

a0005

4.16 Neural Ensembles in Taste Coding

A Fontanini, S E Grossman, B A Reville, and D B Katz, Brandeis University, Waltham, MA, USA

© 2007 Elsevier Inc. All rights reserved.

4.16.1	Introduction	1
4.16.2	Population Coding and Neural Interactions	2
4.16.3	Functional Implications of Interactive Population Coding	3
4.16.4	The Purposes of Neural Interactions in Taste	5
4.16.5	Conclusions	6
References		6

Glossary

g9000	coherence The state of sticking together, here meaning neurons firing (or changing firing) at the same times.	
g9005	context A set of variables having to do with the environment, either internal or external.	
g9010	ensembles Groups of neurons recorded simultaneously.	
g9015	forebrain The rostral-most portion of the brain, including the thalamus, hypothalamus, basal ganglia, limbic system, and of course cerebral cortex.	
g9020	hierarchy Classification for a system containing a series of levels, each of which does a particular job or set of jobs.	
g9025	interactions Activity in one element (here, a neuron or brain region) having an impact on activity in another.	
	pattern completion A property of a neural network architecture, whereby the act of setting a small subset of units into a state reflecting a particular global pattern causes, through time, the rest of the network to complete this global pattern.	g9030
	receptive field The range of stimuli to which a neuron responds.	g9035
	taste space A theoretical organization of the relative similarities between the stimuli within a particular modality.	g9040
	top-down Interregional interactions reflecting the influence of a higher level of a hierarchy on a lower level of the same hierarchy.	g9045

s0005 4.16.1 Introduction

p0005 Two main theories of taste coding, the labeled-line (LL) and across-neuron pattern (ANP) hypotheses, dominate research in gustation. The two theories are similar, in that both explain taste coding in terms of activity in populations of neurons. They differ in only one regard: according to the LL theory, a particular subgroup of neurons communicates information for a particular taste, and therefore a reduction in firing among one subgroup (say, sucrose-best neurons) codes a reduction in that taste (sweetness); according to the ANP theory, the entire population of taste-responsive neurons participates in all codes, and therefore a reduction in the response of sucrose-best neurons is expected to code both a reduction in sweetness and an increase in some other

taste quality (which is coded, in part, by specifically low firing rates in sucrose-best neurons).

It is not our intent to pursue these distinctions p0010 here. Excellent pro-LL (Scott, K., 2004) and pro-ANP (Smith, D. V. and St. John, S. J., 1999) reviews have been written in the last 10 years. Instead, we will discuss a basic aspect of neural population function that is largely lacking from debates over taste coding. In this essay, we will suggest that coding in distributed neural populations is intrinsically interactive, and that future advances in our theories of gustatory population coding will therefore require an accounting of such interactions. We will present data demonstrating that such interactions occur in sensory systems, including the gustatory system. This will lead to a discussion of the spatial and temporal structures that such interactions introduce

2 Neural Ensembles in Taste Coding

into population activity, and finally to our suggestion that dynamic population codes may be best thought of not as coding stimuli themselves, but rather as driving the transformation of sensory-related activity into action-related activity. Guided by seminal theorizing about perception and action (Gibson, J. J., 1966; Erickson, R., 1984) and by data from taste and other sensory systems, we will argue that the time has come to think about gustatory population coding in a way that is orthogonal to the LL–AFP debate.

Data collected in the light of such neural network modeling has suggested that real brain systems engage in exactly this sort of population coding. A variety of vertebrate and invertebrate sensory, cognitive, and motor systems may make explicit use of interactions between neurons (see below). These interactions introduce considerable complexity into single-neuron behavior and do processing work in neural systems. And while most of this work has been done in the visual, auditory, somatosensory, and olfactory systems, it now appears that the same can be said of the gustatory system – neuronal interactions occur both within and between brain regions in the taste neuroaxis. We will now briefly discuss those anatomical and physiological data.

Interactive processing within single brain regions can be revealed in cross-correlogram (CCG) and cross-coherence peaks, which indicate that one neuron produces action potentials in a consistent temporal relationship to those of another (Brody, C. D., 1999). When that correlated activity is specific to particular stimuli, it suggests that neural coding may involve population interactions. Such coding has been observed to occur in the somatosensory (Roy, S. and Alloway, K. D., 1999), auditory (e.g., Eggermont, J. J., 1994; DeCharms, R. C. and Merzenich, M. M., 1996; Eggermont, J. J., 2000), visual (e.g., Brosch, M. *et al.*, 1997; Lampl, I. *et al.*, 1999; Bretzner, F. *et al.*, 2001; Yoshimura, Y. *et al.*, 2005), and olfactory (e.g., Wehr, M. and Laurent, G., 1996; Christensen, T. A. *et al.*, 2003) systems, and similar findings have been reported in the frontal cortex of monkeys performing a GO NO-GO task (Vaadia, E. *et al.*, 1995) and in motor cortex (Hatsopoulos, N. G. *et al.*, 2003).

