Perceptual Maps of Taste Space Using Temporal Coding in the Nucleus of the Solitary Tract of the Rat

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Introduction

It is agreed that neurons in waking brain perform complex and numerous neural computations during neural information processing. **Spike timing** is thought to play a critically functional role during these computational procedures. The temporal structures of neural activities (spike timing or temporal coding) have been widely discussed in the literature. In the taste system, previous studies from our lab showed that neurons in the nucleus of the solitary tract (NTS) reliably generate different temporal patterns in response to different taste stimuli. Moreover, the information conveyed by the temporal structure of a taste response is significantly greater than the information contributed by spike count alone. **Previous studies focused on the role of temporal structure in discriminating various tastants. Here, we focus on the role of temporal structure in *representing* the multidimensional space of tastes.**

Materials and Methods

Surgery and Data Collection

- 23 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 **four single-component tastants: NaCl** (0.1 M), **Sucrose** (0.5 M), **HCl** (0.01 M), and **Quinine** (0.01 M) and **six undiluted binary mixtures: NaCl** (0.1 M) **+ HCl** (0.01 M), **NaCl** (0.1 M) **+ Sucrose** (0.5 M), **NaCl** (0.1 M) **+ Quinine** (0.01 M), **HCl** (0.01 M) **+ Sucrose** (0.5 M), **HCl** (0.01 M) **+ Quinine** (0.01 M), **Sucrose** (0.5 M) **+ Quinine** (0.01M).
- 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 four single tastants and six mixtures 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 stimuli presentation minus the firing rate in the final 5 seconds of the water pre-rinse. Two or Three blocks of the four singular tastants were alternated with two or three blocks of the six binary mixtures in a psedudorandom fashion for as long as the cell remained well isolated.

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.

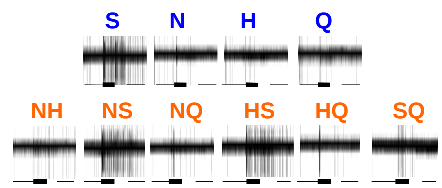


Figure 1: Examples of raw data (Cell 17) recorded from four single-component and six binary mixture taste responses (total 116 trials).

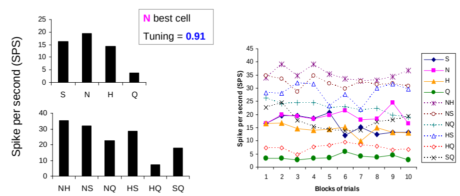


Figure 2: An example of a broadly tuned cell (Cell 7) with response magnitudes to four single-component and six mixture taste stimuli. This N best cell responded vigorously to all taste stimuli except quinine and a mixture of HCl and quinine. Its response magnitudes to these 10 taste stimuli show order reversals across blocks of trials.

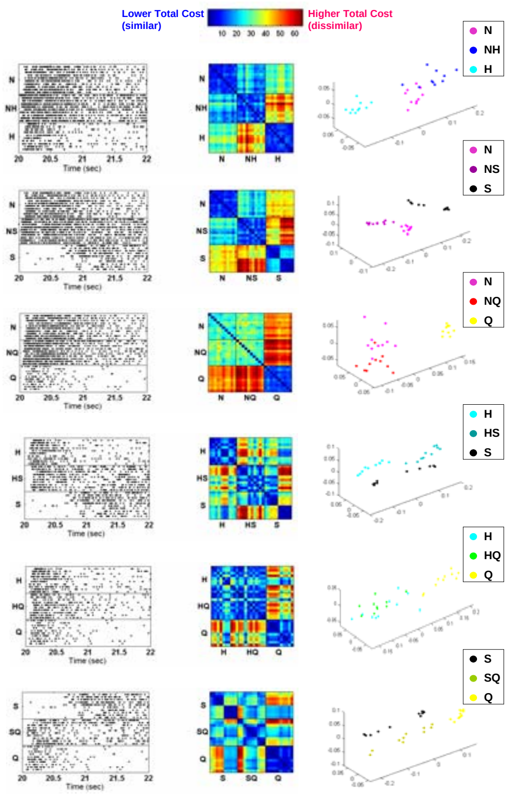


Figure 3: Raster plots, D^{spike} matrices and multidimensional taste spaces of mixture tastes and their single-components for Cell 7. Based on the temporal characteristics of first 2 sec of responses, individual mixtures and their single-components formed their own clusters (clouds). In each taste space, these mixture clusters were generally distinct from other clusters generated by its single-components.

