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Tactile Interaction with Taste Localization: Influence of Gustatory Quality and Intensity

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Abstract

Taste is always accompanied by tactile stimulation, but little is known about how touch interacts with taste. One exception is evidence that taste can be "referred" to nearby tactile stimulation. It was recently found (Lim J, and Green BG. 2007. The psychophysical relationship between bitter taste and burning sensation: evidence of qualitative similarity. Chem Senses. 32:31–39) that spatial discrimination of taste was poorer for bitterness than for other tastes when the perceived intensities were matched. We hypothesized that this difference may have been caused by greater referral of bitterness by touch. The present study tested this hypothesis by comparing localization of quinine sulfate and sucrose under conditions that minimized and maximized the opportunity for referral. In both conditions, stimulation was produced by 5 cotton swabs spaced 1 cm apart and arranged in an arc to enable simultaneous contact with the front edge of the tongue. Only one swab contained the taste stimulus, whereas the rest were saturated with deionized water. In both conditions, the swabs were stroked up-and-down against the tongue 5 times. Subjects were asked to identify which swab contained the taste stimulus 1) 5 s after the fifth stroke (touch-removed condition) and 2) immediately at the end of the fifth stroke, with the swabs still in contact with the tongue (touch-maintained condition). Ratings of taste intensity were obtained to assess the possible effect of perceived intensity on spatial localization. Taste localization was surprisingly accurate, especially for sucrose, with errors of localization in the range of 1 cm or less. For both stimuli, localization tended to be poorer when the tactile stimulus was present while subjects made their judgments, but the difference between conditions was significant only for the lower concentration of quinine. The results are discussed in terms of both the surprisingly good spatial acuity of taste and the possibility of having a close perceptual relationship between touch and bitter taste.

Key words: bitterness, referral, sweetness, tactile, taste, taste localization

Introduction

Taste perception normally takes place within a complex field of mechanical stimulation. The presence of tactile stimulation in parallel with taste stimulation creates the opportunity for perceptual interactions between the modalities. However, little is known about potential interactions between tactile and taste stimulation except an effect of viscosity on the perception of taste and aroma (Cook et al. 2003) and an effect of touch on taste localization (Todrank and Bartoshuk 1991; Green 2002). Taste localization has been shown to be influenced by touch in a manner analogous to the way vision "captures" speech in the ventriloquist effect (Bertelson et al. 2000; Alais and Burr 2004) or, more specifically, the way taste is "referred" to the site of tactile stimulation. In the phenomenon of "thermal referral," sensations of warmth and cold become localized to sites on the fingers or the skin that share a common mechanical stimulus (Green 1977, 1978). Todrank and Bartoshuk (1991) first found evidence of a similar effect in taste when they painted a taste solution on one side of the tongue (an area of relatively low taste papillae density) and then moved it past the tip (an area of high papillae density) to the opposite side of the tongue. Subjects reported stronger taste sensations on the opposite side than on the first side, which was interpreted as evidence that taste sensations evoked on the tongue tip had been "captured" by the tactile stimulus and drawn with it to the less sensitive side of the tongue. Green (2002) later followed up the work of Todrank and Bartoshuk (1991) by using a procedure similar to the original study of thermal referral, in which 3 fingers had simultaneously touched 3 thermodes when only the outer 2 thermodes were heated or cooled. In the analogous taste study, the tongue was touched simultaneously with 3 cotton swabs when only the outer 2 swabs contained a taste stimulus. The results appeared to show that the taste of the outer swabs was referred to the middle swab. Indeed, with the exception of citric acid, the perceived intensities of the referred tastes were quantitatively indistinguishable from the ratings for the actual taste stimuli.

The suggestion by Todrank and Bartoshuk (1991) that taste itself was poorly localized and was normally captured by touch led researchers to investigate whether taste stimuli can be localized without tactile cues (Delwiche et al. 2000; Shikata et al. 2000). Shikata et al. (2000) found that subjects could lateralize (i.e., discriminate which side of the tongue was stimulated) taste stimuli in the absence of any discriminative tactile or mechanical cues. The same authors suggested that the ability to lateralize varied with stimulus concentration. In addition, Delwiche et al. (2000) reported that humans could localize and selectively remove a nearly tasteless gelatin cube from a field of taste-containing "distractor" cubes, although doing so was more difficult than removing a taste-containing cube from a field of tasteless (tactile) distractor cubes. The authors hypothesized that performance in the "1-blank, 3-sweet" condition was significantly worse than in the "1-sweet, 3-blanks" condition because of "tactile capture" of taste by the tasteless target cube.

