

# Taste, Flavor, and Appetite

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## Introduction

A diagram of the taste and related olfactory, somatosensory, and visual pathways in primates is shown in [Figure 1](#). Neurophysiological studies in primates provide a foundation for understanding taste, olfactory, and flavor processing, and neuroimaging in humans, for the investigation of the tuning of individual neurons provides the fundamental information about how these stimuli are encoded in different brain areas using a sparse distributed representation in which each neuron is tuned differently to other neurons ([Kadohisa, Rolls, & Verhagen, 2005](#); [Rolls, 2008a, 2015](#); [Rolls, Grabenhorst, & Parris, 2010](#); [Rolls & Treves, 2011](#)). Studies in nonhuman primates are especially relevant ([Rolls, 2014](#)), for the taste pathways in primates proceed via the thalamus to the taste cortex, whereas in rodents, there is a pontine taste area that has direct subcortical connections ([Small & Scott, 2009](#)); effects of satiety are found peripherally in the nucleus of the solitary tract in rodents ([Rolls & Scott, 2003](#); [Scott & Small, 2009](#)); and rodents do not have the major part of the primate including human orbitofrontal cortex (OFC), the granular part ([Wise, 2008](#)).

## Human Imaging

### Studies Taste

In humans, it has been shown ([Rolls, 2012a, 2014, 2015](#)) in neuroimaging studies using functional magnetic resonance imaging (fMRI) that taste activates an area of the anterior insula/frontal operculum, which is probably the primary taste cortex ([de Araujo, Kringelbach, Rolls, & Hobden, 2003](#); [O'Doherty, Rolls, Francis, Bowtell, & McGlone, 2001](#); [Small, 2010](#)), and part of the OFC, which is probably the secondary taste cortex ([de Araujo, Kringelbach, Rolls, & Hobden, 2003](#); [Francis et al., 1999](#); [O'Doherty et al., 2001](#); [Rolls, 2005b, 2008a](#)). We pioneered the use of a tasteless control with the same ionic constituents as saliva ([de Araujo, Kringelbach, Rolls, & Hobden, 2003](#); [O'Doherty et al., 2001](#)), as water can activate some neurons in cortical taste areas ([Rolls, Yaxley, & Sienkiewicz, 1990](#)) and can activate the taste cortex ([de Araujo, Kringelbach, Rolls, & Hobden, 2003](#)). Within individual subjects, separate areas of the OFC are activated by sweet (pleasant) and by salt (unpleasant) tastes ([O'Doherty et al., 2001](#)).

The primary taste cortex in the anterior insula of humans represents the identity and intensity of taste in that activations there correlate with the subjective intensity of the taste, and the OFC and anterior cingulate cortex (ACC) represent the reward value of taste, in that activations there correlate with the subjective pleasantness of taste ([Grabenhorst & Rolls, 2008](#); [Grabenhorst, Rolls, & Parris, 2008](#); [Figure 2](#)).

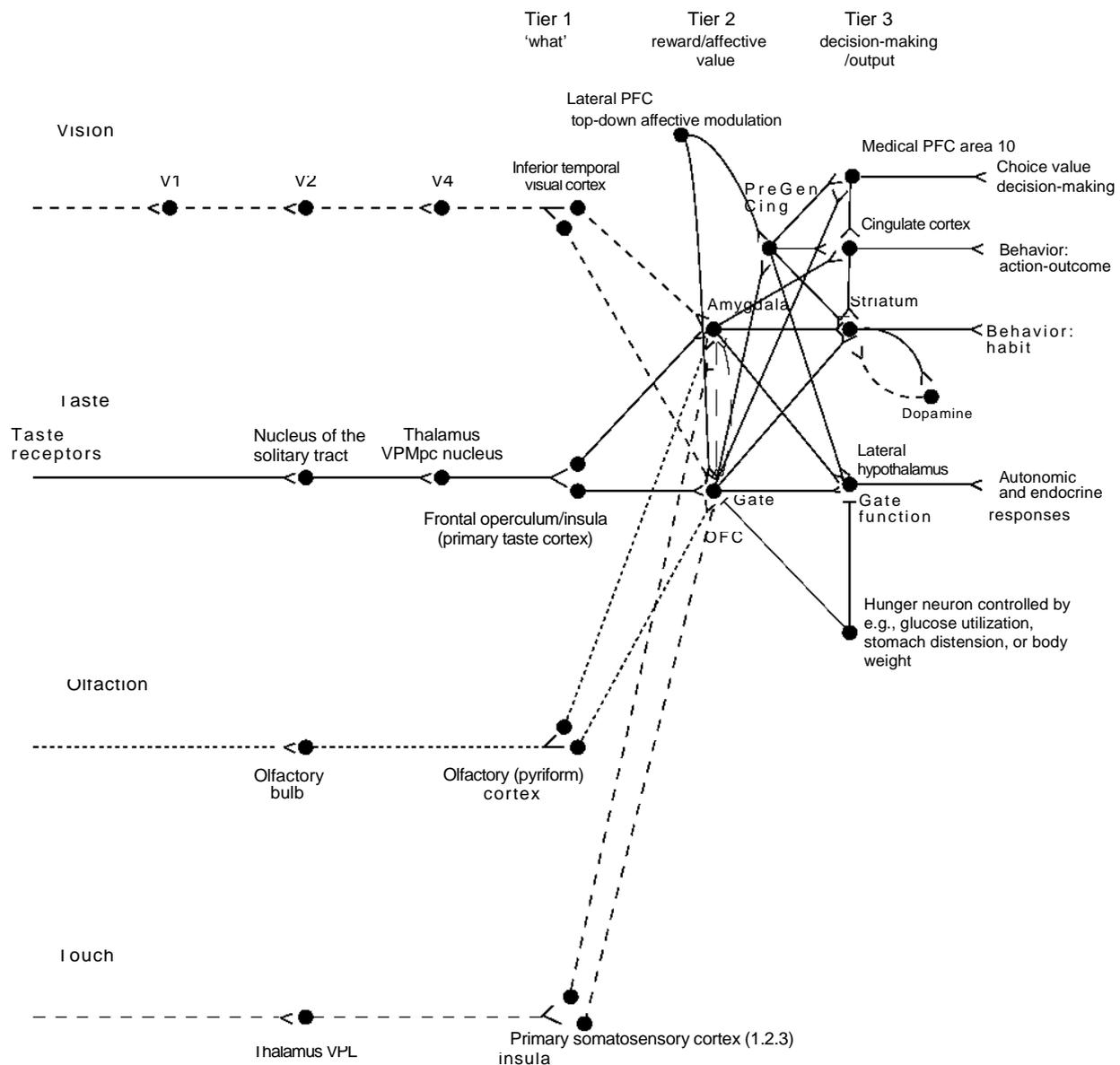
We also found activation of the human amygdala by the taste of glucose ([Francis et al., 1999](#)). Extending this study, [O'Doherty et al. \(2001\)](#) showed that the human amygdala was as much activated by the affectively pleasant taste of glucose

