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More Time to Taste. Focus on “Variability in Responses and Temporal Coding of Tastants of Similar Quality in the Nucleus of the Solitary Tract of the Rat”

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The taste system is ideal for investigations of temporal coding, because neural taste responses are time extensive and often difficult to differentiate by magnitude alone. In a recent article, Roussin et al. 2008 show that spike-time patterning provides a necessary and efficient source of information about tastes that would be otherwise nearly impossible to discriminate—within-type pairs of tastes such as sucrose and fructose, which are both sweet. The authors then go beyond their basic analysis, showing the precision of brain stem taste temporal codes.

The spatial aspect of taste coding is the central focus of most CNS gustatory research—researchers have repeatedly shown that individual neurons respond to particular subsets of taste stimuli (Erickson 1963; Scott and Giza 2000), and various techniques have revealed topographies of taste activation across entire brain regions (Accolla et al. 2007; Chan et al. 2004; Travers et al. 1999). The main theories of taste coding that have emerged in light of these data are spatial theories, whereby an animal knows what taste is on the tongue on the basis of which neurons are activated and to what degree. A major problem for these schemes, however, is the trial-to-trial variability of neural responses: a neuron may respond most strongly to one taste stimulus (say, NaCl) in one trial and respond more strongly to another taste stimulus (say, HCl) in the next trial (Di Lorenzo and Victor 2003; Jones et al. 2007; Lemon and Smith 2006); this problem is particularly acute for tastants that are behaviorally discriminable but that belong to the same category (for example, sucrose and fructose, which both belong to the sweet category). Such stimulus pairs evoke highly similar neural response amplitudes and are therefore indistinguishable based on spike counts alone. In a recent article, Andre Roussin, Patricia Di Lorenzo, Jonathan Victor, and colleagues show that this problem can be solved by considering the possibility that temporal patterning contributes to taste coding.

It has long been known that temporal patterning can contribute information over and beyond that available using magnitude coding in visual, auditory, olfactory, and somatosensory responses (e. g., Friedrich et al. 2004; Ghazanfar and Nicolelis 1997; Mechler et al. 1998; Ringach et al. 1997; Sugase et al. 1999), but recently data have begun to accumulate suggesting that gustation is an ideal system with which to observe the importance of temporal coding (Bahar et al. 2004; Katz et al. 2001, 2002; Lemon and Katz 2007; Stapleton et al. 2006; Yokota and Satoh 2001). Early on, Di Lorenzo and Victor

added to this literature by demonstrating in a rigorous way that even in the first brain stem taste relay (the nucleus of the solitary tract, or NST), many neurons encode tastes using reliable patterns of action potentials (Di Lorenzo and Victor 2003). Simultaneously, this same lab also provided startling insight into the functionality of such spike patterns by showing that rats avoid lick-triggered NTS stimulation when that stimulation temporally mimics the spiking pattern recorded from NTS in response to an aversive bitter stimulus and avoid sucrose after being conditioned to avoid a sucrose-based NTS stimulation pattern (Di Lorenzo and Hecht 1993; Di Lorenzo et al. 2003).

In the recent article, Roussin et al. 2007 have further explored the importance of time in neural taste processing, investigating how NTS neurons respond to repeated applications of similar but discriminable tastes (e.g., salty NaCl vs. salty LiCl, sweet sucrose vs. sweet fructose, and sour HCl vs. sour citric acid) as well as to categorically distinct tastants such as sweet versus sour. As expected (Di Lorenzo and Victor 2003), the authors observed substantial trial-to-trial variance in the number of spikes emitted by each neuron to each taste. This variance caused only moderate problems for the discrimination of tastes from different categories, as the difference in mean rates exceeded the variability for a majority of neurons (but see Di Lorenzo et al. 2003; Lemon and Smith 2006). For tastes belonging to the same category, however, the average amount of spiking was similar enough that a “best stimulus” could seldom be reliably determined. That is, similar but behaviorally discriminable tastes could not be discriminated on the basis of overall spike rate.

The authors go on to show that the resulting conundrum—how can similar tastes be discriminated when responses at the first central taste relay are not reliably different?—can be solved by taking temporal coding into account. They used metric space analysis, a technique that calculates the “cost” of turning one response into another on the basis of adding spikes, moving spikes, or shifting whole chunks of spike trains (Victor and Purpura 1996). From this measurement, the information conveyed by each aspect of the spike trains was calculated. The results show that almost all NTS taste responses carry information within the pattern and sequence of the spike train that can be used to disambiguate stimuli from the same taste category. Where coarse discriminations could rely mainly on rate information, more subtle discriminations appeared to require temporal processes. Furthermore, the analytic technique brought to bear on these neurons allowed Roussin et al. to estimate the time scale of temporal coding to be on the order of hundreds of milliseconds. This finding further illuminates the

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nature of taste processing, by ruling out synchrony-based decoding schemes.

Trial-to-trial variability in taste-responsive spike counts calls simple spatial theories of taste coding into question (Lemon and Smith 2006) and points to the possibility that taste is better conceptualized in terms of single-neuron (Di Lorenzo and Victor 2003) or coherent ensemble (Jones et al. 2006, 2007) dynamics. The current paper makes a strong case for this approach, showing that time-based information can disambiguate stimuli when overall magnitude coding fails. Such data are consistent with work from olfaction suggesting for example that odorant encoding may involve spatiotemporal processes in the mammalian olfactory bulb (Spors et al. 2006) and that the discrimination of similar stimuli requires information concerning spike timing (Stopfer et al. 1997). Work by authors such as Di Lorenzo and Victor heralds in an era of theoretical sophistication in taste coding research.

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