In the taste system as well, pairs of cortical neurons produce correlated spike patterns during the presentation of particular subsets of tastes (Yokota, T. *et al.*, 1996; Nakamura, T. and Ogawa, H., 1997; Yokota, T. and Satoh, T., 2001; Katz, D. B. *et al.*, 2002b). Taste administration recruits taste-specific but overlapping neuronal ensembles, including some neurons that are broadly tuned and some that according to classic single-neuron analyses cannot even be identified as taste responsive, that is, neurons with flat or unremarkable responses to taste administration may still be involved in taste-specific cross-correlations (Katz, D. B. *et al.*, 2002b). Taste-specific cross-correlations have also been observed in the nucleus of the solitary tract (NTS, Adachi, M. *et al.*, 1989) and in the pontine parabrachial nuclei (PbN, Yamada, S. *et al.*, 1990; Adachi, M., 1991). Patterns of

s0010 4.16.2 Population Coding and Neural Interactions

p0015 While the LL and ANP hypotheses both refer to activity in populations of neurons, neither suggests a specific role for interactions between the neurons. Such interactions, embodied at the simplest level by concepts such as lateral or reciprocal inhibition and excitation, would in fact introduce complications into the decoding of a LL or ANP code, because such interactions cause neural activity to be modulated through time (see below). In fact, any purely spatial coding scheme (such as both LL and ANP) proposed to function in a network in which neurons interact must include specification of the operative time period during which the spatial code will be polled for content.

p0020 By comparison, most conceptions of neural population function explicitly rely on convergence and/or feedback between nodes (see, for instance, Nagai, T. *et al.*, 1992; van Vreeswijk, C. and Sompolinsky, H., 1998; Nagai, T., 2000; Masuda, N. and Aihara, K., 2003). The earliest neural network models, founded on basic neuroscientific principles but developed before researchers had the means to do ensemble electrophysiology, suggested that population coding relies on information transfer among an entire set of neural elements (McClelland, J. L. and Rumelhart, D. E., 1981). No individual group of neurons in these models (save the input and output nodes) is profitably described as coding any particular stimulus. Instead, processing is a function of the interactions between neurons. Input to such models – even LL input – is transformed by interconnected neural networks into dynamic patterns in which individual neural elements seldom code stimulus attributes independently of their neighbors (see, for instance, Lumer, E. D. *et al.*, 1997; Rabinovich, M. I. *et al.*, 2000; Sporns, O. *et al.*, 2000).

neural interactions appear to provide an additional source of taste-related information not inherent in single-unit spike trains, suggesting that taste neurons are embedded in interactive ensembles.

p0040 Of course, these intraregional ensembles are themselves embedded in larger interactive networks. Various dye-labeling techniques have demonstrated the existence of reciprocal connections among taste-responsive nuclei in brainstem, thalamic, limbic, and cortical regions. Just as injections of horse-radish peroxidase into PbN have revealed two parallel ascending taste pathways in rodents – a parabrachio-thalamo-cortical and parabrachio-amygdaloid pathway (Halsell, C. B., 1992) – similar methods have revealed descending pathways back to the brainstem (van der Kooy, D. *et al.*, 1984; Huang, T. *et al.*, 2003). Reciprocal connections have been shown to exist between various pairs of taste regions, including gustatory cortex (GC) and thalamus (Nakashima, M. *et al.*, 2000), GC and amygdala (McDonald, A. J. and Jackson, T. R., 1987), and amygdala and PbN (Takeuchi, Y. *et al.*, 1982). These data suggest that taste information is processed in a distributed system of information exchange involving ascending and descending pathways.

p0045 Interregional connectivity in the taste system is both convergent and functional (Di Lorenzo, P. M. and Monroe, S., 1997), just as it is in other systems (e.g., Kay, L. M. *et al.*, 1996; Alonso, J. M. *et al.*, 2001; Alloway, K. D. and Roy, S. A., 2002; Villalobos, M. E. *et al.*, 2005). For example, stimulation of GC, amygdala, or hypothalamus modifies single-neuron PbN responses to lingual application of the four basic tastes (Lundy, R. F. and Norgren, R., 2004; Li, C. S. *et al.*, 2005). A large percentage of the PbN taste neurons that receive any sort of feedback receive it from at least two forebrain sites, suggesting that multiple feedback loops may converge upon single brainstem taste neurons. Modulation of neurons in NTS, the very first central taste relay, via manipulation of both central amygdala and lateral hypothalamus, produces similar results (Cho, Y. K. *et al.*, 2003).

p0050 The specific function of feedback from forebrain to brainstem has been suggested to be a sharpening of receptive field (i.e., forebrain stimulation typically reduces the number of stimuli to which brainstem neurons respond, see Lundy, R. F. and Norgren, R., 2004). It might be tempting to conclude that the ultimately sharpened responses are evidence for a LL code, but in fact these data compellingly demonstrate that feed-forward projections are relatively

broadly tuned (reflecting either broadly receptive transduction mechanisms or very early mixing of pathways), and that the apparent labeling of brainstem neurons represents an interactive network effect, in which the broad responses are tuned up by forebrain populations.

4.16.3 Functional Implications of Interactive Population Coding

s0015

The existence of interactive ensembles has strong **p0055** implications for neural network function. Specifically, within- and between-region interactions affect neural activity by introducing structure – both spatial and temporal – into spontaneous and evoked neural activity. Through such imposition of structure, interneuronal interactions imbue neural activity with contextual and behavioral specificity. We will now discuss studies demonstrating that these phenomena are prominent in many neural systems and, to the extent that they have been studied, in the taste system as well.

Classical analysis of sensory neural coding relies **p0060** on the tacit assumption that spontaneous, prestimulus neural activity is random and uncorrelated – noise with which stimulus-evoked signals must compete. In populations of interacting neural elements, however, spontaneous activity is far from random. Hallmark phenomena of interactive processing, such as pattern completion (Rumelhart, D. E. and McClelland, J. L., 1986), ensure that spontaneous activity can drive a network into preferred coherent states.

Little work on this topic has yet been done in the **p0065** taste neuroaxis, but visual cortex has been shown to spontaneously attain spatially coherent global states (Arieli, A. *et al.*, 1996). Images of intrinsic V1 signals, keyed to the spontaneous firing of individual neurons, are nearly identical to the maps produced when those neurons' best stimuli are presented (Tsodyks, M. *et al.*, 1999; Kenet, T. *et al.*, 2003). Analogously, motor cortical networks have been suggested to attain states, referred to as preshapes, that predict population codes for particular movements well in advance of such movements (Bastian, A. *et al.*, 1998; 2003). Cortex can produce best-stimulus responses both in the presence and absence of these stimuli.