as by the affectively negative taste of NaCl and thus provided evidence that the human amygdala is not especially involved in processing aversive as compared to rewarding stimuli. [Zald, Lee, Fluegel, and Pardo \(1998\)](#) and [Zald, Hagen, and Pardo \(2002\)](#) also showed that the amygdala, as well as the OFC, responds to aversive (e.g., quinine) and to sucrose taste stimuli.

Umami taste stimuli, of which an exemplar is monosodium glutamate (MSG) and which capture what is described as the taste of protein, activate the insular (primary), orbitofrontal (secondary), and anterior cingulate (tertiary [Rolls, 2008a](#)) taste cortical areas ([de Araujo, Kringelbach, Rolls, & McGlone, 2003](#)). When the nucleotide 0.005 M inosine 5<sup>0</sup>-monophosphate (IMP) was added to MSG (0.05 M), the BOLD (blood oxygenation level-dependent) signal in an anterior part of the OFC showed supralinear additivity, and this may reflect the subjective enhancement of umami taste that has been described when IMP is added to MSG ([Rolls, 2009](#)). The supralinear additivity refers to a greater activation to the combined stimulus MSG+IMP than to the sum of the activations to MSG and IMP presented separately. This evidence that the effect of the combination is greater than the sum of its parts indicates an interaction between the parts to form in this case an especially potent taste of umami, which is part of what can make a food taste delicious ([Rolls, 2009](#)). Overall, these results illustrate that the responses of the brain can reflect inputs produced by particular combinations of sensory stimuli with supralinear activations and that the combination of sensory stimuli maybe especially represented in particular brain regions and may help to make the food pleasant.

### Odor

In humans, in addition to activation of the pyriform (olfactory) cortex ([Poellinger et al., 2001](#); [Sobel et al., 2000](#); [Zald & Pardo, 1997](#)), there is strong and consistent activation of the OFC by olfactory stimuli ([Francis et al., 1999](#); [Rolls, Kringelbach, & de Araujo, 2003](#); [Zatorre, Jones-Gotman, Evans, & Meyer, 1992](#)). This region appears to represent the pleasantness of odor, as shown by a sensory-specific satiety experiment with banana versus vanilla odor ([O'Doherty et al., 2000](#)), and this has been confirmed by [Gottfried et al. \(personal communication, see Gottfried \(2013\)\)](#), who also showed that activations in the pyriform (primary olfactory) cortex were not decreased by odor devaluation by satiety. Further, pleasant odors tend to activate the medial, and unpleasant odors the more lateral, OFC ([Rolls et al., 2003](#)), adding to the evidence that there is a hedonic map in the OFC and also in the ACC, which receives inputs from the OFC ([Grabenhorst & Rolls, 2011](#); [Rolls & Grabenhorst, 2008](#)). The primary olfactory (pyriform) cortex represents the identity and intensity of odor in that activations there correlate with the subjective intensity of the odor, and the OFC and ACC represent the reward value of odor, in that activations there correlate with the subjective pleasantness (medially) or unpleasantness (laterally) of odor ([Grabenhorst & Rolls, 2011](#); [Grabenhorst, Rolls, Margot, da Silva, & Velazco, 2007](#);