In a recent study of the relationship between bitter taste and chemesthetic burning sensations (Lim and Green 2007), we confirmed that taste can be surprisingly well discriminated on the tongue but also found that spatial discriminability may depend on taste quality; spatial discrimination of quinine sulfate (QSO_4) was significantly poorer than discrimination of sucrose, NaCl, and citric acid, even though all 4 stimuli produced statistically similar perceived intensities. We speculated that the poorer performance with quinine may have been caused by greater referral of bitterness to tactile stimulation produced by the swabs. This hypothesis was tested in the current study by comparing localization of 2 different stimuli, one bitter and another sweet, under 2 different conditions that minimized and maximized the opportunity for taste referral. The study also provided the opportunity to measure the spatial acuity of taste (i.e., the error of localization) along the anterior edge of the tongue.

Materials and methods

Subjects

A total of 21 subjects (14 females and 7 males) between 19 and 35 years of age (mean = 26 years old) were recruited on the Yale University Campus. All were nonsmokers and free from deficits in taste or smell by self-report and were asked to refrain from eating/drinking for at least 1 h prior to their scheduled session. Informed consent was obtained, and the subjects were paid for their participation.

Stimuli

The test stimuli were 0.32 and 1.8 mM QSO_4 (Fisher Scientific Inc., Fair Lawn, NJ) and 0.1 and 0.56 M sucrose (J.T.Baker, Phillipsburg, NJ). Citric acid (17 mM, Pfaltz & Bauer, Inc., Waterburry, CT), sodium chloride (0.32 M, J.T.Baker), sucrose (0.32 M, J.T.Baker), and QSO_4 (0.32 mM, Fisher Scientific Inc.) were used for the practice session and/or trial (see below). All stimuli were prepared weekly from reagent grade compounds using deionized water and were stored in glass bottles at 4–6 °C. The stimuli were applied to the tip of the tongue using sterile, cotton tip swabs that were saturated just prior to application with the appropriate aqueous solutions. To eliminate thermal sensations as possible cues or confounds, the taste solutions and water were kept at 39 ± 0.5 °C, which was shown in pilot experiments to feel thermally neutral when applied to the tongue.

Procedure

Practice session

All subjects were initially instructed in the use of the general version of the labeled magnitude scale (gLMS) (Green et al. 1993, 1996; Bartoshuk et al. 2003) and given practice using it to rate imagined and actual taste sensations. After receiving the instructions, subjects were asked to rate 15 remembered or imagined oral sensations (i.e., the sweetness of cotton candy, the bitter taste of black coffee) on the gLMS to give them experience using the scale in the broad context of normal oral perception (Green and Schullery 2003). The subjects were then instructed to rate the intensity of sweetness, saltiness, sourness, and bitterness produced by 4 prototypical taste stimuli. The stimuli were applied to the tongue by rolling a saturated cotton swab across the tip for approximately 3 s. The subjects were asked to withdraw the tongue back into their mouth but not to move or touch any other part of the mouth until they finished the rating. Instructions in the practice session required the subjects to rate the intensity of each taste quality separately and to base their ratings on the maximum sensation perceived during stimulus application or immediately afterward. There was 1-min interstimulus interval, during which the subjects rinsed at least 3 times with deionized water (37 ± 0.5 °C). They also rinsed 3 times before testing began.

Discrimination sessions

Taste localization was measured on the anterior edge of the tongue. On each trial, subjects were asked to extend the tongue out of the mouth and hold it immobile between the lips. A set of 5 cotton swabs spaced 1 cm apart in a drilled plastic block (see Figure 1) were then applied simultaneously to the tongue tip in an up-and-down motion for approximately 3 s (5 strokes). Only 1 swab contained a taste stimulus, and the rest contained deionized water. With the tongue

