presentation than did subjects who received repeated lemon juice presentations with no distractor (5). However, the habituation

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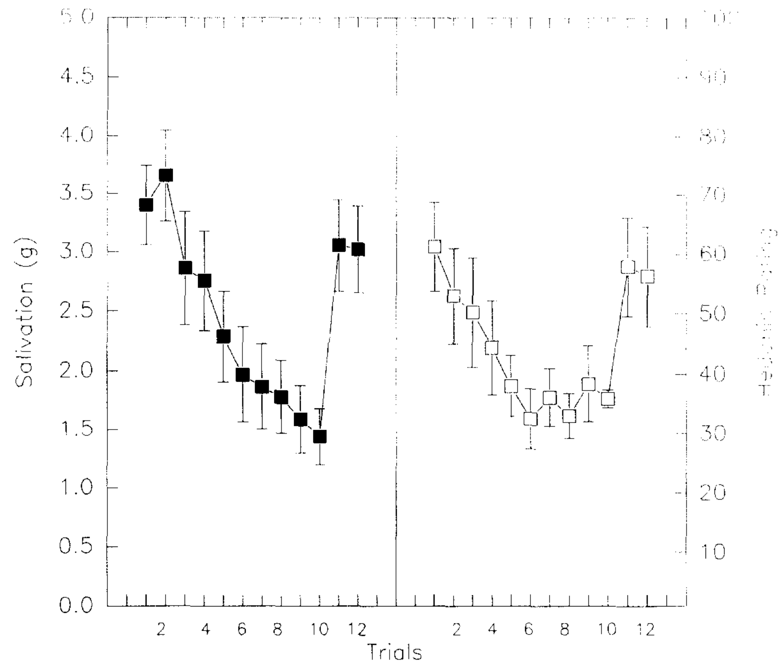

FIG. 1. Salivation and hedonics (mean ± SEM) for subjects who received lemon or lime juice as the habituating stimulus in trials 1–10, the other juice as a dishabituator in trial 11, and presentation of the habituating stimulus in trial 12. ■, salivation; □, hedonic ratings.

may in part be a function of the taste stimuli used. Complete habituation to five presentations of capsaicin was not observed (15), although the response pattern was consistent with the warm-up effect and then initiation of a gradual decrease observed by others (32) to acetic acid. The first and second experiments in the present series evaluated the pattern of habituation to repeated taste stimuli and dishabituation to a novel taste. The third experiment assessed whether a nontaste stimulus could serve as a distractor to influence the development of habituation, and could serve as a dishabituator after habituation had been established.

GENERAL METHOD

Subjects

Subjects were females ages 18–30, in good health, nonobese (14), who took no medications which might influence salivation (e.g., atropine, diphenhydramine, amitriptyline), were not dieting, showed no dietary restraint (10), and rated lemon flavor as at least moderately liked (≥5) on a 1–10 scale. Dietary restraint was included as an exclusionary criterion since it can influence salivary response to food stimuli (13). Subjects were excluded if they were above the mean for standardization samples for restraint.

General Procedures

Subjects were deprived of food, caloric and/or caffeinated beverages for a minimum of 4 hours prior to the experiment. Upon arriving at the laboratory for the 90-minute lunch or dinnertime session, subjects' heights and weights were measured, and they completed scales which assessed liking of various flavors, and the dietary restraint scale.

Measurement of Salivation

Whole mouth parotid salivary flow was measured using the Strongin-Hinsie Peck (SHP) method (16). In this procedure three cotton dental rolls (cylindrical, 10 mm diameter, 38 mm length, Patterson Dental Co., Lancaster, PA) were placed in the subject's mouth under the tongue and on both the left and right side of mouth between the cheek and lower gum after swallowing. The stimulus was applied to the subject's tongue, and saliva was collected for 2-minute periods, followed by 2-minute intertrial intervals. Subjects rinsed their mouths with water after each trial. Saliva was measured to 0.01 grams.

Subjects began the experimental session with two trials in which they were adapted to the measurement of salivation in response to 0.03 ml of water. The habituating taste stimuli used were presentation of 0.03 ml of either lemon (Real Lemon, Borden, Inc., Columbus, OH) or lime (Real Lime, Borden, Inc., Columbus, OH) juice to the middle of the tongue. The taste dishabituation stimuli were lemon or lime juice in Experiment 1 and 0.03 ml of chocolate flavor (Lorann Oils, Inc., Lansing, MI) in Experiment 2.

