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Behavioral Modulation of Gustatory Cortical Activity

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Abstract

Our perception of the sensory world is constantly modulated by the environment surrounding us and by our psychological state; each encounter with the same stimulus can in fact evoke very different perceptions. This phenomenological richness correlates well with the plasticity and the state-dependency observed in neural responses to sensory stimuli. This article reviews recent results on how the processing of sensory inputs varies depending on the internal state of the animal. Specifically it focuses on the gustatory system and on data showing that levels of attention and expectation modulate taste processing and gustatory cortical activity in meaningful ways. Mounting experimental evidence suggesting that expectation-dependent changes in gustatory cortical activity result from changes in the coupling between the amygdala and the cortex will also be discussed. The results presented here begin to paint a complex picture of taste, which goes beyond the framework of classical coding theories.

Keywords

attention; expectation; learning

The Taste Stimulus Underdetermines the Taste Percept

You run into the kitchen, thirsty from your workout. On the counter sits a tall glass of amber fluid. “Ah, ginger ale,” you think, as you grab for it and start to quaff. Too late you realize that it was not ginger ale at all, but apple juice. You are surprised.

And accompanying this surprise is an odd perceptual phenomenon: the first bolus of fluid on your tongue tastes neither like ginger ale nor apple juice; in fact, it tastes bad, even if you normally find both beverages quite palatable. While the apple juice almost certainly activates the same constellation of taste receptors each time it hits the tongue, the perceptual experience engendered by that activation can vary wildly, depending on your expectations.

Attention to Tastes Changes Taste Perception

These well-known (if anecdotal) facts suggest that pretaste activity in the gustatory neuroaxis can have strong and specific impacts on neural coding of the tastes themselves—expectation

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Conflicts of Interest

The authors declare no conflicts of interest.

changes everything. A simple laboratory illustration of such changes can be found in studies performed recently in our lab (Fig. 1). When rats involved in a tasting task suddenly lost interest in this task, the “spontaneous” patterns of activity in gustatory cortex (GC) changed drastically, such that large 10 Hz spikes appeared in prestimulus local field potentials¹ (Fig. 1A). These sudden changes were accompanied by equally sudden modifications to the taste responses of individual GC neurons.² But attention doesn’t simply change GC responses; it changes them in explicable, palatability-specific ways. Responses in inattentive animals emphasize major differences in palatability—pleasant versus aversive tastes—and de-emphasize finer differences within these larger categories (Fig. 1B). As predicted by earlier work,³ these differences are expressed purely in palatability-related portions of the neural codes, more than 0.75 s after taste delivery; earlier aspects of the taste codes are unaltered. Palatability-related orofacial behaviors⁴ (taste reactivity⁵) change in concert with these neural changes,² such that the differences between pleasing and aversive tastes increases and the differences within category (i.e., between two aversive tastes) decreases (Fig. 1C).

Thus, as is true in other modalities,^{6,7} taste responses are very sensitive to even as broad a manipulation as arousal. When an animal focuses on the possibility of taste administration, this focus has a reliable impact on taste perception—an impact that makes evolutionary sense, in that it is adaptive for an “inattentive” animal to remain sensitive to highly positive and negative stimuli, lest the animal fail to respond to food, mates, and threats.

Expectation of Taste Delivery Changes Taste Perception

Given that focusing attention on the taste modality changes taste perception, it should come as no surprise that specific expectation of upcoming taste delivery has even greater effects. Tastes are unique among stimuli in that they are, in nature, always self-administered—an animal seldom if ever finds a taste on the tongue unbidden. Taste self-administration travels hand in hand with taste expectation, and therefore should engender different neural responses, and a different perceptual experience, than those engendered by delivery to a passive animal.