The complementary result has also been shown: **p0070** cortex produces surprisingly variable responses to static stimuli. In fact, the specific spatial structure of cortical responses is less dependent on the exact

4 Neural Ensembles in Taste Coding

physical stimulus than on the cognitive context, that is, the animal's interpretation of the stimulus at a particular moment. In the visual system, for example, attention modulates the magnitude of sensory activity, enhancing responses to the attended object and suppressing responses to unattended ones (e.g., Fischer, B. and Boch, R., 1985; Reynolds, J. H. and Chelazzi, L., 2004). In situations in which a stimulus is bistable (e.g., the figure-ground illusion), meanwhile, cortical neurons shift firing rates in direct relation to changes in perception, despite the fact that the actual sensory stimulus is static (Leopold, D. A. and Logothetis, N. K., 1996; Otterpohl, J. R. *et al.*, 2000). Cognitive states also influence the correlations between neurons responding to simultaneously presented stimuli, modifying spatial patterns of neural interactions in cortical regions (Hatsopoulos, N. G. *et al.*, 1998; 2003), and thereby tagging the ensembles recruited to code particular real-world objects; the visual responses to disconnected line segments that are perceived to be part of a single occluded rod fire in synchrony, for instance, while responses to identical line segments that do not present the percept of an occluded rod do not (Singer, W., 1993; see also Harris, K. D., 2005).

p0075 In the taste system, as well, attentional variables affect cortical coding: when a rat ceases to pay attention to taste stimuli, the responses of 40% of the neurons in taste cortex suddenly change their receptive fields (Fontanini, A. and Katz, D. B., 2006). These changes are not random, but rather represent an interpretable modulation of perceptual taste space – specifically, an increase in the salience of the palatability dimension. Changes in orofacial responses to the tastes (Grill, H. J. and Norgren, R., 1978; Berridge, K. C., 2000) confirm this interpretation (Fontanini, A. and Katz, D. B., 2006). Such placing of coherent responses into a meaningful context has been suggested to have its source in feedback from higher neural centers (Engel, A. K. *et al.*, 2001; Buffalo, E. A. *et al.*, 2005). In other words, inclusion of multiple brain regions in the coding population places the neural code into the motivational and cognitive context, such that sensory responses reflect the meaning of stimuli, and not simply their physical makeup.

p0080 While it has not yet been shown that taste networks organize into analogous spatial coherence (but see Yoshimura, H. *et al.*, 2004), it is becoming clear that neural responses to taste administration, like those to other stimuli (e.g., Golomb, D. *et al.*, 1994; Vaadia, E. *et al.*, 1995; MacLeod, K. and Laurent, G.,

1996; Seidemann, E. *et al.*, 1996; Compte, A. *et al.*, 2000; Kirkland, K. L. *et al.*, 2000; Bazhenov, M. *et al.*, 2001; Miller, P. *et al.*, 2005), do have temporal structure. Such temporal structure has been extensively described in both brainstem (Di Lorenzo, P. M. and Schwartzbaum, J. S., 1982; Erickson, R. P. *et al.*, 1994; Di Lorenzo, P. M. and Victor, J. D., 2003) and cortex (Katz, D. B. *et al.*, 2001; see also Tabuchi, E. *et al.*, 2002). The use of chronic recordings in active, tasting rats has allowed us to observe not only slower dynamics but also oscillations (Fontanini, A. and Katz, D. B., 2005) in taste cortex, a region rife with inhibitory cross-talk (Ogawa, H. *et al.*, 1998). These cortical dynamics have been directly linked to network functioning (Katz, D. B. *et al.*, 2002b), a finding that is consistent with paired-pulse studies showing that two identical inputs, separated by just long enough to allow the processing of information from the first input to begin, cause reliably distinct patterns of response in NTS neurons (Lemon, C. H. and Di Lorenzo, P. M., 2002; Di Lorenzo, P. M. *et al.*, 2003). Gustatory responses are clearly dynamic, as predicted by interactive population models (but not by either the LL or ANP model).

Analogous to the above findings on spatial coherence, perceptual relevance emerges in the temporal structure of cortical taste responses, much as it does in other systems (Sugase, Y. *et al.*, 1999; Friedrich, R. W. and Laurent, G., 2001). While data from primates have suggested that only prefrontal cortical activity is affected by important changes in state (i.e., satiety, Rolls, E. T. *et al.*, 1989), rat primary cortical responses clearly contain both sensory and cognitive components. These responses can be divided in three epochs, each of which reflects a particular stage of gustatory processing – somatosensation, chemosensation, and palatability (Katz, D. B. *et al.*, 2001). Attention-related changes in stimulus palatability are preferentially expressed in changes in late-epoch coding (Fontanini, A. and Katz, D. B., 2006), a fact that reinforces the conclusion that the three epochs represent genuine temporal coding, rather than trivially reflecting the outcome of processing.

