Journal Club

Editor's Note: These short, critical reviews of recent papers in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to summarize the important findings of the paper and provide additional insight and commentary. For more information on the format and purpose of the Journal Club, please see http://www.jneurosci.org/misc/ifa_features.shtml.

A Dynamic Cortical Network Encodes Violations of Expectancy during Taste Perception

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Review of Veldhuizen et al.

The ability to detect and appropriately respond to potentially harmful stimuli in the environment is crucial for the survival of all organisms. As a result, most species have developed reflex-like avoidance behaviors that serve to protect them from external threats. Quick and automatic avoidance reactions are of particular importance during food ingestion. By the time the taste of an ingested object has been assessed, it is already in the mouth, so an immediate reaction is needed to prevent a toxic item from being swallowed. Humans achieve these fast edibility assessments by forming taste predictions based on contextual input that is available before ingestion, taking advantage of learned associations between the senses. Incongruencies between sensory inputs typically result in rapid reallocation of attention to the food stimulus and are perceived as aversive (Stevenson, 2010). This rejection mechanism is so powerful that even food items that are normally perceived as pleasant can appear repulsive when they do not correspond to our visually derived expectations (Yeomans et al., 2008). Top-down error signals from association cortex thus appear to be able to override even our innate preferences for certain tastes, such as sweets. While these

mechanisms are clearly of great evolutionary importance, the functional anatomy and intrinsic connectivity of the underlying neural network have not, until recently, been studied.

An article published in *The Journal of Neuroscience* (Veldhuizen et al., 2011) now offers insight into the neural basis of perceived breaches of taste identity expectation. In a functional magnetic resonance imaging (fMRI) study, the authors presented subjects with a sweet sucrose solution and a tasteless solution, and asked them to indicate via button press when a taste was perceived. In 70% of cases, taste stimuli were preceded by a valid auditory cue of a voice saying “sweet” or “tasteless,” respectively. In 30% of cases, presentation was preceded by an invalid cue, leading subjects to expect the alternate tastant. Effects of expectancy breaches were observed behaviorally, indicated by both slower response times and lower task accuracy. A voxelwise analysis of the neuroimaging data revealed that relative to expected solutions, unexpected solutions led to higher activation of a broad network of cortical regions previously implicated in gustatory perception, attention, and reward processing. Surprisingly, the presentation of both solutions resulted not only in activation changes in gustatory cortex, but also in deactivation of an area in the fusiform gyrus, which is generally associated with visual object processing. This effect was significantly more pronounced for unexpected compared with expected stimuli.

The authors supplemented these analyses of brain activation with analyses of psychophysical interactions (PPI), a method that uses the activation peaks as seed regions to identify inter-regional correlations in the fMRI time series that are explained by task modulation. Such increases in coordinated activity were observed between the anterior insula, where the primary gustatory cortex is located, and both the ventral striatum (VS), a part of the reward network, and the inferior parietal sulcus, a part of the attention network.

To determine the directionality of these interactions, the authors developed a mechanistic model of the brain functions underlying reactions to unexpected taste presentation. Dynamic causal modeling (DCM) was used to compare networks comprising the three nodes identified by PPI analyses with different patterns of intrinsic connections and input paths. The model with the best fit contained bidirectional connections between anterior insula and VS, and unidirectional influences of inferior parietal activity on anterior insula. On the basis of these observations, the authors developed a model for breaches of expectancy in gustatory processing: Unexpected auditory-gustatory combinations modulate top-down influences from attentional networks and reward networks, thereby enhancing activation to the taste in the primary gustatory cortex. This increase in coordinated activity may reflect attentional orientation toward the unexpected stimulus

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and the formation of an expectation-related error signal in the VS.

In the past, the role of the VS in gustation has predominantly been investigated in the context of reward learning. It has been implicated as the potential generator site of a so-called “prediction error” response that occurs as a result of a temporal mismatch between real and expected taste delivery and is thought to subserve the formation of causal associations. Of interest, a recent meta-analysis evaluating evidence for an aversion-processing network in humans and animals has implicated locations in the striatum as important nodes for aversion processing (Hayes and Northoff, 2011). Animal studies provided strong support for a role of the VS in the generation of an aversion response, while activations of the dorsal striatum were primarily reported in humans, also found by Veldhuizen et al. (2011). Hayes and Northoff (2011) speculate that methodological limitations may have resulted in an underestimation of VS contribution in humans and urge further investigation of the subject. Veldhuizen et al.’s study forms an important contribution in our understanding of striatal projections, suggesting that, as previously proposed, they might indeed equally contribute to our learning of an aversive response during mismatches across sensory modalities.