Evidence resoundingly confirms this prediction. In fact, the difference between passive and self-administration is such that it changes the very circuit involved in taste perception. For instance, the neural system underlying conditioned taste aversion (CTA), the process whereby an animal comes to dislike the experience of consuming a taste that has previously caused illness, depends on the nature of stimulus delivery: when the taste is delivered to a passive rat through an intra-oral cannula (IOC) CTA requires basolateral amygdala, but when the animal licks the taste from a spout it does not.^{8,9} Our recent work demonstrates that CTAs are independent of amygdala even when the taste is delivered through an IOC, if the animal triggers delivery by breaking an infrared beam in a nose-poke (Wieskopf *et al.*, submitted). Further work from our laboratory reveals an entire class of taste neurons in basolateral amygdala that respond only to “surprise” deliveries; taste responses in these neurons are largely inhibited when the animal self-administers the stimulus.¹⁰

We are now completing an in-depth examination directly comparing passive- and self-administration in GC, amygdala, and prefrontal responses (Fontanini & Katz, in preparation). This examination demonstrates that taste expectation—not expectation of a particular taste, but simply the anticipation that a taste will soon arrive—changes all aspects of GC taste responses. In fact, GC neurons develop entirely novel responses to stimuli that announce the availability of tastes for self-administration. These stimuli may not be gustatory; in our hands, rats learn to acquire tastes in the presence of a particular tone, and taste neurons come to respond at short latencies to this tone. Our work suggests that both the changes in taste coding and the novel, nontaste responses are related to activity in “higher” structures, as the animal organizes

its cognitive, sensory, and probably motor resources into a single system for the purpose of perceiving a taste stimulus in the complete context of its current situation.

Conclusion

Of course, the purpose of this research is not to suggest that GC exists to process auditory information, or even to provide still more evidence for the already well-documented fact that sensory cortex is intrinsically multimodal.¹¹ What our data ultimately demonstrates is that taste responses, usually argued to reflect either labeled-line¹² or across-fiber coding,^{13,14} may in fact reflect neither: both of the coding schemes debated in the taste literature assume that neural responses supply reliable, faithful reports of the taste on the tongue; the data described here suggest, in contrast, that taste responses are massively variable and sensitive to the specifics of prestimulus activity in GC and “higher” structures. As such, these data suggest, as has been suggested previously at ISOT meetings,¹⁵ that “coding” may be a poor description of what the gustatory system does with tastes. GC activity seems too variable across contexts, and the codebook that a putative decoder would need to understand this activity—the mapping between code and meaning in every context—seems too vast for the taste responses to serve as reliable codes. Whether or not this proves to be the case, or whether instead there is some useful “core” of neurons that respond reliably regardless of context, remains to be seen. What is clear, however, is that the bulk of the taste-related activity in GC has more to do with the performance of associative tasks than with sensory coding *per se*.

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Figure 1.

Attention levels modulate gustatory processing: (A) Left panel: Patterns of local field potential activity observed in the gustatory cortex of rats during different phases of a tasting session. Each trace represents a 2 s long recording during a period characterized by fast, desynchronized activity (top) or during a period dominated by 7–12 Hz mu-like oscillations. Right panel: Correlation between mu-like activity in the early (first hour) and late part of the tasting session and reaction times to the stimulus presented directly in the mouth of the animal. Left y-axis (and light gray histograms): amount of time per s in which mu-like rhythms were observed. Right y-axis (and dark gray points superimposed on the histograms): Latency of the first purposeful orofacial movement following stimulus presentation. (B) Principal components

analysis of neural activity showing how the “distance” between tastes in a hypothetical stimulus space changes depending on attention. Left panel: Distance (i.e., the dissimilarity) between quinine (Q and Q') and sucrose (S and S'), tastes with opposing palatability, increases with inattention (the ' denotes the position of the taste during inattention). Right panel: Distance between quinine (Q and Q') and citric acid (CA and CA') decreases once the animal becomes inattentive. The ' denotes the taste during inattention. (C) Analysis of orofacial behaviors during attention and inattention showing independent evidence for a rearrangement of the taste space according to palatability. Left panel: Ratio between sucrose and quinine for the number of tongue protrusions evoked. The ratio increases during inattention, reflecting an increased dissimilarity between the two stimuli. In contrast, tastes with similar palatability (right panel) show more similar orofacial reactions as the animal becomes inattentive. The ratio between quinine and citric acid for number of gapes evoked decreases with inattention.