The evolution of activity during these three p0090 epochs could be the result of interactions/reverberations between the gustatory system and other high-order areas known to code palatability, such as the amygdala (Nishijo, H. *et al.*, 1998). It has also recently been shown that even later aspects of cortical responses in rats change as a taste becomes familiar (Bahar, A. S. *et al.*, 2004). Thus, cognitive processes are apparent both in the spatial and temporal

structures of sensory responses, as one expects when examining a system functioning via interacting populations of neurons.

s0020 **4.16.4 The Purposes of Neural Interactions in Taste**

p0095 It is clear that the behavior of neurons in primary gustatory cortex must be interpreted in terms of context – both the physical context of the networks (of neurons and brain areas) into which the neuron is connected and the cognitive context of the task. Primary GC is not a passive receiver, but rather a dynamic processor of information constantly engaged in a behaviorally dependent interplay with other regions; taste neurons in cortex interact with populations of neurons throughout the taste neuroaxis in the process of stimulus coding. A fundamental issue that remains to be addressed, however, is the definition of the term coding. Put another way, the question is: what kind of processes are interacting populations of taste neurons involved in?

p0100 It has been suggested that neural ensembles may interact for the purposes of binding and/or effective signal transmission, collapsing neurons into a functional, synchronous ensemble in order that this ensemble may code a context-embedded percept. Intra-regional connectivity is thought to allow flexible assembly of a broad range of possible ensembles, while longer-range connections modulate that assembly according to global (cognitive) states (Brosch, M. *et al.*, 1997). This hypothesis has been further extended to consider time-varying responses, wherein distinct subpopulations of neurons fire synchronously at different times during the response (Vaadia, E. *et al.*, 1995; Wehr, M. and Laurent, G., 1996).

p0105 Synchrony is potentially powerful, because synchronous input can be decoded by coincidence-detecting readout cells whose firing represents a synthetic and sparsened version of the input. Perhaps the most well-studied example comes from the insect olfactory system. Kenyon cells in the mushroom body of the locust and fly receive complex, time-varying inputs from populations of projecting neurons in the antenna lobe (Laurent, G. *et al.*, 2001; Lei, H. *et al.*, 2004; Wilson, R. I. *et al.*, 2004) and respond to this very complex input with relatively few – and very reliable – action potentials following the arrival of synchronous inputs (Perez-Orive, J. *et al.*, 2002). The attractiveness of the synchronization hypothesis lies in the ease with which it

fits into an overall vision of the brain as a coding–decoding device: every area codes the input according to some rules and feeds its output to a higher level area that synthesizes it into a sparser representation. In this framework the brain is treated as a linear hierarchical system, where the output of a level is sent to the next, and where the highest level decodes a fully contextualized percept.

The evidence collected thus far, however, does not provide strong support for such a model of gustatory function. As described above, information traversing the gustatory system is hierarchical only to a first approximation – for every ascending pathway between brainstem and forebrain there is matching feedback. In the context of this recurrent organization it is hard to identify the putative decoding zone in which convergence and sparsening might occur. Recordings confirm that the taste selectivity of neural responses does not increase by a great deal as one ascends through the system (Yamamoto, T. *et al.*, 1985; Ogawa, H. *et al.*, 1990; Nishijo, H. *et al.*, 1998), and there is not much evidence for synchrony or oscillations during gustatory processing. In fact, while oscillations occur prominently in gustatory cortex, they specifically occur when rats are not engaged in taste processing (Fontanini, A. and Katz, D. B., 2005). Significant CCGs between pairs of neurons separated by more than 100 μm , meanwhile, appear to reflect simultaneous changes of firing rate, rather than synchronous firing of action potentials (Katz, D. B. *et al.*, 2002b).

Alternative theories avoid the coding–decoding issue entirely, simply by suggesting that processing of a sensory stimulus can be accomplished in the absence of coding of the sensory stimulus. Several researchers and philosophers (see, for instance, Varela, F. J. *et al.*, 1991; van Gelder, T., 1992; Eggermont, J. J., 1998; Engel, A. K. *et al.*, 2001), including more than one chemosensory scientist (Freeman, W. J. and Skarda, C. A., 1994; Halpern, B. P., 2000), have suggested that coding and representation may be constructs with more relevance to computer function than to brain function. Such a notion is *prima facie* attractive, because all extant concepts of taste coding run into trouble over the fact of the wide range of response latencies produced in gustatory behavior – the fact that some taste responses can be produced as little as 200 ms following taste administration, while others take well over 1 s (Halpern, B. P., 2005). Furthermore, it makes sense from an ecological perspective, in that the function of gustation is to provide information for

6 Neural Ensembles in Taste Coding

the crucial decision of ingesting or rejecting food (Gibson, J. J., 1966). Taste is therefore intimately linked to orofacial motor behavior – a linkage that is explicit in the fact that the brainstem taste relays are almost directly connected into orofacial motor-neuron pools (Travers, J. B. and Norgren, R., 1983; Travers, J. B. *et al.*, 2000). It may be reasonably argued that the job of populations of neurons in the gustatory neuroaxis is not to code tastes at all, but rather to transform taste input into motor output. In such a scheme, the spatial hierarchy in which each successive brain region contains more highly processed information is replaced by a temporal hierarchy in which successive time points contain more highly processed information.

p0120 This, then, would be the function of interacting neural populations – to transform input, through poststimulus time, into a form adequate for driving behavior. Stimulus-related input does not get represented by neural firing (or even by neural synchrony) for any particular finite time, but rather sets in motion a dynamic process of population interaction (Harris, K. D., 2005). This is consistent not only with the recent data on temporal coding and cross-correlations in taste (Katz, D. B. *et al.*, 2002a), but also with data from other systems showing: (1) action-oriented responses in early sensory relays (Kay, L. M. and Laurent, G., 1999, Shuler, M. G. and Bear, M. F., 2006); (2) emergence of perceptual information through time (Sugase, Y. *et al.*, 1999); and (3) intriguing new data suggesting that visual input merely perturbs active processes already underway in V1 (Fiser, J. *et al.*, 2004).

s0025 4.16.5 Conclusions

p0125 These are necessarily speculative musings, because the study of interactive population coding in taste cortex and the larger taste neuroaxis is still in its infancy. We do not write this review in an attempt to resolve the debate between LL and ANP theories – both theories have their adherents, both can be thought to receive support from data, and as of now neither can be disproved in the central nervous system. Our suggestion is that we will need a more explicit account of interacting populations, perhaps adapted from research in other systems, if we are to provide the necessary framework for a complete understanding of the functioning of taste networks. These interactions exist in the taste system, as they do in other, more extensively examined systems and in

realistic neural models. The extant theory and data suggest that they may be central to sensory function – function that may conceivably have more to do with transforming input smoothly into motor output than with actual coding of the stimulus *per se*. It will likely be years before these issues can be completely resolved.

