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Review

Temporal coding in the gustatory system

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Abstract

Hallock, R.M. and Di Lorenzo, P.M. [2006. Temporal coding in the gustatory system. Neurosci. Biobehav. Rev. XX(X) XXX–XXX]. Early investigations of temporal coding in the gustatory system showed that the time course of responses in some neurons showed systematic differences across the various classes of taste stimuli, implying that the temporal characteristics of a response can convey information about a taste stimulus. Studies of temporal coding in the gustatory system have grappled with several unique methodological challenges, including the quantitative description and comparison of temporal patterns as well as the assessment of the relative contributions of spatial and temporal coding to the information contained in a response to a tastant. Other investigations have suggested that the cooperative activity among synchronously firing ensembles of taste-responsive neurons at all levels of processing in the brain can convey information about taste quality (sweet, sour, salty, bitter and umami). Behavioral studies using patterned electrical stimulation of the brain in awake animals have supported the idea that temporal coding of taste stimuli may have functional significance.

Keywords: Taste; Gustatory; Neural coding; Temporal coding; Neurophysiology

Contents

1. Introduction

In the past several years, the study of sensation and perception has been energized by the discovery that some, if not all, sensory systems utilize the temporal parameters of neural responses to convey information about stimuli (e.g. see Lestienne (2001) for a recent review). These discoveries have recast our understanding of neural

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communication in nearly all sensory modalities, including the chemical senses. For example, in the olfactory system, it has been shown that organized oscillations in firing patterns of neurons in the central nervous system of moths are not only correlated with olfactory discrimination (MacLeod et al., 1998) but are necessary for some fine discrimination to take place (Nusser et al., 2001; Stopfer et al., 1997). Collectively, such data can be used to assert the functionality of temporal coding, and thus its relevance to neural processing of sensory stimuli. In this context, the taste system is an attractive model for the study of temporal coding because there are relatively few categories of similar tasting stimuli, called the "basic" taste qualities (sweet, sour, salty, bitter and possibly umami), and because the successful encoding of taste stimuli can often be gauged by both innate and learned behavioral reactivity.

Here we define "temporal coding" as any neural representation in which the distribution of neural activity over time contains information about a stimulus that is meaningful to an organism. For example, information about taste quality could be conveyed by systematic changes in the firing rate over time (i.e. the rate envelope or time course) within a response, by the timing of spikes during the response (Di Lorenzo and Victor, 2003), or by the frequency distribution or particular sequence of interspike intervals during the response. Temporal coding may be contrasted with "spatial coding" in that a spatial code relies on the identity of a neural element to convey information, e.g. two stimuli evoke responses in different subsets of cells. "Population coding," where all neurons in a population contribute to the code for a given stimulus, would be one example of spatial coding. This might take the form of a population vector constructed by the weighted average firing rates across neurons that would specify the identity of a stimulus (Georgopoulos et al., 1986; Nicolelis and Chapin, 1994; Wilson and McNaughton, 1993). Obviously, both spatial and temporal coding may be utilized by the same population of neurons.

The definition of temporal coding can be broadened to include the interactions among neurons as a source of information. Coincident firing of one or more neurons, for example, may convey information about a taste stimulus. In this regard, Katz et al. (2002a, b) have shown that small groups of cortical neurons form cohesive ensembles by firing synchronously during a response to a tastant. Because these dynamic ensembles convey information both by virtue of the timing of their spikes, i.e. simultaneous with respect to each other, and by their identity, i.e. different ensembles are formed according to the particular tastant, this type of representation would be an example of a "spatiotemporal" code.

The idea that temporal coding might be used by the gustatory system originated from the observation that different tastants can evoke neural responses of equal magnitude but with different temporal patterns of firing both across neurons and in a single neuron (Mistretta, 1972). For example, in Fig. 1, responses to sucrose and quinine are shown from a cell recorded in the nucleus of the solitary tract (NTS), the first synapse in the central pathway for taste in the rat (Di Lorenzo and Victor, 2003). It can be seen that each stimulus evokes a different temporal pattern of firing, even though the number of spikes over the response interval are nearly identical. Such observations have fueled several decades of investigation and speculation about the significance of the temporal parameters of taste responses in the neural representation of taste stimuli.

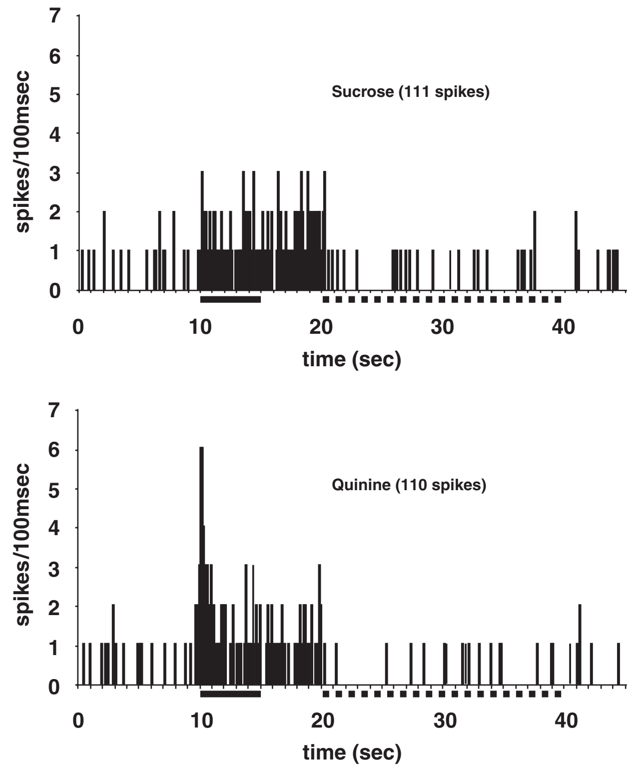

Fig. 1. Peristimulus-time histograms (PSTHs) of responses to sucrose (top) and quinine (bottom) recorded from a single cell in the NTS of an anesthetized rat (Di Lorenzo and Victor, 2003). For each PSTH, the number of spikes in successive 100 ms bins over the time course of the response is shown. The number of spikes that occurred between the onset of the stimulus and the onset of the distilled water rinse is indicated in parentheses for each stimulus. Solid line indicates presence of the stimulus on the tongue and dashed line indicates distilled water rinse.

2. Neural coding of taste—what is encoded?

In the study of neural coding in the gustatory system, it is necessary to define what properties of a stimulus the system must encode, a task that is not nearly as straightforward as one might expect. Consider, for example, taste quality. It has been argued that each of the basic taste qualities represents a taste "primary" in the sense that any gustatory sensation could, in theory, be analyzed and reconstructed as a combination of these basic taste qualities. The most active challenge to this idea has been offered by Erickson (2000) and Schiffman (2000) who assert that taste stimuli can be arranged along a