SHORT COMMUNICATION

Influence of Stimulus Duration on a Regional Measure of NaCl Taste Sensitivity

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Abstract

The present study demonstrates that perithreshold temporal integration occurs in the human taste system across stimulus durations ranging from 200 to 1500 ms in a manner analogous to that seen in other major sensory systems. Thus, the notion that gustation is comparatively insensitive to temporal stimulus parameters at threshold levels is disproved. **Chem. Senses 22: 171–175, 1997.**

Introduction

Although it is well established that the visual, auditory and tactile sensory systems integrate perithreshold stimulus energy over time to enhance signal detectability (Marks, 1974), this is not the case for the chemical senses. In gustation, for example, little attention has been paid to the possibility of perithreshold temporal integration, due, in part, to technical difficulties in accurately controlling temporal aspects of the stimulus, and the general belief that the taste system is comparatively insensitive to temporal stimulation parameters (McBurney, 1976; Lester and Halpern, 1979).

Only one study has addressed the influences of stimulus duration on perithreshold detection using chemical tastants (Bujas, 1934). In this work, which presented data from only one subject, taste thresholds for several compounds (sucrose, citric acid, sodium chloride and quinine hydrochloride) seemed to decrease in a 'hyperbolic-like' manner as stimulus duration increased up to a point of asymptote (for NaCl, ~2.8 s). Unfortunately, specifics of the study are not presented, such as the size and location of the tongue region stimulated.

As a result of the development of the University of Pennsylvania Regional Taste Testing System (RATTS)—a computerized system which allows for presentation of a wide range of discretely timed stimuli to well-defined regions of the tongue—it is now possible to reliably test the influences of stimulus duration on the chemical gustatory detection threshold. This device allows for the accurate presentation of taste stimuli for brief (e.g. 100 ms) durations, as well as intertrial and rinse intervals of known extent.

The purpose of this study was to investigate, using the

RATTS, whether temporal summation occurs in the human taste system at the threshold level and, if so, the nature of the functional relationship between stimulus duration and taste sensitivity. Sodium chloride was chosen as the test stimulus, given its importance to the economy of the organism, the fact that it appears to be easier to detect than many sweet, sour and bitter taste stimuli, and the large psychophysical literature on this agent (Meiselman, 1967; Doty, 1990; Mistretta and Hill, 1995). Stimulus durations were chosen to fall clearly below the duration suggested by Bujas (1934), where asymptotic identification of NaCl presented to a small region of the tongue occurs.

Materials and methods

Six men and six women between the ages of 20 and 29 years (mean age ± SD = 21.833 ± 2.69) served as subjects and were paid $45.00 each for their participation in four 1 h long test sessions. All were non-smokers in good health at the time of testing. Each abstained from eating or drinking anything but water 1 h prior to testing. All provided informed written consent, in accordance with the requirements of the University of Pennsylvania's Committee for the Study of Human Beings, and participated in a practice session to become familiar with the procedures of the experiment. Seven of the subjects were Caucasian Americans and five were Asian Americans.

The taste stimuli were 11 concentrations of reagent-grade NaCl (Fisher Scientific, Fairlawn, NJ) spaced in 0.5 log unit dilution steps. The solutions ranged in concentration from 3.16×10^{-5} M to 3.16 M, and were chosen because they were within the general threshold region of humans for localized testing (McBurney, 1969; Smith, 1971; Collings, 1974; Linschoten and Kroeze, 1992). Each solution was prepared in double-distilled deionized water, stored by refrigeration (4°C), replaced every week and brought to room temperature (20°C) before use. Deionized water alone served as the blank stimulus.

RATTS was used to present the stimuli. This device is a further development of a microprocessor-controlled gustometer described by Matsuda and Doty (1995), and was designed to allow precise presentation of a wide range of

Figure 1 A picture of the University of Pennsylvania Regional Automated Taste Testing System showing the glass stimulation device held to the subject's tongue tip.

taste stimuli to discrete regions of the tongue. The system automatically delivers timed trains of stimulus boluses and water rinses from 13 gravity-fed solution reservoirs to a glass stimulation device held to the surface of the tongue by a mild vacuum surround (Figures 1 and 2). Stimulus delivery is controlled, via a series of Teflon™ GVC solenoid valves (General Valve Corp., Fairfield, NJ), by a microprocessor (ATCOM Interactive Controller 64, Automatic Timing and Controls Company, Inc., King of Prussia, PA) which stores programs related to stimulus presentation (e.g. flow rates, durations, intertrial intervals) and subject responses.