References

- Adachi, M. 1991. The mechanism of taste quality discrimination in rat pontine parabrachial nucleus. *Aichi Gakuin Daigaku Shigakkai Shi* 29, 283–299. [b0005](#)
- Adachi, M., Ohshima, T., Yamada, S., and Satoh, T. 1989. Cross-correlation analysis of taste neuron pairs in rat solitary tract nucleus. *J. Neurophysiol.* 62, 501–509. [b0010](#)
- Alloway, K. D. and Roy, S. A. 2002. Conditional cross-correlation analysis of thalamocortical neurotransmission. *Behav. Brain Res.* 135, 191–196. [b0015](#)
- Alonso, J. M., Usrey, W. M., and Reid, R. C. 2001. Rules of connectivity between geniculate cells and simple cells in cat primary visual cortex. *J. Neurosci.* 21, 4002–4015. [b0020](#)
- Arieli, A., Sterkin, A., Grinvald, A., and Aertsen, A. 1996. Dynamics of ongoing activity: explanation of the large variability in evoked cortical responses. *Science* 273, 1868–1871. [b0025](#)
- Bahar, A. S., Dudai, Y., and Ahissar, E. 2004. Neural signature of taste familiarity in the gustatory cortex of the freely behaving rat. *J. Neurophysiol.* 92, 3298–3308. [b0030](#)
- Bastian, A., Riehle, A., Erhagen, W., and Schoner, G. 1998. Prior information preshapes the population representation of movement direction in motor cortex. *Neuroreport* 9, 315–319. [b0035](#)
- Bastian, A., Schoner, G., and Riehle, A. 2003. Preshaping and continuous evolution of motor cortical representations during movement preparation. *Eur. J. Neurosci.* 18, 2047–2058. [b0040](#)
- Bazhenov, M., Stopfer, M., Rabinovich, M., Abarbanel, H. D., Sejnowski, T. J., and Laurent, G. 2001. Model of cellular and network mechanisms for odor-evoked temporal patterning in the locust antennal lobe. *Neuron* 30, 569–581. [b0045](#)
- Berridge, K. C. 2000. Measuring hedonic impact in animals and infants: microstructure of affective taste reactivity patterns. *Neurosci. Biobehav. Rev.* 24, 173–198. [b0050](#)
- Bretzner, F., Aitoubah, J., Shumikhina, S., Tan, Y. F., and Molotchnikoff, S. 2001. Modulation of the synchronization between cells in visual cortex by contextual targets. *Eur. J. Neurosci.* 14, 1539–1554. [b0055](#)
- Brody, C. D. 1999. Disambiguating different covariation types. *Neural Comput.* 11, 1527–1535. [b0060](#)
- Brosch, M., Bauer, R., and Eckhorn, R. 1997. Stimulus-dependent modulations of correlated high-frequency oscillations in cat visual cortex. *Cereb. Cortex* 7, 70–76. [b0065](#)
- Buffalo, E. A., Bertini, G., Ungerleider, L. G., and Desimone, R. 2005. Impaired filtering of distracter stimuli by TE neurons following V4 and TEO lesions in macaques. *Cereb. Cortex* 15, 141–151. [b0070](#)
- Cho, Y. K., Li, C. S., and Smith, D. V. 2003. Descending influences from the lateral hypothalamus and amygdala converge onto medullary taste neurons. *Chem. Senses* 28, 155–171. [b0075](#)
- Christensen, T. A., Lei, H., and Hildebrand, J. G. 2003. Coordination of central odor representations through transient, non-oscillatory synchronization of glomerular