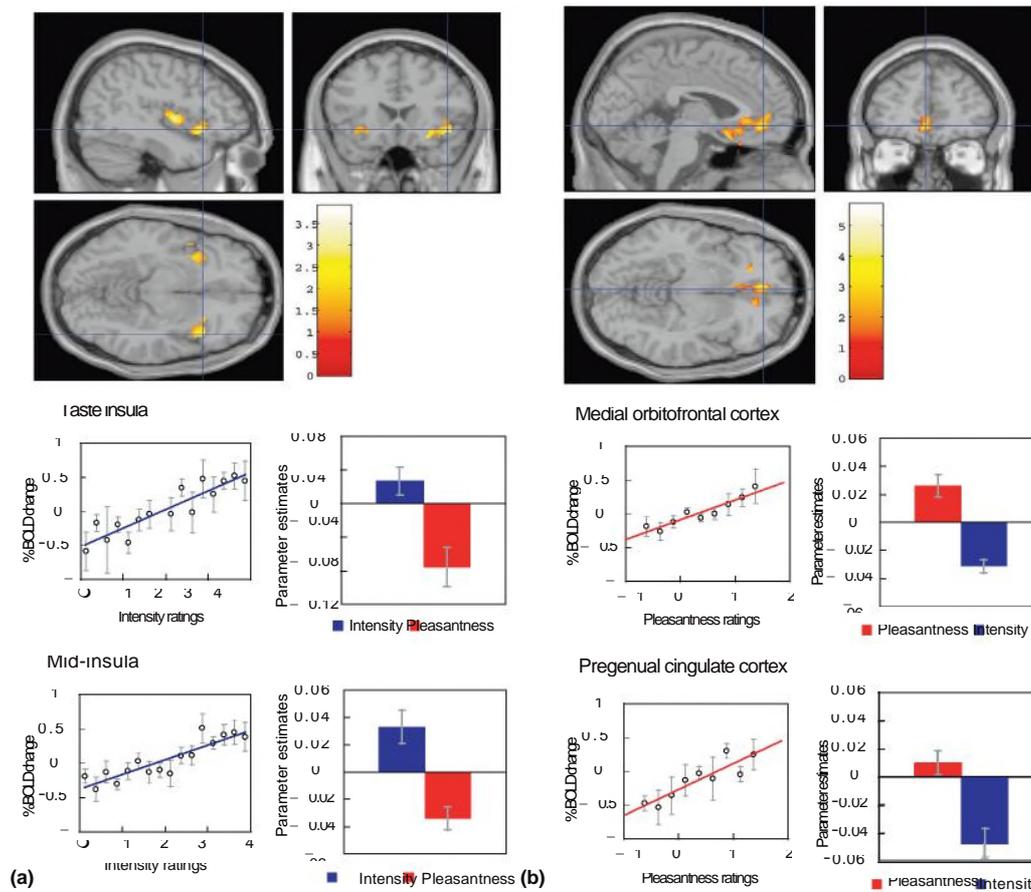
**Figure 1** Schematic diagram showing some of the gustatory, olfactory, visual, and somatosensory pathways to the orbitofrontal cortex (OFC), and some of the outputs of the OFC, in primates. The secondary taste cortex and the secondary olfactory cortex are within the OFC. V1, primary visual cortex; V4, visual cortical area V4; PreGen Cing, pregenual cingulate cortex. 'Gate' refers to the finding that inputs such as the taste, smell, and sight of food in some brain regions only produce effects when hunger is present (Rolls, 2005a). Tier 1: The column of brain regions including and below the inferior temporal visual cortex represents brain regions in which 'what' stimulus is present is made explicit in the neuronal representation, but not its reward or affective value that is represented in the next tier of brain regions (tier 2), the OFC and amygdala, and in the anterior cingulate cortex. In Tier 3 areas beyond these such as medial prefrontal cortex area 10, choices or decisions about reward value are taken, with the mechanisms described elsewhere (Rolls, 2008b, 2014; Rolls & Deco, 2010). Top-down control of affective response systems by cognition and by selective attention from the dorsolateral prefrontal cortex is also indicated. Medial PFC area 10, medial prefrontal cortex area 10; VPMpc, ventral posteromedial thalamic nucleus.

Rolls & Grabenhorst, 2008; Rolls, Grabenhorst, & Franco, 2009; Rolls, Grabenhorst, Margot, da Silva, & Velazco, 2008; Rolls et al., 2003).

#### Olfactory–Taste Convergence to Represent Flavor and the Influence of Satiety on Flavor Representations

Taste and olfactory conjunction analyses, and the measurement of supra-additive effects indicating convergence and

interactions, showed convergence for taste (sucrose) and odor (strawberry) in the OFC and ACC, and activations in these regions were correlated with the pleasantness ratings given by the participants (de Araujo, Rolls, Kringelbach, McGlone, & Phillips, 2003; Small & Prescott, 2005; Small et al., 2004). These results provide evidence on the neural substrate for the convergence of taste and olfactory stimuli to produce flavor in humans and on where the pleasantness of flavor is represented in the human brain. The first region where the effects of this



**Figure 2** Effect of paying attention to the pleasantness versus the intensity of a taste stimulus. (a) Top: A significant difference related to the taste period was found in the taste insula at  $[42\ 18\ -14]$   $z = 2.42$   $p < 0.05$  (indicated by the cursor) and in the midinsula at  $[40\ -2\ 4]$   $z = 3.03$   $p < 0.025$ . Middle: Taste insula. Right: The parameter estimates (mean  $\pm$  sem across subjects) for the activation at the specified coordinate for the conditions of paying attention to pleasantness or to intensity. The parameter estimates were significantly different for the taste insula  $t = 4.5$ ,  $df = 10$ ,  $p = 0.001$ . Left: The correlation between the intensity ratings and the activation (% BOLD change) at the specified coordinate ( $r = 0.91$ ,  $df = 14$ ,  $p < 0.001$ ). Bottom: Midinsula. Right: The parameter estimates (mean  $\pm$  sem across subjects) for the activation at the specified coordinate for the conditions of paying attention to pleasantness or to intensity. The parameter estimates were significantly different for the midinsula  $t = 5.02$ ,  $df = 10$ ,  $p = 0.001$ . Left: The correlation between the intensity ratings and the activation (% BOLD change) at the specified coordinate ( $r = 0.89$ ,  $df = 15$ ,  $p < 0.001$ ). The taste stimulus, monosodium glutamate (MSG), was identical on all trials. (b) Top: A significant difference related to the taste period was found in the medial OFC at  $[-6\ 14\ -20]$   $z = 3.81$   $p < 0.003$  (toward the back of the area of activation shown) and in the pregenual cingulate cortex at  $[-4\ 46\ -8]$   $z = 2.90$   $p < 0.04$  (at the cursor). Middle: Medial OFC. Right: The parameter estimates (mean  $\pm$  sem across subjects) for the activation at the specified coordinate for the conditions of paying attention to pleasantness or to intensity. The parameter estimates were significantly different for the OFC  $t = 7.27$ ,  $df = 11$ ,  $p < 10^{-4}$ . Left: The correlation between the pleasantness ratings and the activation (% BOLD change) at the specified coordinate ( $r = 0.94$ ,  $df = 8$ ,  $p < 0.001$ ). Bottom: Pregenual cingulate cortex. Conventions as above. Right: The parameter estimates were significantly different for the pregenual cingulate cortex  $t = 8.70$ ,  $df = 11$ ,  $p < 10^{-5}$ . Left: The correlation between the pleasantness ratings and the activation (% BOLD change) at the specified coordinate ( $r = 0.89$ ,  $df = 8$ ,  $p = 0.001$ ). The taste stimulus, 0.1 M MSG, was identical on all trials. After Grabenhorst, F. and Rolls, E. T. (2008) Selective attention to affective value alters how the brain processes taste stimuli. *European Journal of Neuroscience*, 27, 723–729.

convergence are found is in an agranular part of what cytoarch-itecturally is the insula (Ia) that is topologically found in the posterior OFC, though it is anterior to the insular taste cortex and posterior to the granular OFC (see Figure 2; de Araujo, Rolls, Kringelbach, McGlone, & Phillips, 2003).