Methods of Analysis

Salivary flow and rating scale data were analyzed using separate mixed analyses of variance for the habituation trials (trials 1–10), and for changes from the final habituation trial to the dishabituation trial. Anovas for the repeated measure habituation data used the Greenhouse-Geiser correction, to minimize problems in sphericity due to correlated nature of the data (30). Statistical analysis was completed using SYSTAT (33).

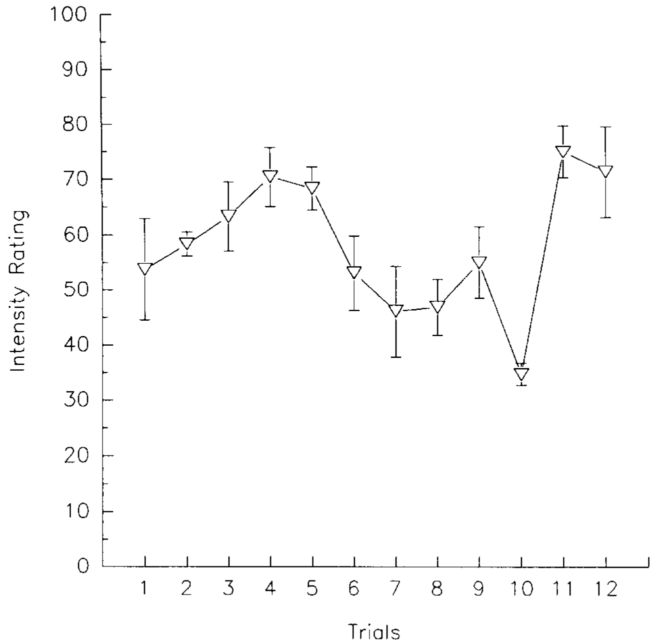

FIG. 2. Subjective stimulus intensity ratings (mean ± SEM) for subjects who received lemon or lime juice as the habituating stimulus in trials 1–10, the other juice as a dishabituator in trial 11, and presentation of the habituating stimulus in trial 12.

EXPERIMENT 1

METHOD

Subjects were eight females. Upon arriving at the laboratory, subjects' heights and weights were measured and they completed the dietary restraint scale (10) and scales which assessed liking of various flavors by placing a mark on a 100-mm line. Subjects began the experimental session with two water adaptation trials, and then were provided 10 habituation trials. Four subjects received lemon juice and four received lime juice as the habituating stimulus. On trial 11 subjects received the other juice stimulus as a dishabituator. On trial 12 subjects received the habituating stimulus they had received on trials 1–10. Subjects rated how much they liked the taste (hedonics) and how intensely they experienced the stimulus (intensity) of the habituating and dishabituating stimuli both prior to the experiment and after each trial.

RESULTS AND DISCUSSION

As shown in Fig. 1, significant decreases from trials 1–10 were shown for both salivary flow, $F(9, 54) = 23.47, p < 0.001$, and hedonic ratings, $F(9, 54) = 4.80, p = 0.018$. The dishabituator produced significant increases from trial 10 to trial 12 for both salivation, $F(1, 6) = 51.83, p < 0.001$, and hedonics $F(1, 6) = 5.82, p = 0.05$. Subjects salivated more to lemon juice than to lime juice, $F(1, 6) = 6.46, p = .04$, but no other effects of juice, or interaction of juice by trials for any of the effects reported were observed.

Ratings of intensity also varied significantly over time, $F(9, 54) = 3.47, p = 0.039$, though as shown in Fig. 2, the changes during the first 10 habituation trials did not follow the same pattern as the changes in salivation. As with salivation and hedonics, a significant increase in intensity, $F(1, 6) = 16.47, p = 0.007$, was observed from trial 10 to trial 12 after the dishabituator was presented.

This experiment showed that salivary response to a repeated taste stimulus habituates, and presentation of a taste dishabituator restored response to the initial stimulus. It has been previously observed that responses to habituating stimuli after dishabituation are often restored to initial levels (9). Hedonic ratings changed with salivation, such that recovery of salivation was associated with recovery of taste hedonics. The relationship between taste intensity and changes in salivation and hedonics is not clear. Intensity changed in a variable fashion over time, with an initial increase followed by a decrease. However, after the decrease in intensity, increases were observed during the presentation of the dishabituating stimulus and on the final dishabituation test trial and were similar to those seen with salivation and hedonics. Thus, on the basis of these data, the role of change in the perception of stimulus intensity cannot be ruled out for either the taste habituation or dishabituation observed, which is inconsistent with previous theorizing about the relationship between stimulus intensity and recovery of hedonics (17).