- output neurons. *Proc. Natl. Acad. Sci. U. S. A.* 100, 11076–11081.
- b0085** Compte, A., Brunel, N., Goldman-Rakic, P. S., and Wang, X. J. 2000. Synaptic mechanisms and network dynamics underlying spatial working memory in a cortical network model. *Cereb. Cortex* 10, 910–923.
- b0090** DeCharms, R. C. and Merzenich, M. M. 1996. Primary cortical representation of sounds by the coordination of action-potential timing. *Nature* 381, 610–613.
- b0095** Di Lorenzo, P. M. and Monroe, S. 1997. Transfer of information about taste from the nucleus of the solitary tract to the parabrachial nucleus of the pons. *Brain Res.* 763, 167–181.
- b0100** Di Lorenzo, P. M. and Schwartzbaum, J. S. 1982. Coding of gustatory information in the pontine parabrachial nuclei of the rabbit: temporal patterns of neural response. *Brain Res.* 251, 245–257.
- b0105** Di Lorenzo, P. M. and Victor, J. D. 2003. Taste response variability and temporal coding in the nucleus of the solitary tract of the rat. *J. Neurophysiol.* 90, 1418–1431.
- b0110** Di Lorenzo, P. M., Lemon, C. H., and Reich, C. G. 2003. Dynamic coding of taste stimuli in the brainstem: effects of brief pulses of taste stimuli on subsequent taste responses. *J. Neurosci.* 23, 8893–8902.
- b0115** Eggermont, J. J. 1994. Neural interaction in cat primary auditory cortex II. Effects of sound stimulation. *J. Neurophysiol.* 71, 246–270.
- b0120** Eggermont, J. J. 1998. Is there a neural code? *Neurosci. Biobehav. Rev.* 22, 355–370.
- b0125** Eggermont, J. J. 2000. Sound-induced synchronization of neural activity between and within three auditory cortical areas. *J. Neurophysiol.* 83, 2708–2722.
- b0130** Engel, A. K., Fries, P., and Singer, W. 2001. Dynamic predictions: oscillations and synchrony in top-down processing. *Nat. Rev. Neurosci.* 2, 704–716.
- b0135** Erickson, R. 1984. On the neural bases of behavior. *Am. Sci.* 72, 233–241.
- b0140** Erickson, R. P., Di Lorenzo, P. M., and Woodbury, M. A. 1994. Classification of taste responses in brain stem: membership in fuzzy sets. *J. Neurophysiol.* 71, 2139–2150.
- b0145** Fischer, B. and Boch, R. 1985. Peripheral attention versus central fixation: modulation of the visual activity of prelunate cortical cells of the rhesus monkey. *Brain Res.* 345, 111–123.
- b0150** Fiser, J., Chiu, C., and Weliky, M. 2004. Small modulation of ongoing cortical dynamics by sensory input during natural vision. *Nature* 431, 573–578.
- b0155** Fontanini, A. and Katz, D. B. 2005. 7 to 12 Hz activity in rat gustatory cortex reflects disengagement from a fluid self-administration task. *J. Neurophysiol.* 93, 2832–2840.
- b0160** Fontanini, A. and Katz, D. B. 2006. State-dependent modulation of time-varying gustatory responses. *J. Neurophysiol.* 96, 3183–3193.
- b0165** Freeman, W. J. and Skarda, C. A. 1994. Representations: Who Needs Them? In: *Brain Organization and Memory: Cells, Systems, and Circuits* (eds. J. L. McGaugh, N. Weinberger, and G. Lynch), pp. 375–380. Oxford University Press.
- b0170** Friedrich, R. W. and Laurent, G. 2001. Dynamic optimization of odor representations by slow temporal patterning of mitral cell activity. *Science* 291, 889–894.
- b0175** van Gelder, T. 1992. What might cognition be if not computation? *J. Philo.* 91, 345–381.
- b0180** Gibson, J. J. 1966. *The Senses Considered as Perceptual Systems*. Houghton Mifflin.
- b0185** Golomb, D., Wang, X. J., and Rinzel, J. 1994. Synchronization properties of spindle oscillations in a thalamic reticular nucleus model. *J. Neurophysiol.* 72, 1109–1126.
- b0190** Grill, H. J. and Norgren, R. 1978. The taste reactivity test. I. Mimetic responses to gustatory stimuli in neurologically normal rats. *Brain Res.* 143, 263–279.
- Halpern, B. P. 2000. Sensory coding, decoding, and representations. Unnecessary and troublesome constructs? *Physiol. Behav.* 69, 115–118.
- Halpern, B. P. 2005. Temporal characteristics of human taste judgments as calibrations for gustatory event-related potentials and gustatory magnetoencephalographs. *Chem. Senses* 30(Suppl. 1), i228–i229.
- Halsell, C. B. 1992. Organization of parabrachial nucleus efferents to the thalamus and amygdala in the golden hamster. *J. Comp. Neurol.* 317, 57–78.
- Harris, K. D. 2005. Neural signatures of cell assembly organization. *Nat. Rev. Neurosci.* 6, 399–407.
- Hatsopoulos, N. G., Ojakangas, C. L., Paninski, L., and Donoghue, J. P. 1998. Information about movement direction obtained from synchronous activity of motor cortical neurons. *Proc. Natl. Acad. Sci. U. S. A.* 95, 15706–15711.
- Hatsopoulos, N. G., Paninski, L., and Donoghue, J. P. 2003. Sequential movement representations based on correlated neuronal activity. *Exp. Brain Res.* 149, 478–486.
- Huang, T., Yan, J., and Kang, Y. 2003. Role of the central amygdaloid nucleus in shaping the discharge of gustatory neurons in the rat parabrachial nucleus. *Brain Res. Bull.* 61, 443–452.
- Katz, D. B., Nicolelis, M. A., and Simon, S. A. 2002a. Gustatory processing is dynamic and distributed. *Curr. Opin. Neurobiol.* 12(4), 448–454.
- Katz, D. B., Simon, S. A., and Nicolelis, M. A. 2001. Dynamic and multimodal responses of gustatory cortical neurons in awake rats. *J. Neurosci.* 21, 4478–4489.
- Katz, D. B., Simon, S. A., and Nicolelis, M. A. 2002b. Taste-specific neuronal ensembles in the gustatory cortex of awake rats. *J. Neurosci.* 22, 1850–1857.
- Kay, L. M. and Laurent, G. 1999. Odor- and context-dependent modulation of mitral cell activity in behaving rats. *Nat. Neurosci.* 2, 1003–1009.
- Kay, L. M., Lancaster, L. R., and Freeman, W. J. 1996. Reafference and attractors in the olfactory system during odor recognition. *Int. J. Neural Syst.* 7, 489–495.
- Kenet, T., Bibitchkov, D., Tsodyks, M., Grinvald, A., and Arieli, A. 2003. Spontaneously emerging cortical representations of visual attributes. *Nature* 425, 954–956.
- Kirkland, K. L., Sillito, A. M., Jones, H. E., West, D. C., and Gerstein, G. L. 2000. Oscillations and long-lasting correlations in a model of the lateral geniculate nucleus and visual cortex. *J. Neurophysiol.* 84, 1863–1868.
- van der Kooy, D., Koda, L. Y., McGinty, J. F., Gerfen, C. R., and Bloom, F. E. 1984. The organization of projections from the cortex, amygdala, and hypothalamus to the nucleus of the solitary tract in rat. *J. Comp. Neurol.* 224, 1–24.
- Lampl, I., Reichova, I., and Ferster, D. 1999. Synchronous membrane potential fluctuations in neurons of the cat visual cortex. *Neuron* 22, 361–374.
- Laurent, G., Stopfer, M., Friedrich, R. W., Rabinovich, M. I., Volkovskii, A., and Abarbanel, H. D. 2001. Odor encoding as an active, dynamical process: experiments, computation, and theory. *Annu. Rev. Neurosci.* 24, 263–297.
- Lei, H., Christensen, T. A., and Hildebrand, J. G. 2004. Spatial and temporal organization of ensemble representations for different odor classes in the moth antennal lobe. *J. Neurosci.* 24, 11108–11119.
- Lemon, C. H. and Di Lorenzo, P. M. 2002. Effects of electrical stimulation of the chorda tympani nerve on taste responses in the nucleus of the solitary tract. *J. Neurophysiol.* 88, 2477–2489.
- Leopold, D. A. and Logothetis, N. K. 1996. Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature* 379, 549–553.
- Li, C. S., Cho, Y. K., and Smith, D. V. 2005. Modulation of parabrachial taste neurons by electrical and chemical