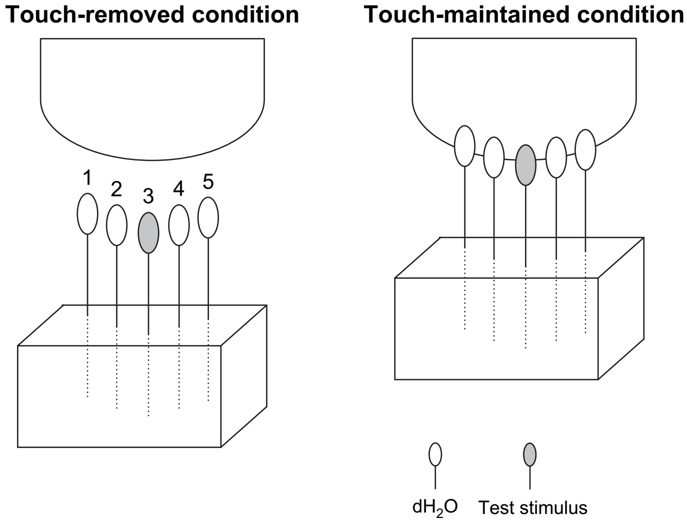

Figure 1 The diagrams for testing conditions. The subjects made discriminations 1) 5 s after the last stroke for the touch-removed condition and 2) when the swabs stayed lightly against the tongue on the fifth stroke for the touch-maintained condition.

still protruded, the subject's task was to indicate which swab had the strongest taste. They did this by consulting a diagram in which the 5 swabs were numbered 1 through 5 then by holding up the appropriate number of fingers. Immediately before the stimulus was applied, subjects were told which taste quality they should attempt to localize on that trial, for example, "which swab is the most bitter"? The phrase "most bitter" or "most sweet" was used to indicate to the subject that they may perceive taste sensations from more than one swab but should indicate which swab had the most intense taste. On a given trial, the experimenter signaled the subject to localize the most intense taste stimulus at one of 2 conditions: 1) 5 s after the fifth stroke, when the swabs were no longer in contact with the tongue (touch-removed condition) or 2) immediately at the end of the fifth stroke, as the swabs were held immobile against the tongue (touch-maintained condition). Thus, taste and tactile stimulation were initially identical in the 2 conditions (see Figure 1). The key difference was the absence versus the continued presence of tactile stimulation when the judgment was made because the presence of tactile stimulation should maximize the opportunity for taste referral to tactile stimulation. The subjects were asked to rinse with deionized water at least 3 times during the 1-min intertrial intervals.

The 2 testing conditions were tested in separate sessions. Both sessions began with one warm-up trial using NaCl to acquaint the subject with the task. Each session included 20 test trials [2 taste stimuli (QSO_4, sucrose) × 2 stimulus concentrations (low, high) × 5 stimulus sites (1–5)]. After finishing 10 trials, the subjects took a 3-min break and then completed the rest of 10 trials. The order of stimulus concentrations and sites were completely randomized within each session with the constraint that the same site was never stimulated twice in succession. In addition, 2 taste stimuli were presented alternately to prevent adaptation.

All the discrimination tests under both testing conditions were repeated twice, which meant that each subject participated in 4 sessions. The order in which the 2 conditions were tested was counterbalanced across subjects (ABAB vs. BABA), and sessions were separated by at least 1 day but no more than 2 weeks.

Intensity ratings

After a 5-min break at the end of the last session, intensity ratings were obtained for the sucrose and QSO_4 stimuli at 3 different swab sites: the middle swab (site 3) and the 2 outer swabs (sites 1 and 5). These sites were selected to detect possible spatial differences in taste perception on the tongue. There were a total of 12 trials (2 taste stimuli × 2 stimulus concentrations × 3 stimulus sites). The stimulation procedure was the same as in the touch-removed condition, except rather than localize the taste stimulus the subjects rated the intensity of sweetness, saltiness, sourness, and bitterness on the gLMS.

Data analysis

The binomial test would be appropriate to determine whether taste stimulus could be localized significantly above chance on each combination of stimulus-testing condition. The binomial model assumes a single source of variation, that is, the stimulus-testing condition. However, there were 2 more sources of variation in the present experiment: stimulus site and replicate. Ennis and Bi (1998) suggested using the beta-binomial model, an extension of the binomial distribution, to fit binomial data with multiple sources of variation. Therefore, a beta-binomial test was first performed after combining individual data across the stimulus sites and across the replicates to determine if the binomial assumption was appropriate for the current data using the IFProgram (Institute for Perception, Richmond, VA, 2003). The results indicated that the gamma values for both touch-removed and touch-maintained conditions were zero, which meant that the beta-binomial model did not fit the data significantly better than the binomial model. In other words, response probabilities did not vary by stimulus site and/or by replicate. The data from each subject were, therefore, pooled across stimulus sites and replicates.