The unexpected finding of decreased fusiform activation during taste processing is of high relevance in the context of current efforts to elucidate the role of resting state activity in this area. Two recent papers (Zhang et al., 2009; Turk-Browne et al., 2010) have reported that under resting conditions, default activity in the fusiform gyrus and other core face-processing areas is elevated and increased network connectivity can be observed. Thus, activation in the absence of visual input may reflect a latent readiness for task-related processing of faces, some of the most frequently encountered stimuli in our environment. Veldhuizen et al. (2011) report a reduction of this activity relative to resting state in a purely auditory-gustatory task. Interestingly, the reduction was higher in the conditions in which increased attention was allocated to the gustatory modality, implicating a suppression of brain areas involved in visual object recognition. Most multisensory research to date focuses on understanding brain activation during events in which visual stimuli are

presented in combination with other sensory stimulation. The findings reported by Veldhuizen et al. (2011) provide evidence that cortical multisensory coordination can draw attention away from our dominant sense to dedicate directed attention to non-visual tasks. Understanding these dynamics of mutual inhibition and mutual enhancement will provide a challenge for multisensory research.

A critical question that remains is how the choice of stimulus material, particularly taste quality and valence, affected the results reported by Veldhuizen et al. (2011). The authors chose to only compare one intrinsically rewarding sweet taste to a tasteless solution. This might have been done in an effort to dissociate the negative affect associated with a breach of expectation from negative affect caused by an intrinsic negative taste. As a next step, it is imperative to investigate whether similar mechanisms can be observed for tastes of negative valence. Expectations about taste valence, elicited by a visual cue, indeed affect bitter and sweet taste perception differently (Nitschke et al., 2006), indicating that the hedonic quality of a taste affects the extent to which expectancy acts upon taste perception. The complex interactions between taste quality and hedonics can yield different perceptual experiences of the same taste depending on how deviations from expectations are subjectively perceived. Therefore, hedonic taste differences may obfuscate expectancy effects. For example, the same mildly unpleasant taste can evoke negative affect or disgust if a pleasant taste is expected. By contrast, positive affect or relief can result when a very unpleasant taste is expected. The extent of such differential processing associated with breaches of expectancy for tastes of baseline and negative valence could be assessed relative to a hedonically neutral taste.

In addition to taste hedonics, the magnitude of deviations from expectancy determines the direction in which expectations alter perception. It appears that subtle differences between expectations about the food and the actual food properties result in assimilation effects, i.e., the merging of actual and expected experiences, whereas strong discrepancies between expectations and actual stimuli can elicit contrast effects, i.e., the enhancement of unexpected stimulus prop-

erties (Zellner et al., 2004; Yeomans et al., 2008). Using qualitatively different tastes within the same study would allow strong violations of expectancy to be elicited through an enlarged discrepancy between the stimuli. To control for these diverging perceptual consequences of breaches of expectancy and to assess whether assimilation or contrast occurred, trial-by-trial subjective ratings of taste properties including hedonics should complement future investigations.

In summary, Veldhuizen et al. (2011) provide important insights into the neural underpinnings of violations of expectations about taste by revealing a network comprising attentional, reward-related, and primary taste areas. These findings are of high ecological relevance given that under real life conditions, the ingestion of a spoiled or novel food would often be the cause of a breach of expectancy reaction. Future studies are warranted to replicate and extend these findings with stimuli of different sensory and hedonic taste properties.

References

- Hayes DJ, Northoff G (2011) Identifying a network of brain regions involved in aversion-related processing: a cross-species translational investigation. *Front Integr Neurosci* 5:49.
- Nitschke JB, Dixon GE, Sarinopoulos I, Short SJ, Cohen JD, Smith EE, Kosslyn SM, Rose RM, Davidson RJ (2006) Altering expectancy dampens neural response to aversive taste in primary taste cortex. *Nat Neurosci* 9:435–442.
- Stevenson RJ (2010) An initial evaluation of the functions of human olfaction. *Chem Senses* 35:3–20.
- Turk-Browne NB, Norman-Haignere SV, McCarthy G (2010) Face-specific resting functional connectivity between the fusiform gyrus and posterior superior temporal sulcus. *Front Hum Neurosci* 4:176.
- Veldhuizen MG, Douglas D, Aschenbrenner K, Gitelman DR, Small DM (2011) The anterior insular cortex represents breaches of taste identity expectation. *J Neurosci* 31:14735–14744.
- Yeomans MR, Chambers L, Blumenthal H, Blake A (2008) The role of expectancy in sensory and hedonic evaluation: the case of smoked salmon ice-cream. *Food Quality and Preference* 19:9p.
- Zellner DA, Strickhouser D, Tornow CE (2004) Disconfirmed hedonic expectations produce perceptual contrast, not assimilation. *Am J Psychol* 117:363–387.
- Zhang H, Tian J, Liu J, Li J, Lee K (2009) Intrinsically organized network for face perception during the resting state. *Neurosci Lett* 454:1–5.