Experiment 1 was designed to maximize dishabituation by presentation of a taste dishabituator that itself stimulated salivation. This stimulatory action of the dishabituator may have activated salivation to the next presentation of the initial stimulus. In the next experiment the influence of a taste dishabituating stimulus that does not elicit salivation was assessed.

EXPERIMENT 2

METHOD

Subjects were 24 females randomly assigned to the control and experimental groups. Upon arriving at the laboratory, heights and weights were measured and subjects completed the dietary restraint scale (10); in addition they completed scales which assessed liking of various flavors, and current hunger and fullness ratings by placing a mark on a 100-mm line. Subjects began the session with two water adaptation trials, and were then provided sandwich(es), based on previously expressed preference, of either ham or turkey luncheon meats and either American, provolone, or Swiss cheese and 8 oz of water (mean kcal consumed = 316.7; SD = 74.0). Subjects were provided lunch equal to recent eating patterns, and minimize the influence of hunger on the taste cues that were studied.

Fifteen minutes after meal completion the habituation trials began. Trials 1–10 utilized the lemon juice stimulus. On trial 11 control subjects received the lemon juice stimulus, while the experimental group was presented with the novel chocolate flavor. The lemon juice stimulus was delivered to both groups during trial 12. Additional scales which assessed liking for lemon and chocolate flavor, and hunger and fullness scales were completed after trials 10 and 12.

RESULTS AND DISCUSSION

As shown in Fig. 3, salivary flow decreased from baseline during trials 1–10 for both groups $F(9, 198) = 28.17, p < 0.001$. Differential change by groups from trial 10 to trial 12 was observed, $F(1, 22) = 24.70, p < 0.001$. Subjects given the dishabituator showed a recovery of salivary flow to levels observed during the initial presentations of lemon, while those given the same lemon stimulus showed a further decrease. Chocolate on trial 11 for the experimental group did not increase salivation on trial 11.

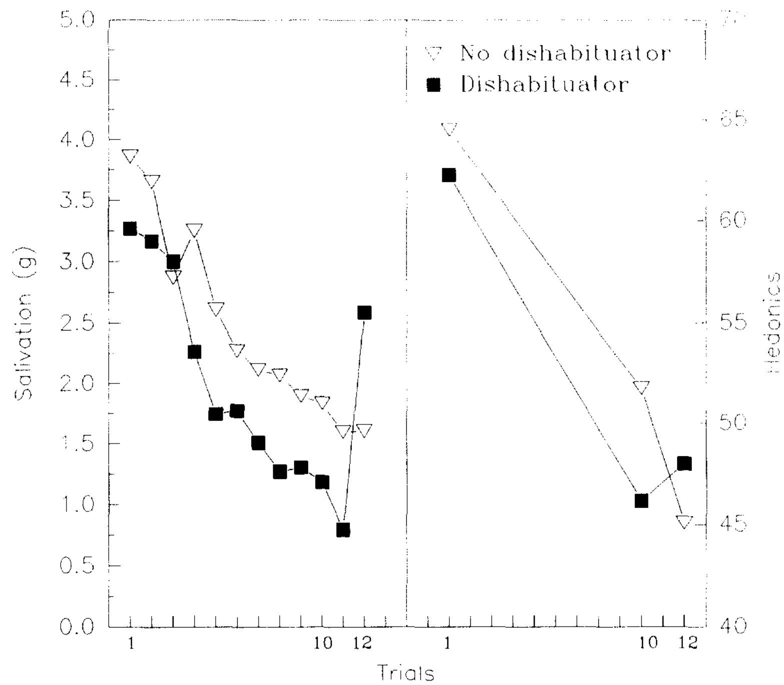

FIG. 3. Salivation and hedonic ratings (mean ± SEM) for subjects who received lemon juice on all trials and subjects who received lemon juice in trials 1–10, chocolate in trial 11, and lemon juice in trial 12.

Subjects in both groups showed significant, $F(1, 22) = 4.62$, $p = 0.04$, and similar decreases in liking for lemon flavor from trials 1–10, with ratings across groups changing from 63.4 ± 3.3 mm to 49.0 ± 5.3 mm. After subjects in the experimental group received chocolate, their hedonic ratings for lemon increased on trial 12, while subjects who had received the same lemon stimulus showed a further decrease, $F(1, 22) = 6.36$, $p = 0.02$.