McCabe and Rolls (2007) had shown that the convergence of taste and olfactory information appears to be important for the delicious flavor of umami. They showed that when glutamate is given in combination with a consonant, savory, odor (vegetable), the resulting flavor can be much more pleasant than the glutamate taste or vegetable odor alone and that this reflected

activations in the pregenual cingulate cortex and medial OFC. The principle is that certain sensory combinations can produce very pleasant food stimuli, which may of course be important in driving food intake, and that these combinations are formed in the brain far beyond the taste or olfactory receptors (Rolls, 2009).

To assess how satiety influences the brain activations to a whole food that produces taste, olfactory, and texture stimulation, we measured brain activation by whole foods before and after the food is eaten to satiety. The food eaten to satiety was either chocolate milk or tomato juice. A decrease in activation by the food eaten to satiety relative to the other food was found in

the OFC (Kringelbach, O'Doherty, Rolls, & Andrews, 2003) but not in the primary taste cortex. This study provided evidence that the pleasantness of the flavor of food and sensory-specific satiety that is an important component of appetite and the control of food intake (Rolls, 2014) are represented in the OFC.

### Oral Viscosity and Fat Texture

The viscosity of food in the mouth is represented in the human primary taste cortex (in the anterior insula) and also in a mid-insular area that is not taste cortex, but that represents oral somatosensory stimuli (de Araujo & Rolls, 2004). Oral viscosity is also represented in the human orbitofrontal and perigenual cingulate cortices, and it is notable that the perigenual cingulate cortex, an area in which many pleasant stimuli are represented, is strongly activated by the texture of fat in the mouth and also by oral sucrose (de Araujo & Rolls, 2004). We have shown that the pleasantness and reward value of fat texture are represented in the mid OFC and ACC, where activations are correlated with the subjective pleasantness of oral fat texture (Grabenhorst, Rolls, Parris, & D'Souza, 2010; Rolls, 2009, 2010b; Figure 3). This provides a foundation for studies of whether activations in the fat reward system are heightened in people who tend to become obese (Rolls, 2012a). Interestingly, high-fat stimuli with a pleasant flavor increase the coupling of activations between the OFC and the somatosensory cortex, suggesting a role for the somatosensory cortex in processing the sensory properties of food in the mouth (Grabenhorst & Rolls, 2013).

### The Sight of Food

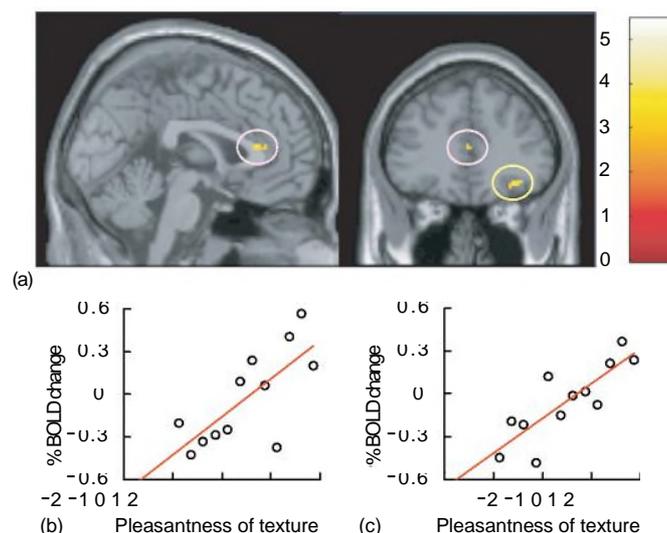
O'Doherty, Deichmann, Critchley, and Dolan (2002) showed that visual stimuli associated with the taste of glucose activated the OFC and some connected areas, consistent with the primate neurophysiology. Simmons et al. (2005) found that showing pictures of foods, compared to pictures of places,

can also activate the OFC. Similarly, the OFC and connected areas were also found to be activated after presentation of food stimuli to food-deprived subjects (Wang et al., 2004).

