Temporal Coding of Intensity of Salty and Sour Tastants in the Nucleus of the Solitary Tract of the Rat

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Introduction

It is clear that most taste sensitive cells in the central gustatory system respond to more than one primary taste quality (sweet, salt, sour, bitter, and umami). Furthrmore, increasing stimulus concentration generally results in increments of a cell's response magnitude. **How taste sensitive neurons convey information about taste quality and intensity simultaneously by response magnitude is an important issue in the study of taste coding**. The purpose of the present study was to test whether temporal patterns of taste responses can convey more information about taste quality and intensity than response frequency (spike count) alone. Single neuron responses to three different concentrations of NaCl (0.6M, 0.1M, 0.01M) and HCl (0.06M, 0.01M, 0.001M) and their undiluted binary mixtures were recorded from the nucleus of the solitary tract (NTS) of anesthetized rats. By applying the methods of metric space analyses (Victor and Purpura, 1997) and multidimensional scaling analysis, the results show that **the temporal structure of taste responses can convey more information about both taste quality and intensity than can the spike count alone.**

Materials and Methods

▪ Surgery and Data Collection

▪ 17 adult male Sprague-Dawley rats (300-450g) were subjects in this experiment. All subjects were fully anesthetized with urethane (1.5 ml/kg) and prepared surgically for electrophysiological recording in the NTS. Extracellular recordings were made from single cells in the NTS with etched tungsten microelectrodes. Waveforms associated with single cells were isolated using the software package Spike2 (CED).

▪ Taste stimuli consisted of NaCl and HCl and their undiluted mixtures at various concentrations. These stimuli were:

(1) High NaCl (0.6M)	(7) High NaCl + High HCl
(2) Medium NaCl (0.1M)	(8) Medium NaCl + Medium HCl
(3) Low NaCl (0.01M)	(9) Low NaCl + Low HCl
(4) High HCl (0.06 M)	(10) High NaCl + Low HCl
(5) Medium HCl (0.01 M)	(11) Low NaCl + High HCl.
(6) Low HCl (0.001 M)	

▪ Each trial consisted of a 10 sec baseline (no stimulus presented), 10 sec distilled water, 5 sec stimulus presentation, 5 sec wait, and 20 sec distilled water rinse. Each block of 11 tastants as described above was repeated for as long as the cell was well isolated. Response magnitude was measured as the rate of firing in spikes per second (SPS) during stimulus presentation minus the firing rate in the final 5 sec of the water pre-rinse.

▪ Quantitative Analysis of Temporal Coding

I. Metric Space Analyses:

▪ The distance between two spike trains was measured by the "**minimum total cost**" of changing one spike train into the other. Each spike that was deleted or added incurred a cost of 1. In addition, the cost of moving a spike by an amount of time "t" was counted as "qt", where q was the "cost" to move a spike per unit time. If q is set at zero, the distance (cost) between the two trains would simply be the difference in the number of spikes (Victor and Purpura, 1997).

▪ In this analysis, shifting a spike by $1/q$ costs as much as deleting the spike. Thus, if we define the "**temporal precision**" of coding as the difference in the timing of the occurrence of two spikes that makes just as much of a difference to the nervous system as the deletion of a spike, then "$1/q$" is the measure of the temporal precision or temporal resolution. Spike trains are considered similar only if they have approximately the same number of spikes, and these spikes occur at approximately the same times, i.e., $1/q$ or less.

▪ Information is then calculated by determining the extent to which responses to each stimulus from distinct clusters based on the distance (cost) among them. The value of q at which the information reaches its maximum is denoted as q_{max}. At the value of q equal to q_{max}, the distances (cost) among taste responses are calculated. These distances are then **used as inputs to a multidimensional scaling analysis (MDS)**. The results of the MDS thus indicate the organization of taste responses in terms of the **similarity of their temporal patterns**.

II. Multidimensional Scaling Analysis (MDS):

▪ MDS is often used in **data visualization** to explore **data similarities or dissimilarities**. Objects (trials of taste responses in this study) are arranged in a **hypothetical taste space** such that the distances from one another correspond to the relative similarity of their temporal patterns, in the sense of the distance defined by the cost q.