The number of correct responses for each stimulus in each condition was compared with values in binomial tables (Lawless and Heymann 1998) to assess statistical significance. The criterion for the group to be regarded as capable of discriminating the target stimulus was 53 correct out of 210 total observations (1-tailed binomial test, $P < 0.05$). Although a statistical analysis using d' values would also be proper to test for significant differences between the testing conditions, this analysis could not be performed because no tables exist to estimate the variance of d' values for 5-alternative forced choice tests.

For additional analysis, the average error of localization (Greenspan and Bolanowski 1996; Hollins 2002) was calculated for each stimulus and site based on the distance between where the stimulus was presented and where the subjects reported it to be (0 for the correct location and 1–4 for the incorrect locations). A repeated measures of analysis of variance (ANOVA) was performed to examine the effect of testing condition, stimulus, concentration, and stimulus site. Student's t-tests were further carried out as a post hoc test to examine the difference between the means from the 2 testing conditions for each stimulus without any other variables (stimulus and/or concentration) present. The alpha value for each t-test was adjusted by the Bonferroni correction.

Prior to statistical analysis, individual intensity ratings were log transformed because responses on the LMS tend to be log-normally distributed (Green et al. 1993, 1996). The arithmetic means of log-transformed intensity ratings were calculated across replicates within subjects. A repeated measures of ANOVA and the Tukey's honestly significantly different (HSD) post hoc tests were performed. All the statistical analyses were conducted with Statistica 6.1 (StatSoft Inc. Tulsa, OK).

Results

The results of the spatial localization tasks are shown in Figure 2. The 1-tailed binomial tests conducted on each of the 8 stimulus-condition combinations showed that subjects were able to localize the test stimuli significantly above chance ($P < 0.05$). However, based on the nominal center-to-center spacing between swabs of 1 cm, calculations of the average error of localization indicated that performance varied from 0.40 to 0.96 cm depending on testing condition and stimulus. An ANOVA was initially performed on the error of localization with following factors: 1) testing condition, 2) stimulus, 3) concentration, and 4) stimulus site. Because there was no significant effect of stimulus site, mean errors of localization were calculated for each stimulus by averaging across the 5 stimulus sites. A repeated measures ANOVA showed that there were significant main effects of testing condition [$F(1,20) = 5.64$, $P = 0.028$], stimulus [$F(1,20) = 11.77$, $P = 0.003$], concentration [$F(1,20) = 32.18$, $P < 0.0001$], and a marginal interaction effect between the testing condition and concentration [$F(1,20) = 4.29$, $P = 0.051$].

For both stimuli, the error of localization tended to be greater when tactile stimulation was present at the time the judgment was made (touch-maintained condition). The further statistical test (1-tailed t-test for dependent samples, $P < 0.0125$) revealed that the difference was significant only for the lower concentration of QSO_4. Consistent with our previous data, localization tended to be poorer for QSO_4 than for sucrose (Lim and Green 2007) and the errors of localization were significantly less at the higher concentrations.

The dependence of localization on concentration raises the question of whether differences in perceived intensity may have led to the differences in performance between 2 taste stimuli. The mean log taste intensity ratings for QSO_4 and sucrose are shown in Figure 3. A repeated measures ANOVA