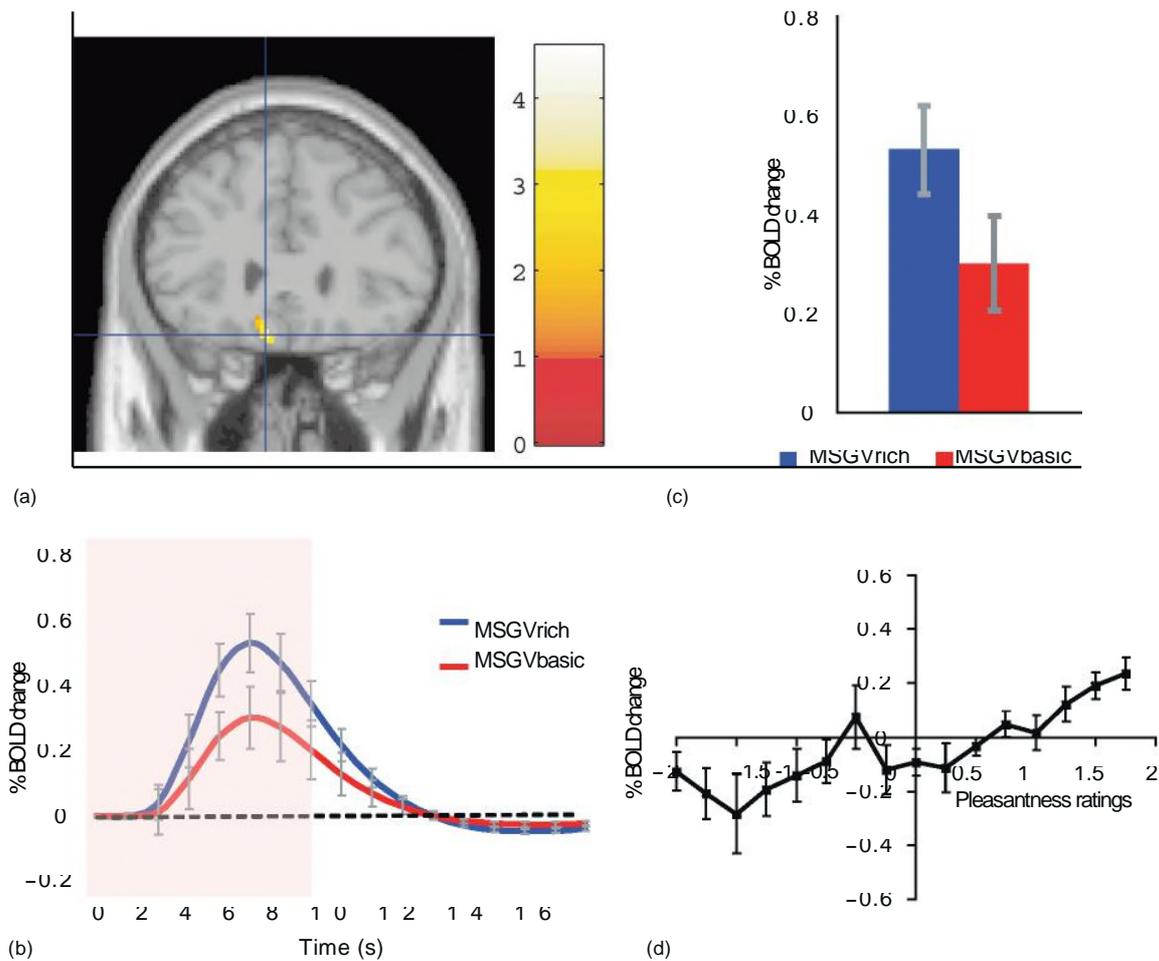
### Top-Down Cognitive Effects on Taste, Olfactory, and Flavor Processing

To what extent does cognition influence the hedonics of food-related stimuli, and how far down into the sensory system does the cognitive influence reach? To address this, we performed an fMRI investigation in which the delivery of a standard test odor (isovaleric acid combined with cheddar cheese odor, presented orthonasally using an olfactometer) was paired with a descriptor word on a screen, which on different trials was 'Cheddar cheese' or 'Body odor.' Participants rated the affective value of the test odor as significantly more pleasant when labeled 'Cheddar cheese' than when labeled 'Body odor,' and these effects reflected activations in the medial OFC/rostral ACC that had correlations with the pleasantness ratings (de Araujo, Rolls, Velasco, Margot, & Cayeux, 2005). The implication is that cognitive factors can have profound effects on our responses to the hedonic and sensory properties of food, in that these effects are manifest quite far down into sensory and hedonic processing (in the OFC, see Figure 1), so that hedonic representations of odors are affected (de Araujo et al., 2005).

Similar cognitive effects and mechanisms have now been found for the taste and flavor of food, where the cognitive word-level descriptor was, for example, 'rich delicious flavor' and activations to flavor were increased in the OFC and regions to which it projects including the perigenual cingulate cortex and ventral striatum, but were not influenced in the insular primary taste cortex where activations reflected the intensity (concentration) of the stimuli (Grabenhorst, Rolls, & Parris, 2008; see Figure 4).



**Figure 3** Brain regions in which the activations were correlated with the subjective pleasantness of fat texture: Mid-OFC ( $[32\ 34\ -14]$   $z^1_{,3.38}$   $p^1_{,0.013}$ ) (a, yellow circle, and c showing the relation between the % change in the BOLD signal and the rating of the pleasantness of the texture) and anterior cingulate cortex ( $[2\ 30\ 14]$   $z^1_{,3.22}$   $p^1_{,0.016}$ ) (a, pink circles, and b). After Grabenhorst, F., Rolls, E. T., Parris, B. A., & D'Souza, A. (2010). How the brain represents the reward value of fat in the mouth. *Cerebral Cortex*, 20, 1082–1091.



**Figure 4** Cognitive modulation of flavor reward processing in the brain. (a) The medial orbitofrontal cortex (OFC) was more strongly activated when a flavor stimulus was labeled 'rich and delicious flavor' (MSGVrich) than when it was labeled 'boiled vegetable water' (MSGVbasic) ( $[-8\ 28\ -20]$ ). (The flavor stimulus, MSGV, was the taste 0.1 M MSG + 0.005 M inosine 5'-monophosphate combined with a consonant 0.4% vegetable odor.) (b) The time course of the BOLD signals for the two conditions. (c) The peak values of the BOLD signal (mean across subjects  $\pm$  sem) were significantly different ( $t = 3.06$ ,  $df = 11$ ,  $p = 0.01$ ). (d) The BOLD signal in the medial OFC was correlated with the subjective pleasantness ratings of taste and flavor, as shown by the SPM analysis and as illustrated (mean across subjects  $\pm$  sem,  $r = 0.86$ ,  $p < 0.001$ ). After Grabenhorst, F., Rolls, E. T., & Parris, B. A. (2008). From affective value to decision-making in the prefrontal cortex. *European Journal of Neuroscience*, 28, 1930–1939.

### Effects of Selective Attention to Affective Value Versus Intensity on Representations of Taste, Olfactory, and Flavor Processing

We have found that with taste, flavor, and olfactory food-related stimuli, selective attention to pleasantness modulates representations in the OFC (see Figure 2), whereas selective attention to intensity modulates activations in areas such as the primary taste cortex (Grabenhorst & Rolls, 2008; Rolls et al., 2008). Thus, depending on the context in which tastes and odors are presented and whether affect is relevant, the brain responds to a taste, odor, or flavor differently. These findings show that when attention is paid to affective value, the brain systems engaged to represent the stimulus are different from those engaged when attention is directed to the physical properties of a stimulus such as its intensity.