8 Neural Ensembles in Taste Coding

- stimulation of the lateral hypothalamus and amygdala. *J. Neurophysiol.* 93, 1183–1196.
- [b0300](#) Lumer, E. D., Edelman, G. M., and Tononi, G. 1997. Neural dynamics in a model of the thalamocortical system. I. Layers, loops and the emergence of fast synchronous rhythms. *Cereb. Cortex* 7, 207–227.
- [b0305](#) Lundy, R. F., Jr. and Norgren, R. 2004. Activity in the hypothalamus, amygdala, and cortex generates bilateral and convergent modulation of pontine gustatory neurons. *J. Neurophysiol.* 91, 1143–1157.
- [b0310](#) MacLeod, K. and Laurent, G. 1996. Distinct mechanisms for synchronization and temporal patterning of odor-encoding neural assemblies. *Science* 274, 976–979.
- [b0315](#) Masuda, N. and Aihara, K. 2003. Duality of rate coding and temporal coding in multilayered feedforward networks. *Neural Comput.* 15, 103–125.
- [b0320](#) McClelland, J. L. and Rumelhart, D. E. 1981. An interactive activation model of context effects in letter perception. Part 1. An account of basic findings. *Psychol. Rev.* 88, 375–407.
- [b0325](#) McDonald, A. J. and Jackson, T. R. 1987. Amygdaloid connections with posterior insular and temporal cortical areas in the rat. *J. Comp. Neurol.* 262, 59–77.
- [b0330](#) Miller, P., Brody, C. D., Romo, R., and Wang, X. J. 2005. A recurrent network model of somatosensory parametric working memory in the prefrontal cortex. *Cereb. Cortex* 15, 679.
- [b0335](#) Nagai, T. 2000. Artificial neural networks estimate the contribution of taste neurons to coding. *Physiol. Behav.* 69, 107–113.
- [b0340](#) Nagai, T., Yamamoto, T., Katayama, H., Adachi, M., and Aihara, K. 1992. A novel method to analyse response patterns of taste neurons by artificial neural networks. *Neuroreport* 3, 745–748.
- [b0345](#) Nakamura, T. and Ogawa, H. 1997. Neural interaction between cortical taste neurons in rats: a cross-correlation analysis. *Chem. Senses* 22, 517–528.
- [b0350](#) Nakashima, M., Uemura, M., Yasui, K., Ozaki, H. S., Tabata, S., and Taen, A. 2000. An anterograde and retrograde tract-tracing study on the projections from the thalamic gustatory area in the rat: distribution of neurons projecting to the insular cortex and amygdaloid complex. *Neurosci. Res.* 36, 297–309.
- [b0355](#) Nishijo, H., Uwano, T., Tamura, R., and Ono, T. 1998. Gustatory and multimodal neuronal responses in the amygdala during licking and discrimination of sensory stimuli in awake rats. *J. Neurophysiol.* 79, 21–36.
- [b0360](#) Ogawa, H., Hasegawa, K., Otawa, S., and Ikeda, I. 1998. GABAergic inhibition and modifications of taste responses in the cortical taste area in rats. *Neurosci. Res.* 32, 85–95.
- [b0365](#) Ogawa, H., Ito, S., Murayama, N., and Hasegawa, K. 1990. Taste area in granular and dysgranular insular cortices in the rat identified by stimulation of the entire oral cavity. *Neurosci. Res.* 9, 196–201.
- [b0370](#) Otterpohl, J. R., Haynes, J. D., Emmert-Streib, F., Vetter, G., and Pawelzik, K. 2000. Extracting the dynamics of perceptual switching from ‘noisy’ behaviour: an application of hidden Markov modelling to pecking data from pigeons. *J. Physiol. Paris* 94, 555–567.
- [b0375](#) Perez-Orive, J., Mazor, O., Turner, G. C., Cassenaer, S., Wilson, R. I., and Laurent, G. 2002. Oscillations and sparsening of odor representations in the mushroom body. *Science* 297, 359–365.
- [b0380](#) Rabinovich, M. I., Huerta, R., Volkovskii, A., Abarbanel, H. D., Stopfer, M., and Laurent, G. 2000. Dynamical coding of sensory information with competitive networks. *J. Physiol. Paris* 94, 465–471.
- [b0385](#) Reynolds, J. H. and Chelazzi, L. 2004. Attentional modulation of visual processing. *Annu. Rev. Neurosci.* 27, 611–647.
- [b0390](#) Rolls, E. T., Sienkiewicz, Z. J., and Yaxley, S. 1989. Hunger modulates the responses to gustatory stimuli of single neurons in the caudolateral orbitofrontal cortex of the macaque monkey. *Eur. J. Neurosci.* 1, 53–60.
- Roy, S. and Alloway, K. D. 1999. Synchronization of local neural networks in the somatosensory cortex: a comparison of stationary and moving stimuli. *J. Neurophysiol.* 81, 999–1013.
- [b0395](#) Rumelhart, D. E. and McClelland, J. L. 1986. *Parallel Distributed Processing: Explorations in the Microstructure of Cognition*, MIT Press.
- [b0400](#) Scott, K. 2004. The sweet and the bitter of mammalian taste. *Curr. Opin. Neurobiol.* 14, 423–427.
- [b0405](#) Seidemann, E., Meilijson, I., Abeles, M., Bergman, H., and Vaadia, E. 1996. Simultaneously recorded single units in the frontal cortex go through sequences of discrete and stable states in monkeys performing a delayed localization task. *J. Neurosci.* 16, 752–768.
- [b0410](#) Shuler, M. G. and Bear, M. F. 2006. Reward timing in the Primary Visual Cortex. *Science* 311, 1606–1609.
- [b0415](#) Singer, W. 1993. Synchronization of cortical activity and its putative role in information processing and learning. *Annu. Rev. Physiol.* 55, 349–374.
- [b0420](#) Smith, D. V. and St. John, S. J. 1999. Neural coding of gustatory information. *Curr. Opin. Neurobiol.* 9, 427–435.
- [b0425](#) Sporns, O., Tononi, G., and Edelman, G. M. 2000. Connectivity and complexity: the relationship between neuroanatomy and brain dynamics. *Neural Netw.* 13, 909–922.
- [b0430](#) Sugase, Y., Yamane, S., Ueno, S., and Kawano, K. 1999. Global and fine information coded by single neurons in the temporal visual cortex. *Nature* 400, 869–873.
- [b0435](#) Tabuchi, E., Yokawa, T., Mallick, H., Inubushi, T., Kondoh, T., Ono, T., and Torii, K. 2002. Spatio-temporal dynamics of brain activated regions during drinking behavior in rats. *Brain Res.* 951, 270–279.
- [b0440](#) Takeuchi, Y., McLean, J. H., and Hopkins, D. A. 1982. Reciprocal connections between the amygdala and parabrachial nuclei: ultrastructural demonstration by degeneration and axonal transport of horseradish peroxidase in the cat. *Brain Res.* 239, 583–588.
- [b0445](#) Travers, J. B. and Norgren, R. 1983. Afferent projections to the oral motor nuclei in the rat. *J. Comp. Neurol.* 220, 280–298.
- [b0450](#) Travers, J. B., DiNardo, L. A., and Karimnamazi, H. 2000. Medullary reticular formation activity during ingestion and rejection in the awake rat. *Exp. Brain Res.* 130, 78–92.
- [b0455](#) Tsodyks, M., Kenet, T., Grinvald, A., and Arieli, A. 1999. Linking spontaneous activity of single cortical neurons and the underlying functional architecture. *Science* 286, 1943–1946.
- [b0460](#) Vaadia, E., Haalman, I., Abeles, M., Bergman, H., Prut, Y., Slovin, H., and Aertsen, A. 1995. Dynamics of neuronal interactions in monkey cortex in relation to behavioural events. *Nature* 373, 515–518.
- [b0465](#) Varela, F. J., Thompson, E. T., and Rosch, E. 1991. *The Embodied Mind: Cognitive Science and Human Experience*. MIT Press.
- [b0470](#) Villalobos, M. E., Mizuno, A., Dahl, B. C., Kemmotsu, N., and Muller, R. A. 2005. Reduced functional connectivity between V1 and inferior frontal cortex associated with visuomotor performance in autism. *Neuroimage* 25, 916–925.
- [b0475](#) van Vreeswijk, C. and Sompolinsky, H. 1998. Chaotic balanced state in a model of cortical circuits. *Neural Comput.* 10, 1321–1371.
- [b0480](#) Wehr, M. and Laurent, G. 1996. Odour encoding by temporal sequences of firing in oscillating neural assemblies (w/ commentary). *Nature* 384, 162–166.
- [b0485](#) Wilson, R. I., Turner, G. C., and Laurent, G. 2004. Transformation of olfactory representations in the *Drosophila* antennal lobe. *Science* 303, 366–370.
- [b0490](#) Yamada, S., Ohshima, T., Oda, H., Adachi, M., and Satoh, T. 1990. Synchronized discharge of taste neurons recorded