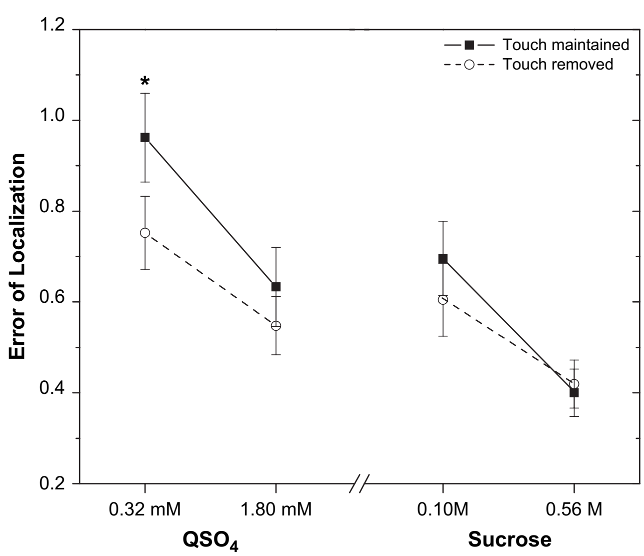

Figure 2 The error of localization ± standard error for the spatial discrimination tests for each testing condition. The errors of localization between 2 testing conditions for the each stimulus were compared by the t-test for dependent sample. The asterisk indicates a significant difference at $P < 0.01$ (1-tailed).

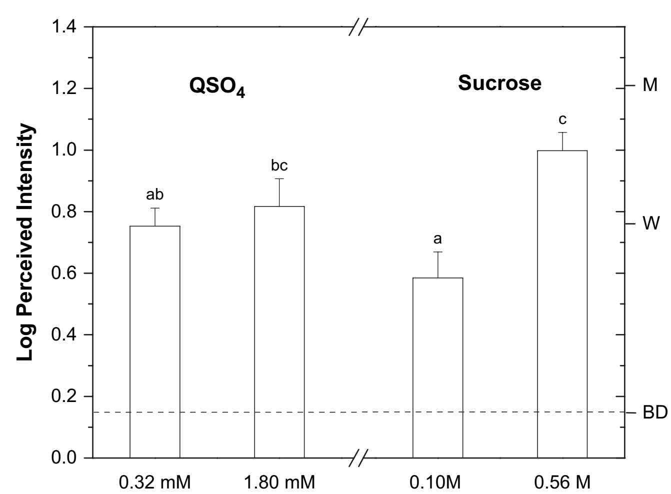

Figure 3 The log-mean taste intensity ratings of bitterness for QSO_4 and sweetness for sucrose under touch-removed condition are shown. Vertical bars denote standard errors of the means. Letters on the right y axis represent semantic labels of the LMS (BD, barely detectable; W, weak; M, moderate). The different letters indicate significant differences on perceived taste intensities by the Tukey's Honestly Significantly Different test ($P < 0.05$).

showed that there was a main effect of concentration [$F(1,20) = 29.00$, $P < 0.0001$] and an interaction between the effects of stimulus and concentration [$F(1,20) = 9.32$, $P < 0.01$]. Tukey's HSD tests ($P < 0.05$) confirmed that the perceived sweetness of sucrose increased significantly with concentration, whereas the perceived bitterness of QSO_4 did not differ significantly between the 2 concentrations. More importantly, the perceived intensities of bitterness of QSO_4 and sweetness of sucrose were not significantly different from one another in either concentration.

Discussion

The present results reinforce and extend recent findings, which indicate that taste localization is surprisingly acute (Shikata et al. 1997, 2000; Breslin et al. 1998; Delwiche et al. 2000; Lim and Green 2007). Subjects discriminated all the test stimuli significantly above chance and the average error of localization for taste on the front of the tongue was less than 1 cm. Although this result is in good agreement with a very early estimation of taste localization (von Skramlik 1924), it is in sharp contrast to the evidence from studies of regional taste loss in humans, which implied that taste localization was extremely poor (Pfaffmann and Bartoshuk 1989; Kveton and Bartoshuk 1994). In those studies, patients were often unaware of having lost taste sensitivity on a specific area of the tongue and noticed no overall difference in taste perception. The absence of complaints of overall taste loss was attributed to the release of inhibition of input from unimpaired gustatory areas that effectively preserved total taste sensitivity (Lehman et al. 1995). Failure to detect regional deficits in taste perception was hypothesized to be masked by a combination of poor taste localization and tactile capture (or referral) of taste. Specifically, it was hypothesized that referral of taste sensations to the sites of tactile stimulation throughout the tongue and palate gave the impression that taste sensitivity was uniform and normal (Todrank and Bartoshuk 1991; Kveton and Bartoshuk 1994). However, the occurrence of tactile capture or referral does not necessarily mean that taste localization is inherently poor. Theoretically, for capture or referral to occur requires only that tactile localization be more acute than taste localization. As good as taste localization appears to be in the present study, tactile spatial acuity on the anterior tongue is still better, rivaling the acuity of the most sensitive regions of the body (Van Boven and Johnson 1994; Essick et al. 1999). Thus, when tactile and taste stimulation are spatially and temporally correlated, touch may serve to further sharpen taste localization by bringing it into closer spatial registration with the mechanical stimulus. Such spatial sharpening, together with the referral of taste throughout the area of mechanical contact, may have the additional effect of heightening the perceptual coherence between tastes and the food matrix or liquid that gives rise to them (Green 2002).