The source of the top-down modulation by attention of the OFC appears to be the lateral prefrontal cortex, as shown by

psychophysiological interaction analyses (Grabenhorst & Rolls, 2010) and by Granger causality analyses (Ge, Feng, Grabenhorst, & Rolls, 2012; Luo, Ge, Grabenhorst, Feng, & Rolls, 2013). The mechanism probably involves a weak top-down biased competition effect on the taste and olfactory processing (Deco & Rolls, 2005; Desimone & Duncan, 1995; Rolls, 2008b). Because whole streams of cortical processing are influenced (OFC and cingulate cortex, and even their coupling to the primary taste cortex, by pleasantness-related processing and insular taste cortex and the midinsula by intensity-related processing Grabenhorst & Rolls, 2010; Luo et al., 2013), the process has been described as a biased activation model of attention (Grabenhorst & Rolls, 2010; Rolls, 2013).

This differential biasing by prefrontal cortex attentional mechanisms (Ge et al., 2012; Grabenhorst & Rolls, 2010) of brain regions engaged in processing a sensory stimulus depending on whether the cognitive demand is for affect-related versus more sensory-related processing may be an important aspect of

cognition and attention that have implications for how strongly the reward system is driven by food and thus for eating and the control of appetite (Grabenhorst & Rolls, 2008, 2011; Rolls, 2012a; Rolls et al., 2008). The top-down modulations of processing have many implications for the investigations of taste, olfactory, and other sensory processing and for the development of new food and perfumery products.

### Beyond Reward Value to Decision-Making

Representations of the reward value of food, and their subjective correlate the pleasantness of food, are fundamental in determining appetite and processes such as economic decision-making (Padoa-Schioppa, 2011; Padoa-Schioppa & Cai, 2011; Rolls, 2005a, 2014). But after the reward evaluation, a decision has to be made about whether to seek for and consume the reward. We are now starting to understand how the brain takes decisions as described in *The Noisy Brain* (Rolls & Deco, 2010) and *Emotion and Decision-Making Explained* (Rolls, 2014), and this has implications for whether a reward of a particular value will be selected (Deco, Rolls, Albantakis, & Romo, 2013; Grabenhorst & Rolls, 2011; Rolls, 2008b, 2011b, 2014; Rolls & Deco, 2010; Rolls & Grabenhorst, 2008).

A tier of processing beyond the OFC, in the medial prefrontal cortex area 10, becomes engaged when choices are made between odor stimuli based on their pleasantness (Grabenhorst, Rolls, & Bilderbeck, 2008; Rolls, Critchley, Verhagen, & Kadohisa, 2010; Rolls, Grabenhorst, & Deco, 2010b; tier 3 in Figure 1). The choices are made by a local attractor network in which the winning attractor represents the decision, with each possible attractor representing a different choice and each attractor receiving inputs that reflect the evidence for that choice. The attractor network is formed in a part of the cerebral cortex by strengthening of the recurrent collateral excitatory synapses between nearby pyramidal cells. One group of neurons with strengthened synapses between its members can form a stable attractor with high firing rates, which competes through inhibitory interneurons with other possible attractors formed by other groups of excitatory neurons (Rolls, 2008b, 2010a). The word attractor refers to the fact that inexact inputs are attracted to one of the states of high firing that are specified by the synaptic connections between the different groups of neurons. The result in this nonlinear system is that one attractor wins, and this implements a mechanism for decision-making with one winner (Deco et al., 2013; Rolls, 2008b, 2014; Rolls & Deco, 2010; Wang, 2008). The decisions are probabilistic as they reflect the noise in the competitive nonlinear decision-making process that is introduced by the random spiking times of neurons for a given mean rate that reflect a Poisson process (Rolls & Deco, 2010; Rolls, Grabenhorst, & Deco, 2010a). The costs of each reward need to be subtracted from the value of each reward to produce a net reward value for each available reward before the decision is taken (Grabenhorst & Rolls, 2011; Rolls, 2008b; Rolls & Grabenhorst, 2008). The reasoning or rational system with its long-term goals (introducing evidence such as “scientific studies have shown that fish oils rich in omega 3 may reduce the probability of Alzheimer’s disease”) then competes with the rewards such as the pleasant flavor of food (which are gene-specified (Rolls, 2005a, 2014), though subject to conditioned

effects (Booth, 1985; Rolls, 2005a)) in a further decision process that may itself be subject to noise (Rolls, 2005a, 2008b; Rolls & Deco, 2010). This can be described as a choice between the selfish phenotype (standing for phenotype) and the selfish gene (Rolls, 2011b, 2012b, 2014). In this context, the findings described here that the cognitive system can have a top-down influence on the reward system are important advances in our understanding of how these decisions are reached.

### Synthesis

These investigations show that a principle of brain function is that representations of the reward/hedonic value and pleasantness of sensory including food-related stimuli are formed separately from representations of what the stimuli are. The pleasantness/reward value is represented in areas such as the OFC and pregenual cingulate cortex, and it is here that hunger/satiety signals modulate the representations of food to make them implement reward. The satiety signals that help in this modulation may reach the OFC from the hypothalamus, and in turn, the OFC projects to the hypothalamus where neurons are found that respond to the sight, smell, and taste of food if hunger is present (Rolls, 2014; Rolls & Grabenhorst, 2008). We have seen earlier some of the principles that help to make the food pleasant, including particular combinations of taste, olfactory, texture, visual, and cognitive inputs.

A hypothesis is developed elsewhere that obesity is associated in part with overstimulation of these reward systems by very rewarding combinations of taste, odor, texture, visual, and cognitive inputs (Rolls, 2005a, 2011a, 2012a, 2014).