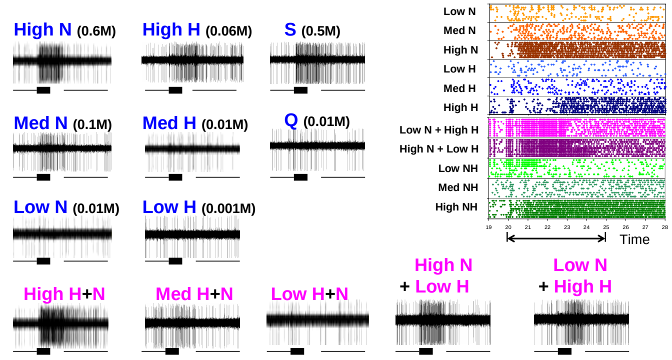

Figure 1: Example of raw data and raster plots including high, medium and low concentrations of NaCl and HCl and their binary mixtures. (Example: Cell 12 which contains a total of 117 trials)

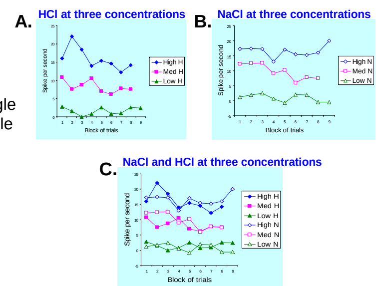

Figure 2: For most cells recorded from the NTS, the response magnitudes for different concentrations of HCl or NaCl are reliably distinguishable as shown in (A) and (B). As the response magnitudes of different qualities and intensities were presented together as in (C), order reversals were common at each concentration level. (Example: Cell 16)

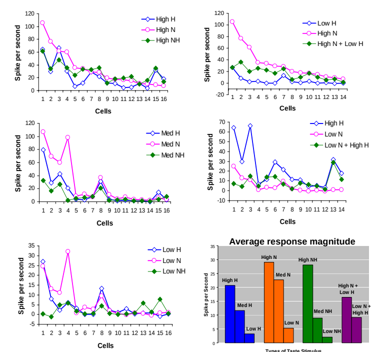

Figure 3: Response magnitudes of NaCl-HCl mixtures with various intensities were mostly less than the MEC. On average, higher intensities of a single taste stimulus (NaCl or HCl) evoked stronger response magnitudes. In mixtures, the order of response magnitudes also obeyed the order of strength of taste intensity (High NH > Med NH> Low NH). Interestingly, the response magnitude of (High N + Low H) was higher than (Low N + High H).

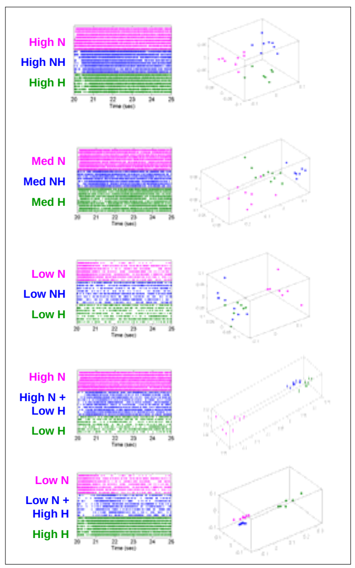

Figure 4: Responses to five mixtures with their single-component (different intensities of NaCl and HCl) were analyzed with metric space analyses and represented in multidimensional taste space based on their temporal firing features. The results show distinguishable individual clusters (clouds) in the taste space for each mixture and its single-components. (Example: Cell 5).