The design of this study was straightforward. Detection thresholds were determined in each subject for each of four stimulus durations (200, 400, 750 and 1500 ms) during four test sessions. The order of the test sessions, each of which lasted from 30 min to 1 h, was counterbalanced using Latin squares (Zimney, 1961). The sessions were separated from one another by a minimum of 24 h.

A two-alternative, forced-choice, single staircase detection threshold procedure was employed. Stimuli were presented using a two-down one-up rule (Levitt, 1970), with the exception of the first reversal, for which the subject had to make five consecutive correct responses. The procedure started at the $-3.5 \log_{10}$ M concentration, which is below normal detection threshold levels for localized testing (see Brosvic and McLaughlin, 1989). The stimuli were administered to the tongue at a flow rate of 1.6 ml/s for all the durations. Subjects were instructed to choose the NaCl stimulus from a pair of solutions: a blank (deionized water) and NaCl solution dissolved in deionized water. For each test trial the solutions were presented in random order, with a rinse of deionized water preceding each test solution. The intertrial interval was ~20 s. The subject indicated which solution was stronger by pressing a button ~5 s into this interval. The geometric mean of the last four of seven total reversals served as the threshold estimate.

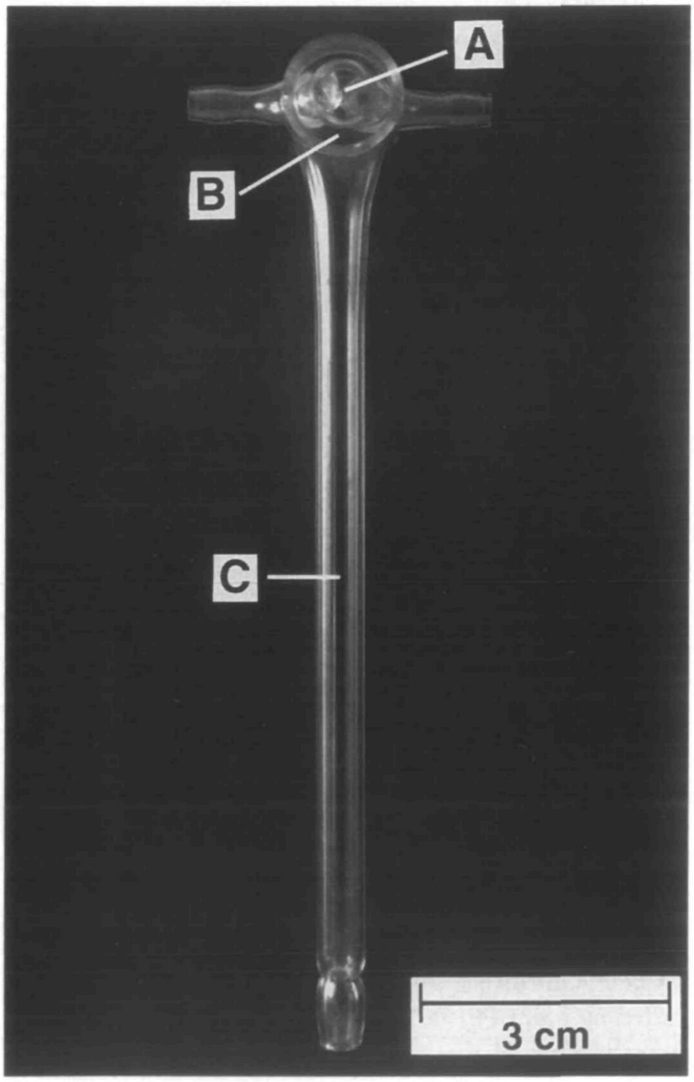

Figure 2 Glass stimulation device viewed from its bottom. The stimuli flow through the 25 mm^2 central chamber **(A)**. A negative pressure present in the annular chamber **(B)** holds the device accurately on the tongue. The pressure (~40 mm Hg) was calibrated using a DWYER Minihelic-2 differential pressure gage connected to distal end of the vacuum chamber **(C)**. The inner and outer diameters of the flow chamber are 5.6 and 11.6 mm respectively.