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### References

- Booth, D. A. (1985). Food-conditioned eating preferences and aversions with interoceptive elements: Learned appetites and satieties. *Annals of the New York Academy of Sciences*, 443, 22–37.
- de Araujo, I. E. T., Kringelbach, M. L., Rolls, E. T., & Hobden, P. (2003). The representation of umami taste in the human brain. *Journal of Neurophysiology*, 90, 313–319.
- de Araujo, I. E. T., Kringelbach, M. L., Rolls, E. T., & McGlone, F. (2003). Human cortical responses to water in the mouth, and the effects of thirst. *Journal of Neurophysiology*, 90, 1865–1876.
- de Araujo, I. E. T., & Rolls, E. T. (2004). The representation in the human brain of food texture and oral fat. *Journal of Neuroscience*, 24, 3086–3093.
- de Araujo, I. E. T., Rolls, E. T., Kringelbach, M. L., McGlone, F., & Phillips, N. (2003). Taste-olfactory convergence, and the representation of the pleasantness of flavour, in the human brain. *European Journal of Neuroscience*, 18, 2059–2068.
- de Araujo, I. E. T., Rolls, E. T., Velazco, M. I., Margot, C., & Cayeux, I. (2005). Cognitive modulation of olfactory processing. *Neuron*, 46, 671–679.