- simultaneously in rat parabrachial nucleus. *J. Neurophysiol.* 63, 294–302.
- b0495 Yamamoto, T., Yuyama, N., Kato, T., and Kawamura, Y. 1985. Gustatory responses of cortical neurons in rats. II. Information processing of taste quality. *J. Neurophysiol.* 53, 1356–1369.
- b0500 Yokota, T. and Satoh, T. 2001. Three-dimensional estimation of the distribution and size of putative functional units in rat gustatory cortex as assessed from the inter-neuronal distance between two neurons with correlative activity. *Brain Res. Bull.* 54, 575–584.
- Yokota, T., Eguchi, K., and Satoh, T. 1996. Correlated discharges of two neurons in rat gustatory cortex during gustatory stimulation. *Neurosci. Lett.* 209, 204–206. b0505
- Yoshimura, Y., Dantzker, J. L., and Callaway, E. M. 2005. Excitatory cortical neurons form fine-scale functional networks. *Nature* 433, 868–873. b0510
- Yoshimura, H., Sugai, T., Fukuda, M., Segami, N., and Onoda, N. 2004. Cortical spatial aspects of optical intrinsic signals in response to sucrose and NaCl stimuli. *Neuroreport* 15, 17–20. b0515

ELSEVIER SECOND PROOF