The occurrence of a statistically significant effect of touch only on localization of the QSO_4 might be interpreted as evidence that taste referral occurs for bitterness of QSO_4 but not for sweetness of sucrose. This conclusion is unwarranted based on the present data, which were obtained in a psychophysical paradigm in which subjects were specifically instructed to ignore weak taste sensations and to report only where the "strongest" taste sensation was perceived. The forced-choice localization procedure therefore provided no direct information about the presence or absence of referred tastes. By contrast, in a previous study of taste referral in our laboratory, subjects were instructed to rate the perceived intensity of taste at a site of tactile stimulation adjacent to (or bracketed by) sites of taste stimulation (Green 2002). Those instructions encouraged reports of referred taste sensations but provided no direct information about taste spatial acuity. Referral would be expected to have a significant effect in the forced-choice task only if referral were strong enough to spread qualitatively and quantitatively equivalent taste sensations across multiple tactile sites. The present data suggest this may have occurred only for the lower concentration of QSO_4. Based on the previous evidence that taste referral occurs for both sucrose and quinine (Green 2002), it is likely that superior performance for the higher concentration of QSO_4 and for both concentrations of sucrose reflects the occurrence of less than "complete" taste referral rather than no referral at all. Thus, the localization task of the present study provided a much more stringent test of spatial interactions between taste and touch than did previous studies of referral (Todrank and Bartoshuk 1991; Green 2002).

At the same time, the evidence that taste stimuli can be localized with an error of 1 cm or less argues against the previously posited hypothesis that taste referral was simply a by-product of poor taste localization. If the source of taste stimulation can be localized to an area approaching the width of a cotton-tipped swab, reports of taste referral from water-only swabs spaced 1 cm or more from the nearest taste stimulus must owe to a perceptual interaction rather than to poor localization. Just as visual capture and the ventriloquist effect occur despite normally accurate auditory localization, taste referral appears to occur despite surprisingly good taste localization.

It is somewhat puzzling that the significant effect of concentration on localization of QSO_4 occurred even though there was no significant difference in the rated bitterness of the high and low concentrations. One explanation may lie in the sensitivity of the 2 different tasks that were used to obtain the 2 kinds of data. Force-choice discrimination tasks are generally recognized to be more sensitive than scaling tasks and would therefore be expected to detect smaller perceptual differences. The failure of the scaling task to reveal a significant difference in intensity despite a 3-quarter-log step in QSO_4 concentration is consistent with this interpretation. It is also possible that QSO_4 concentration simply has a relatively larger effect on the ability to localize bitter taste than it does on the perception of bitterness intensity. In other words, the neural mechanism underlying perceived intensity and localization may not be equally sensitive to changes in stimulus concentration.

The findings that tactile stimulation significantly worsened localization of a weak bitter taste but not an equivalent weak sweet taste imply that bitterness may share a uniquely close physiological and perceptual relationship with touch. It has long been known that gustatory neurons in mammals, including humans, are sensitive to mechanical and thermal stimulation as well as to chemical stimulation (Zotterman 1935; Oakley 1967; Robinson 1988). Evidence of convergent cortical processing of touch and chemical taste has become evident in studies of primate cortical neurophysiology (Yamamoto et al. 1988; Ogawa et al. 1990) and in functional magnetic resonance imaging and positron emission tomography studies in humans (Zald and Pardo 2000; de Araujo and Rolls 2004; Verhagen et al. 2004; Kadohisa et al. 2005). However, the relationship between the neural processing of specific taste qualities and tactile stimulation has not yet been systematically investigated in either peripheral or central nervous system (CNS) neurons. The present results suggest that in regions of the CNS where neurons are found that respond to both taste and touch, a disproportionate number of these neurons may be selectively responsive to bitter-tasting substances.

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