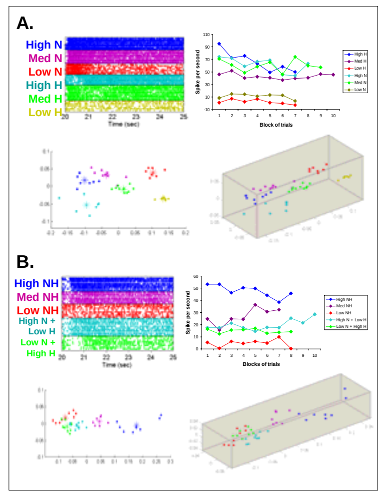

Figure 5: Responses to different intensities of NaCl and HCl (A) and different mixtures (B) were characterized by metric space analyses and represented in multidimensional taste space based on their temporal firing features. The results show distinguishable individual clusters for each stimulus in the taste space. Interestingly, in multidimensional taste space of six single-component (Figure 5A), one coordinate appears to distinguish taste intensities (high, medium or low), and another coordinate distinguishes taste qualities (NaCl or HCl) (Example: Cell 5).

Summary of Results

▪ Multiple repetition of taste responses to different intensities of NaCl and HCl were recorded from **30 cells** in the rat NTS. In addition, in **15 of these cells**, taste responses of binary mixtures with various intensities of NaCl and HCl were recorded. Based on response magnitude, **all cells (100%)** responded to the high concentrations of NaCl and HCl and medium concentrations of NaCl. **28 cells (93%)** responded to the medium concentration HCl. **15 cells (50%)** responded to the low concentrations of either NaCl or HCl.

▪ Overall, the response magnitudes of different concentrations of HCl or NaCl were **reliably distinguishable** as shown in Figure 2A and 2B. There were **5 cells (17%) in the HCl concentration series** and **1 cell (3%) in the NaCl concentration series that showed order reversals of their response magnitudes across blocks of trials.** However, when the response magnitudes evoked by **different qualities and intensities were compared** (Figure 2C), **23 cells (77%) showed order reversals across blocks of trials.**

▪ Mixtures of NaCl and HCl with various concentrations were also recorded from 16 cells. By comparing response magnitudes for a mixtures with the response to its more effective component (MEC), mixture suppression (mixture < MEC) was most commonly observed. Results are summarized as follows:

High NH: enhancement (6/16), similar resp. (3/16), suppression (7/16), order reversal (9/16)

Med NH: enhancement (1/16), similar resp. (1/16), suppression (14/16), order reversal (5/16)

Low NH: enhancement (0/16), similar resp. (2/16), suppression (14/16), order reversal (11/16)

High N + Low H: enhancement (0/15), similar resp. (1/15), suppression (14/15), order reversal (2/15)

Low N + High H: enhancement (2/15), similar resp. (1/15), suppression (12/15), order reversal (4/15)

▪ The contribution of temporal coding to distinguish taste quality and intensity is shown in Figures 4 and 5. In Figure 4, **the clusters (clouds) of mixture tastes occupied separate regions compared with their single components** in the taste space based on their temporal firing characteristics.

▪ The taste spaces for the 6 single-component and 5 mixture stimuli are shown individually in Figure 5. Generally, **each taste stimulus (single-component or mixture) formed its own individual cluster (cloud) in the taste space and those clusters (clouds) occupied separate areas of the space.** When the **spatial arrangement** of individual clouds of single-component taste stimuli were further investigated, we found that the clouds of responses to different taste qualities (NaCl or HCl) generally **occupied different sides of the taste space**. In each side of this quality-dependent taste space, clouds followed **similar (ascending or descending) order** based on the strength of their intensities.

Discussion and Conclusions

▪ Repeated taste responses to three concentrations each of NaCl and HCl and their binary mixtures were recorded from 30 cells in the NTS of anesthetized rats. Most cells showed higher response magnitudes at higher concentrations of NaCl, HCl or their mixtures. However, the **response magnitudes can not provide unambiguous information about taste quality and intensity simultaneously because they are not reliably distinguishable.**

▪ Temporal coding of various intensities of salty and sour tastants was further evaluated by applying metric space analyses and multidimensional scaling analysis. Tastants representing different taste qualities and intensities **formed distinct individual clusters (clouds)** in the taste space. The clusters (clouds) of different taste qualities most often **occupied different sides of the taste space**. Furthermore, the spatial arrangement of clouds for different intensities of each taste quality were generally **parallel** with **the same orderly arrangement based on their intensities**. These results showed that temporal patterns of taste responses convey more information about taste **quality and intensity simultaneously** than response magnitude.

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