

The Many Flavors of Temporal Coding in Gustatory Cortex

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Why temporal coding?

Environmental stimuli are temporally extensive. They typically (at the very least) wax and wane, and their time-varying aspects are further shaped by the behavioral responses they engender, as animals engage in approach or avoidance. Thus, neural activity related to sensation must be intrinsically time varying as well. Even if sensory stimuli were somehow punctate and static, however, neural activity would still be dynamic, because it is the job of neural brain systems to transform responses to those stimuli into activity appropriate for driving behavior, which itself unfolds as a function of time.

These statements, true in general, are particularly true of the gustatory system, where the coupling between perception and action is virtually unbreakable: it is impossible for an awake animal to passively observe a taste stimulus (Grill and Norgren, 1978a; Travers and Norgren, 1986). This fact, and the purely neural evidence of functional feedback and convergence in forebrain and brainstem taste relays (Smith and Li, 2000; Lundy and Norgren, 2004), should lead researchers to expect some sort of temporal coding in gustatory activity.

But to say that gustation involves temporal coding is to say little, because the term ‘temporal coding’ means many things to many researchers. To some the phrase connotes ‘fast’ dynamics: the synchronous firing of neurons (e.g. deCharms and Merzenich, 1996; Hatsopoulos *et al.*, 1998; Christensen *et al.*, 2000; Steinmetz *et al.*, 2000) or neural oscillations in the ~10, ~20, or ~40 Hz range (e.g. Eckhorn, 1994; MacLeod *et al.*, 1998). To others, it refers to ‘slower’ rate changes, either in single neurons or among coherent groups of neurons (Seidemann *et al.*, 1996; Friedrich and Laurent, 2004). What shall we say about temporal coding in the gustatory system?

Several labs including mine are currently seeking answers to this question. Thus far, the data tell the story of temporal coding being apparent mostly (but not solely) at the level of coherent rate changes among neural ensembles, perhaps driving the system toward (or reflecting) response specification. Gustatory cortical (GC) involvement in this process may extend to preparatory coding that develops across trials in learning situations.

‘Fast’ temporal codes—oscillations and synchrony

Several groups of researchers have linked perception to neural oscillations or synchrony (here called ‘fast’ temporal codes because both have to do with precise timing relationships of action potential firing between neurons). It appears, in fact, that both can be observed in gustatory neural structures. Local field potentials recorded from GC reveal high-amplitude spike-and-wave activity in the 7–12 Hz range (Simon, personal communication). This phenomenon, however, appears to reflect neither oral rhythms nor taste processing; rather, experimenter-applied taste stimuli appear to halt these oscillations for however long it takes the animal to process and consume the fluid.

A number of studies have now shown taste-specific cross-correlations between pairs of cortical (Nakamura and Ogawa, 1997; Yokota and Satoh, 2001; Katz *et al.*, 2002) or brainstem (Adachi *et al.*, 1989; Di Lorenzo and Monroe, 1997) neurons. Those studies examining pairs of neurons separated by <100 μm have revealed synchrony, and have been interpreted in terms of common ascending influences and spatial, columnar-like processing in GC (Yokota and Satoh, 2001). GC neurons separated by much greater distances may also fire in a coherent fashion as well, but this phenomenon is poorly described as synchrony—instead, it appears that at a broad spatial scale taste neurons will change their firing rates together, but that the timing of specific action potentials are stochastic (Katz *et al.*, 2002). Thus, it appears that fast dynamics may play a local role in taste processing, and that ‘slower’ temporal coding may have an independent function at the level of whole-system processes.

‘Slow’ temporal codes: firing rate dynamics

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Such a conclusion accords with the work of computationally minded researchers studying a range of systems, many of whom have questioned the evidence for temporal coding in precise times of action potentials (Shadlen and Newsome, 1998; Baker and Lemon, 2000), instead suggesting that time-varying firing rates may be more closely associated with stimulus processing (Seidemann *et al.*, 1996; Oram *et al.*, 1999). Recent exciting work in the taste field has similarly suggested that information-rich temporal codes in the brainstem function at the time-scale of shifting firing rates (Di Lorenzo and Victor, 2003). According to these analyses of NTS neuron taste responses, spike time shifts interfere with discriminability, but only if the shift is larger than 200 ms; this work is consistent with findings described above concerning GC cross-correlations (Katz *et al.*, 2002). In my own analysis of single GC neurons, I have found further evidence that taste-specific information exists in firing-rate dynamics (Katz *et al.*, 2001). Not only can valuable gustatory information be found in temporal codes, in addition this information appears to evolve: in the first 100 ms following taste administration, GC coding is purely chemosensory, but in the next second it develops a palatability-specific quality (Katz *et al.*, 2001). This, together with preliminary evidence collected in my lab, suggests that the temporal codes in GC may reflect the transformation of a perceptual code into an action code.

These musings suggest a possible distinction that could be made between brainstem and cortical taste activity. It is known that brainstem neurons respond more robustly to tastants than do cortical neurons (e.g. Nishijo and Norgren, 1997; Katz *et al.*, 2001); perhaps this is because cortical neurons only fleetingly engage in stimulus processing, and then turn their energies to using experience-generated plasticity in the transformation of stimulus to response.

Conclusion

Clearly, the investigation of temporal coding in taste is still new, and much remains to be done. As is frequently noted, rats are capable of producing basic behavioral responses to tastes with relatively little neural machinery (Grill and Norgren, 1978b), and are able to

respond extremely quickly in some situations (Halpern and Tapper, 1971). While it is possible that only the early portions of brainstem responses are 'important' for tasting (perhaps later parts of the responses are important solely for peculiarly human processes related to gourmet enjoyment of flavors!), it is also possible that the importance of temporal coding in gustatory cortex is revealed in more complex uses of taste stimuli, and that the known cortical involvement in experience-dependent processing of tastes (Berman and Dudai, 2001) will prove to be accompanied by changes in the temporal codes that support early responses.

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