Results and discussion

As shown in Figure 3, the NaCl thresholds were inversely

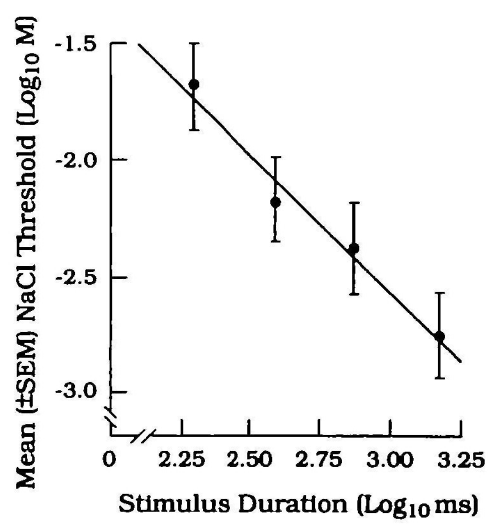

Figure 3 The mean NaCl detection threshold (± SEM) as a function of stimulus duration plotted on log–log axes. The four data points, from left to right, correspond to 200, 400, 750 and 1500 ms. The relationship between threshold and stimulus duration represents a power function. See text for details.

related to stimulus duration across a range of 200–1500 ms. A sex (male, female) by stimulus duration (200, 400, 750, 1500 ms) analysis of variance with repeated measures on the second factor revealed a significant stimulus duration main effect [$F(3, 30) = 15.55$, $P < 0.0001$]. Neither the sex [$F(1, 10) = 0.27$, $P = 0.616$] nor the sex by stimulus duration interaction [$F(3, 30) = 0.65$, $P = 0.592$] was significant. Post-hoc contrasts indicated that the 200 ms stimulus differed significantly from all others (respective P values for 200 versus 400, 200 versus 750, 200 versus 1500 = 0.010, 0.0001 and 0.0001) and that the 400 ms stimulus duration differed significantly from the 1500 ms stimulus ($P = 0.037$).

The function shown in Figure 3 was comprised of linear [$F(1, 10) = 45.90$, $P < 0.0001$], but not quadratic [$F(1, 10) = 0.25$, $P = 0.628$] or cubic [$F(1, 10) = 1.13$, $P = 0.313$], components. This line is well described by the power function, $c = 9.638d^{-1.18}$, where c is the molar concentration at threshold and d is the stimulus duration in ms ($r^2 = 0.979$, $P = 0.011$). This function is in accord with the earlier general observation by Bujas (1934) of a 'hyperbolic-like' relationship between stimulus duration and threshold, and demonstrates that the taste system integrates perithreshold temporal information in a precise and sensitive manner. Such integration appears to be analogous to that seen in other major sensory systems and disproves the notion that gustation is comparatively insensitive to brief temporal stimulus parameters.

Despite the fact that only one previous study examined the influences of stimulus duration on chemical taste thresholds, several studies have examined such influences on electrical taste thresholds. For example, Bujas (1936), using 5 mm diameter Ag–AgCl electrodes, found that sensation magnitude on the tip of the tongue increased with stimulus duration up to a presentation time of ~0.6 s, a finding later confirmed by Krarup (1965). More recently, Føns and Osterhammel (1968) reported, using similar electrodes, that electrical taste thresholds in three subjects decreased over the stimulus duration range of 2–150 ms; longer durations did not lower the threshold further. The latter observation differs from the finding of the present study, in that there is a significant decrease in NaCl thresholds (i.e. higher sensitivity) for stimulus durations as high as 1500 ms. This discrepancy lends further credence to the idea that taste responses due to electrical and chemical stimulation are not directly comparable. Unlike the case with chemical stimuli, the mode of action of electrical taste stimulation is not clear, and it is well established that classic taste qualities are difficult, if not impossible, to produce using this procedure (see Herness, 1985).

The neurophysiological basis for the perithreshold temporal summation observed in the present study is unknown. Presumably, the longer a NaCl solution is present in the vicinity of the taste bud, the more likely Na^+ ions will diffuse to the sodium-sensitive elements of the receptor cells, thereby resulting in more neural activity. Such increased activity could result from greater firing of a given set of neural elements, from the activation of a larger set of neural elements, or from both. It is currently believed that Na^+ salts activate both apical and submucosal pathways within the taste bud (e.g. Ye *et al.*, 1993; Ossebaard and Smith, 1995). It would seem reasonable that, at longer durations, Na^+ ions are more likely to activate ion channels in the apical membranes of taste cells as well as penetrate the tight junctions between taste cells within the basolateral membrane.

In summary, the present study demonstrates that considerable temporal summation occurs at the threshold level for NaCl across stimulus durations ranging from 200 to 1500 ms. Such summation suggests that the taste system, like other primary sensory systems, integrates information across time to enhance its performance at the lower end of the stimulus continuum.

ACKNOWLEDGEMENTS

We thank Mr James Graham, Mr Paul Hebhardt and Ms Solange Chadda for their technical or literary contributions to the project and Dr William Lee for his statistical suggestions. Supported by grant P01 00161 from the National Institute on Deafness and Other Communication Disorders, National Institutes of Health.

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Received on June 18, 1996; accepted on November 11, 1996