After eating, hunger significantly decreased, $F(2, 44) = 12.70$, $p < 0.001$, from 56.7 mm to 26.8 mm, and fullness significantly increased from 28.3 mm to 62.8 mm, $F(2, 44) = 51.09$, $p < 0.001$, with no differences observed between groups. No changes in hunger or fullness were observed during the habituation trials.

This experiment again showed that salivation to a repeated taste stimulus habituates, and salivation can be restored by presentation of a novel taste. In addition, hedonic ratings decreased with repeated presentation of lemon; after presentation of chocolate, experimental subjects showed a small increase in hedonic rating to lemon, while control subjects showed a further decrease. While the changes in hedonic ratings after dishabituation to chocolate showed a similar pattern to those observed to lemon or lime in Experiment 1, the effect was smaller. The reduced effect may be due to the fact that the dishabituating stimulus in Experiment 1 itself stimulated salivation, while in Experiment 2 the dishabituating stimulus did not elicit salivation.

Previous salivation research suggests that the pattern of habituation of salivary responding is not only influenced by the presentation of taste stimuli, but also by presentation of stimuli in other sense modalities (5,32). One paradigm for testing the stimulus specificity of habituation is to present distractors prior to presentation of the habituating stimuli. The presentation of distractors requires allocation of short-term memory from the habituating stimulus to the distractor, which should inhibit the development of habituation (31). Experiment 3 was designed to assess whether a computer game distractor would influence habituation to salivation, and if this distractor could serve as a dishabituator after habituation had been observed.

EXPERIMENT 3

METHOD

Sixteen women who met criteria similar to those of previous experiments were studied. Before the two adaptation trials, subjects in both groups played a popular computer game for 5 minutes to familiarize themselves with the game. Subjects in the experimental group then repeatedly played the game for 1-minute periods during the 2-minute intertrial interval that occurred between each of the first 10 lemon habituation trials. Subjects in the control group sat quietly during the intertrial intervals, as in the first two experiments. After the first two control subjects were run, it was decided to assess whether the stimulus that had been used as a distractor for the experimental group could serve as a dishabituating stimulus for the control subjects. Thus, after completing trial 10, the final 6 of 8 subjects in the control group played the computer game again, and were given an additional lemon juice trial to assess whether the distractor would produce dishabituation.

The computer game was Lode Runner (Broderbund Software, San Rafael, CA). The objective in Lode Runner is to maneuver through an obstacle-filled screen using a joystick while trying to acquire boxes of gold and elude the opponents who constantly chase you. The computer game was paused after each 1-minute playing period so that the subject could resume playing during the next intertrial interval. This kept the subjects interested in the task.

RESULTS

The salivation results (Fig. 4) showed a significant interaction of groups by trials, $F(9, 126) = 4.69$, $p = 0.002$. No changes

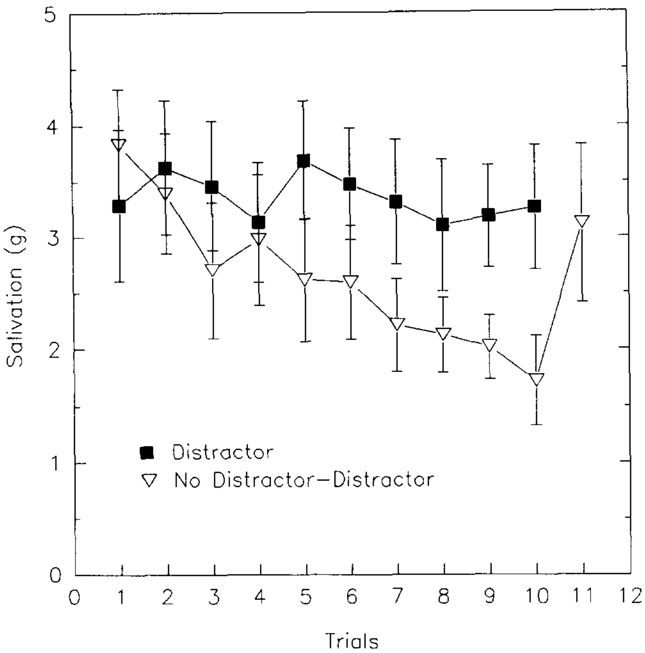

FIG. 4. Salivation (mean ± SEM) for subjects who received a distractor before trials 1–10, or subjects who received a distractor before trial 1, no distractor before trials 2–10 and a distractor before trial 11. All subjects received lemon juice on all trials.

in salivation were observed over the 10 trials for subjects who received the distractor, while subjects who did not receive the distractor habituated. Subjects in the control group showed a recovery of salivation to initial levels when lemon juice was presented on the 11th trial, $F(1, 5) = 13.85$, $p = 0.01$, after the distractor.

