editorial focus

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Making Time With Taste. Focus on "Taste Response Variability and Temporal Coding in the Nucleus of the Solitary Tract of the Rat"

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Until recently, almost all debates concerning the neural coding of taste have focused on the labeled line (LL) and across neuron pattern (ANP) hypotheses. The former theory postulates that the identity of a taste on the tongue is signaled by activity in the particular subset of neurons dedicated to that task (the sodium neurons, for example); the latter postulates that tastant identity is signaled by the pattern of activity levels across neurons. Both explanations are purely spatial in that the taste code has to do with *which* neurons are active (and to what magnitude). A new paper by Di Lorenzo and Victor (this issue, pgs. 1418–1431) presents evidence that the time course of responses in the rat brain stem contains taste information above and beyond that present in the response magnitudes and in so doing demonstrates that neither LL nor ANP theory provides a full account of the manner in which the taste system processes information (Di Lorenzo and Victor 2003). The researchers go on to suggest that temporal codes for taste probably have little to do with now-classic notions such as synchrony but rather that precise spike times are stochastic and empty of information. Thus their results have implications for the way we think about both gustation and temporal coding in general.

The technical difficulty of taste experiments—the challenge of controlling a turbulent stimulus flow, the long waits for activity to return to baseline (Katz et al. 2001)—have for the most part deprived taste researchers of the statistical power necessary to bring analyses of time course to bear on electrophysiology. What Di Lorenzo and Victor have done is, at its root, simple. They have killed the size of the stimulus array in favor of multiple trial presentations, while recording from the nucleus of the solitary tract (NST), the first brain stem taste relay. This has allowed them to show the trial-to-trial response variability and thus to reveal that for some neurons the overall response magnitude—the currency of both LL and ANP codes—was an unreliable indicator of taste identity. Even when this was not the case, however, further information theoretic analyses revealed that the time course of activity was frequently more information-rich than was the overall response magnitude. Their analysis compared the "costs" of transforming a single trial response to a particular tastant (say, Na) to a different single trial response, either that of another Na trial or that of a response to a different taste (say, quinine). A higher cost means more difference between spike trains and thus more taste-specific information. The analysis could be varied with regard to how much the incurred cost depended on moving spikes around as opposed to simply adding or removing spikes (equivalent to testing the importance of overall response magnitude).

Di Lorenzo and Victor found that, for more than half of their sample of NST neurons, spike trains for different tastants were more distinguishable when temporal patterns were taken into account then when they were not. That is, the time courses of NST responses contained taste-specific information. Furthermore, the importance of the temporal pattern had a limited precision—moving spikes less than 250 ms often had little impact—and varying the cost of changing the sizes of particular intervals *between* spikes (a manipulation that lengthened or shortened the entire train) made little difference compared with changing rates within the same length of time. These facts make it likely that the population temporal code has little to do with the occurrence of synchronous or precisely timed spikes, a finding that is consistent with recent analyses of multi-neuron responses in taste cortex (Katz et al. 2002b), and that makes this paper an important new addition to the evolving debate over the nature of temporal codes in the nervous system (see Baker and Lemon 2000; Gutig et al. 2002; Oram et al. 1999; Shadlen and Newsome 1998). Simply put, the temporal codes observed here cannot be decoded by classic coincidence detectors.

This paper joins a small but growing literature suggesting that taste processing is more complex and dynamic than has previously been assumed (for review, see Katz et al. 2002a) and goes beyond previous work by examining, in finer detail, *how* time may work in taste coding. Given the increasing ubiquity with which temporal coding is reported in studies of sensory physiology (for review, see Ghazanfar and Nicolelis 2000) and the fact that notions similar to LL and ANP thrive across neuroscience, the findings of Di Lorenzo and Victor should be on the reading list of any systems neuroscientist studying sensation and perception.

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