Summary of Results

Figure 4: Taste spaces for Cell 1 and Cell 7 were constructed from their four single-component and six mixture taste responses by multidimensional scaling. Based on their temporal firing characteristics during 5 sec taste responses, each single and mixture taste stimulus formed its own cluster (cloud) in the taste space, and these clouds occupied separate areas of the space.

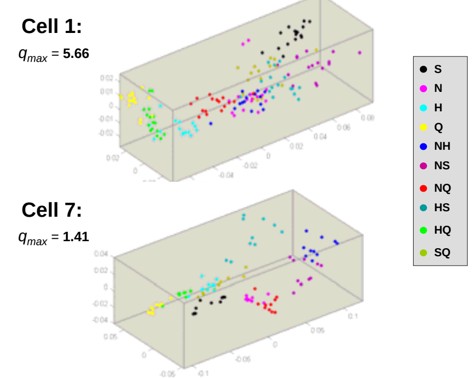
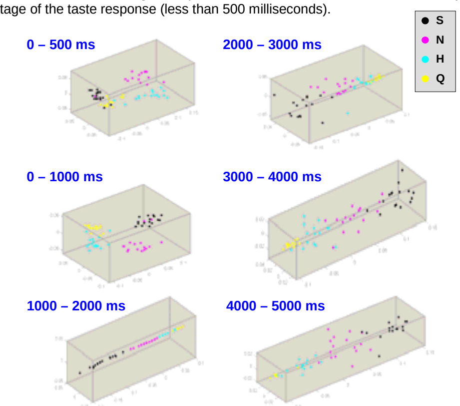


Figure 5: The taste spaces of four single-component taste stimuli at different time epochs of response were constructed for Cell 1. Clusters (clouds) associated with each single-component taste stimuli were formed at an early stage of the taste response (less than 500 milliseconds).



- **35 cells** were recorded from the NTS. Stimuli were repeated between 5 and 23 times (median = 10) for each single-component and mixture stimulus.
- **18** cells (**51%**) responded to all four single-component tastants, **15** cells (**43%**) responded to three tastants, **1** cell (**3%**) responded to two tastants and **1** cell (**3%**) responded to a single tastant. Mixture taste responses were most often similar to the response magnitude of the **more effect component** (**MEC**) (**60%**), but mixture enhancement (**15%**) and mixture suppression (**25%**) were also observed.
- Results of metric space analysis showed that the information conveyed by the **temporal structure** of a taste response is significantly greater than the information contributed by spike count alone.
- It was also evident that the **broadly tuned cells** contribute more information about taste stimuli based on spike timing than do narrowly tuned cells.
- When the temporal characteristics of taste responses were represented in multidimensional taste space, each taste stimulus formed its own **cluster** (**cloud**), and these clusters (clouds) were **distinguishable from clusters generated by other taste stimuli**.
- The results of separate MDS analyses for different time epochs of the response showed that cloud associated with taste stimulus were formed at an **early stage of the taste response** (**less than 500 ms**). These results match the observations from behavioral studies showing that subjects can recognize taste stimuli at an early stage of contact with the tongue.
- The results of MDS also showed that **three dimensions are necessary** to capture the geometry of the clouds, and clouds of responses to tastants of similar quality are **near each other**. This indicated that the **corresponding neural responses are similar in temporal patterns**.

Discussion and Conclusions

- Repeated taste responses of four primary taste qualities and their undiluted binary mixture were recorded from **35** taste sensitive neurons in the NTS of anesthetized rats. Most of these cells showed variable response magnitudes across stimulus repetitions and around 50% **changed their "best stimulus"** across blocks of trials.
- However, when the temporal patterns of taste responses were considered, neurons in the NTS reliably generated different **temporal patterns** in response to different taste stimuli. Moreover, the information contributed by the temporal characteristics of the taste responses was significantly greater than that conveyed by spike count alone.
- When the similarity of the temporal pattern of taste responses, as well as their response magnitudes, were used as input for an MDS analysis, responses associated with individual taste stimuli formed their own clusters (clouds) in the resulting taste space. Clusters for each tastant were distinct from clusters formed by other tastants.
- When taste spaces of different response epochs were constructed, different taste qualities (single-component or mixture) can reliably form distinct individual clusters (cloud) at very **early stages of the taste response** (in a few hundred milliseconds). This result was consistent with behavioral observations that rats can discriminate or recognize taste stimuli in a few hundred milliseconds.
- These results support the ideas that the **temporal characteristics of neural activity in the NTS may convey significant information that may be applied to taste perception.**

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