These results show salivation to a taste stimulus is affected by allocation of attention to nontaste stimuli. Experiment 3 suggests that taste stimuli may not have special characteristics that facilitate dishabituation, but rather they may reflect a more general cognitive or attentional process that underlies all habituation or dishabituation phenomena.

GENERAL DISCUSSION

In these experiments we showed that taste and nontaste stimuli can influence the pattern of habituation of salivation. In addition, the dishabituation and distractor results suggest that the decrease in salivation is not a function of fatigue or neural adaptation, since the response is easily recovered after presentation of a taste or nontaste dishabituating stimulus. Hedonic responses studied in Experiments 1 and 2 also showed a pattern of habituation with repeated taste presentations and dishabituation after presentation of a new taste dishabituator.

These results for salivation and hedonics in humans are consistent with neurophysiological and behavioral changes observed in monkeys (23,24). These studies have shown that food consumption and responses in the lateral hypothalamus, substantia innominata, and caudolateral orbitofrontal cortex decrease with repeated presentation of one food, consistent with habituation. In addition, they showed recovery of neurophysiological activity and eating when a new food was presented.

The paradigm used in the monkey studies (23,24) documents the stimulus specificity of habituation by demonstrating a recovery of neuronal responding with a change in stimulus characteristics. Recent research from our laboratory using a similar paradigm has also shown the stimulus specificity of salivation in humans by observing recovery of salivation after presentation of a new, palatable food (34). We also showed that changes in hedonics and salivation are related to increased food consumption after presentation of a new food, but changes in hedonics without changes in salivation were not related to intake.

The habituation model provides a variety of useful paradigms for studying how sensory factors influence changes in palatability and intake for repeated presentation of the same food. Habituation may also be useful in understanding how changes in both taste and nonfood related sensory stimuli influence intake. While it has been repeatedly demonstrated that presentation of a new food after satiety can result in resumption of eating (17–20,34), we showed in Experiment 3 that nontaste stimuli can also influence habituation of salivation, consistent with the hypothesis (31) that a distractor can influence habituation if it requires allocation of attention from the habituating stimulus. This finding suggests that presentation of nontaste stimuli that require allocation of attention may influence the amount of food eaten. This may be relevant to explain why subjects will eat excess amounts of food when they are watching television (6), since the sensory habituation normally associated with eating is interfered with due to repeatedly attending to nontaste sensory cues. This finding also suggests dishabituation to taste stimuli may be indicative of more general attentional processes operating, and taste stimuli may represent only one class of stimuli that may cause dishabituation to taste stimuli.

In addition to the acute changes in salivation and hedonics observed after repeatedly presenting the same taste in this study, or the same food in other studies from our laboratory (34), more chronic changes may be observed over meals. The habituation model may also facilitate understanding how repeated consumption of the same or similar food over days can influence intake or hedonic ratings. The rate of habituation to taste of a food, and related changes in palatability of the food, may be influenced by previous experience with the stimulus, by the intensity of the taste or affective characteristics of the stimulus, by the interstimulus interval or intervals between meals, and by generalizability of the habituating stimulus to other taste stimuli (8). For example, in a noncontrolled field experiment, greater hedonic ratings were shown when novel foods were presented to a group of subjects who had been eating a regular and limited diet for 6 months than when presented to subjects who had been eating the regular diet for only 2 days (22). Other investigators (28) had subjects eat the same foods for up to 44 meals over 22 days. Subjects were allowed to discontinue participation in the experiment by the 10th day. All subjects showed a reliable decline in palatability over time, but the decline was greatest for subjects who dropped out of the experiment earlier, and the amount of food not eaten was greater for the subjects who dropped out earlier. The decline in palatability was greatest for the foods that subjects found least palatable. More controlled animal research also documents that (21,29) food intake is influenced by repeated presentations of a food across meals.

The experiments in the present report suggest the habituation model may be useful in generating hypotheses about how taste and other sensory variables affect eating, and may be heuristic for understanding how eating is influenced by sensory factors.

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