- Deco, G., & Rolls, E. T. (2005). Neurodynamics of biased competition and co-operation for attention: A model with spiking neurons. *Journal of Neurophysiology*, 94, 295–313.
- Deco, G., Rolls, E. T., Albantakis, L., & Romo, R. (2013). Brain mechanisms for perceptual and reward-related decision-making. *Progress in Neurobiology*, 103, 194–213.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222.
- Francis, S., Rolls, E. T., Bowtell, R., McGlone, F., O'Doherty, J., Browning, A., et al. (1999). The representation of pleasant touch in the brain and its relationship with taste and olfactory areas. *Neuroreport*, 10, 453–459.
- Ge, T., Feng, J., Grabenhorst, F., & Rolls, E. T. (2012). Componential Granger causality, and its application to identifying the source and mechanisms of the top-down biased activation that controls attention to affective vs. sensory processing. *NeuroImage*, 59, 1846–1858.
- Gottfried, J. A. (2013). Structural and functional imaging of the human olfactory system. In R. L. Doty (Ed.), *Handbook of Olfaction and Gustation* (3rd ed.). New York: Wiley-Liss.
- Grabenhorst, F., & Rolls, E. T. (2008). Selective attention to affective value alters how the brain processes taste stimuli. *European Journal of Neuroscience*, 27, 723–729.
- Grabenhorst, F., & Rolls, E. T. (2010). Attentional modulation of affective vs sensory processing: Functional connectivity and a top-down biased activation theory of selective attention. *Journal of Neurophysiology*, 104, 1649–1660.
- Grabenhorst, F., & Rolls, E. T. (2011). Value, pleasure, and choice in the ventral prefrontal cortex. *Trends in Cognitive Sciences*, 15, 56–67.
- Grabenhorst, F., & Rolls, E. T. (2013). The representation of oral fat texture in the human somatosensory cortex. *Human Brain Mapping*, 35(6), 2521–2530.
- Grabenhorst, F., Rolls, E. T., & Bilderbeck, A. (2008). How cognition modulates affective responses to taste and flavor: Top down influences on the orbitofrontal and pregenual cingulate cortices. *Cerebral Cortex*, 18, 1549–1559.
- Grabenhorst, F., Rolls, E. T., Margot, C., da Silva, M. A. A. P., & Velazco, M. I. (2007). How pleasant and unpleasant stimuli combine in different brain regions: Odor mixtures. *Journal of Neuroscience*, 27, 13532–13540.
- Grabenhorst, F., Rolls, E. T., & Parris, B. A. (2008). From affective value to decision-making in the prefrontal cortex. *European Journal of Neuroscience*, 28, 1930–1939.
- Grabenhorst, F., Rolls, E. T., Parris, B. A., & D'Souza, A. (2010). How the brain represents the reward value of fat in the mouth. *Cerebral Cortex*, 20, 1082–1091.
- Kadohisa, M., Rolls, E. T., & Verhagen, J. V. (2005). Neuronal representations of stimuli in the mouth: The primate insular taste cortex, orbitofrontal cortex, and amygdala. *Chemical Senses*, 30, 401–419.
- Kringelbach, M. L., O'Doherty, J., Rolls, E. T., & Andrews, C. (2003). Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness. *Cerebral Cortex*, 13, 1064–1071.
- Luo, Q., Ge, T., Grabenhorst, F., Feng, J., & Rolls, E. T. (2013). Attention-dependent modulation of cortical taste circuits revealed by Granger causality with signal-dependent noise. *PLoS Computational Biology*, 9, e1003265.
- McCabe, C., & Rolls, E. T. (2007). Umami: A delicious flavor formed by convergence of taste and olfactory pathways in the human brain. *European Journal of Neuroscience*, 25, 1855–1864.
- O'Doherty, J. P., Deichmann, R., Critchley, H. D., & Dolan, R. J. (2002). Neural responses during anticipation of a primary taste reward. *Neuron*, 33, 815–826.
- O'Doherty, J., Rolls, E. T., Francis, S., Bowtell, R., & McGlone, F. (2001). The representation of pleasant and aversive taste in the human brain. *Journal of Neurophysiology*, 85, 1315–1321.
- O'Doherty, J., Rolls, E. T., Francis, S., Bowtell, R., McGlone, F., Kobal, G., et al. (2000). Sensory-specific satiety related olfactory activation of the human orbitofrontal cortex. *Neuroreport*, 11, 893–897.
- Padoa-Schioppa, C. (2011). Neurobiology of economic choice: A good-based model. *Annual Review of Neuroscience*, 34, 333–359.
- Padoa-Schioppa, C., & Cai, X. (2011). The orbitofrontal cortex and the computation of subjective value: Consolidated concepts and new perspectives. *Annals of the New York Academy of Sciences*, 1239, 130–137.
- Poellinger, A., Thomas, R., Lio, P., Lee, A., Makris, N., Rosen, B. R., et al. (2001). Activation and habituation in olfaction – An fMRI study. *NeuroImage*, 13, 547–560.
- Rolls, E. T. (2005a). *Emotion explained*. Oxford: Oxford University Press.
- Rolls, E. T. (2005b). Taste, olfactory, and food texture processing in the brain, and the control of food intake. *Physiology and Behavior*, 85, 45–56.
- Rolls, E. T. (2008a). Functions of the orbitofrontal and pregenual cingulate cortex in taste, olfaction, appetite and emotion. *Acta Physiologica Hungarica*, 95, 131–164.
- Rolls, E. T. (2008b). *Memory, attention, and decision-making: A unifying computational neuroscience approach*. Oxford: Oxford University Press.
- Rolls, E. T. (2009). Functional neuroimaging of umami taste: What makes umami pleasant. *American Journal of Clinical Nutrition*, 90, 803S–814S.
- Rolls, E. T. (2010a). Attractor networks. *WIREs Cognitive Science*, 1, 119–134.
- Rolls, E. T. (2010b). Neural representation of fat texture in the mouth. In J.-P. Montmayeur, & L. J. Coutre (Eds.), *Fat detection: Taste, texture, and postingestive effects* (pp. 197–223). Boca Raton, FL: CRC Press.
- Rolls, E. T. (2011a). Taste, olfactory, and food texture reward processing in the brain and obesity. *International Journal of Obesity*, 35, 550–561.
- Rolls, E. T. (2011b). Consciousness, decision-making, and neural computation. In V. Cutsuridis, A. Hussain, & J. G. Taylor (Eds.), *Perception-action cycle: Models, algorithms and systems* (pp. 287–333). Berlin: Springer.
- Rolls, E. T. (2012a). Taste, olfactory, and food texture reward processing in the brain and the control of appetite. *Proceedings of the Nutrition Society*, 71, 488–501.
- Rolls, E. T. (2012b). *Neuroculture. On the implications of brain science*. Oxford: Oxford University Press.
- Rolls, E. T. (2013). A biased activation theory of the cognitive and attentional modulation of emotion. *Frontiers in Human Neuroscience*, 7(74), 1–15.
- Rolls, E. T. (2014). *Emotion and decision-making explained*. Oxford: Oxford University Press.
- Rolls, E. T. (2015). Central neural integration of taste, smell and other sensory modalities. In R. L. Doty (Ed.), *Handbook of olfaction and gustation: Modern perspectives* (3rd ed.). New York: Dekker.
- Rolls, E. T., Critchley, H. D., Verhagen, J. V., & Kadohisa, M. (2010). The representation of information about taste and odor in the orbitofrontal cortex. *Chemosensory Perception*, 3, 16–33.
- Rolls, E. T., & Deco, G. (2010). *The noisy brain: Stochastic dynamics as a principle of brain function*. Oxford: Oxford University Press.
- Rolls, E. T., & Grabenhorst, F. (2008). The orbitofrontal cortex and beyond: From affect to decision-making. *Progress in Neurobiology*, 86, 216–244.
- Rolls, E. T., Grabenhorst, F., & Deco, G. (2010a). Decision-making, errors, and confidence in the brain. *Journal of Neurophysiology*, 104, 2359–2374.
- Rolls, E. T., Grabenhorst, F., & Deco, G. (2010b). Choice, difficulty, and confidence in the brain. *NeuroImage*, 53, 694–706.
- Rolls, E. T., Grabenhorst, F., & Franco, L. (2009). Prediction of subjective affective state from brain activations. *Journal of Neurophysiology*, 101, 1294–1308.
- Rolls, E. T., Grabenhorst, F., Margot, C., da Silva, M. A. A. P., & Velazco, M. I. (2008). Selective attention to affective value alters how the brain processes olfactory stimuli. *Journal of Cognitive Neuroscience*, 20, 1815–1826.
- Rolls, E. T., Grabenhorst, F., & Parris, B. A. (2010). Neural systems underlying decisions about affective odors. *Journal of Cognitive Neuroscience*, 22, 1069–1082.
- Rolls, E. T., Kringelbach, M. L., & de Araujo, I. E. T. (2003). Different representations of pleasant and unpleasant odors in the human brain. *European Journal of Neuroscience*, 18, 695–703.
- Rolls, E. T., & Scott, T. R. (2003). Central taste anatomy and neurophysiology. In R. L. Doty (Ed.), *Handbook of olfaction and gustation* (2nd ed., pp. 679–705). New York: Dekker.
- Rolls, E. T., & Treves, A. (2011). The neuronal encoding of information in the brain. *Progress in Neurobiology*, 95, 448–490.
- Rolls, E. T., Yaxley, S., & Sienkiewicz, Z. J. (1990). Gustatory responses of single neurons in the caudolateral orbitofrontal cortex of the macaque monkey. *Journal of Neurophysiology*, 64, 1055–1066.
- Scott, T. R., & Small, D. M. (2009). The role of the parabrachial nucleus in taste processing and feeding. *Annals of the New York Academy of Sciences*, 1170, 372–377.
- Simmons, W. K., Martin, A., & Barsalou, L. W. (2005). Pictures of appetizing foods activate gustatory cortices for taste and reward. *Cerebral Cortex*, 15, 1602–1608.
- Small, D. M. (2010). Taste representation in the human insula. *Brain Structure and Function*, 214, 551–561.
- Small, D. M., & Prescott, J. (2005). Odor/taste integration and the perception of flavor. *Experimental Brain Research*, 166, 345–357.
- Small, D. M., & Scott, T. R. (2009). Symposium overview: What happens to the pontine processing? Repercussions of interspecies differences in pontine taste representation for tasting and feeding. *Annals of the New York Academy of Sciences*, 1170, 343–346.
- Small, D. M., Voss, J., Mak, Y. E., Simmons, K. B., Parrish, T., & Gitelman, D. (2004). Experience-dependent neural integration of taste and smell in the human brain. *Journal of Neurophysiology*, 92, 1892–1903.
- Sobel, N., Prabhakaran, V., Zhao, Z., Desmond, J. E., Glover, G. H., Sullivan, E. V., et al. (2000). Time course of odorant-induced activation in the human primary olfactory cortex. *Journal of Neurophysiology*, 83, 537–551.
- Wang, X. J. (2008). Decision making in recurrent neuronal circuits. *Neuron*, 60, 215–234.

- Wang, G. J., Volkow, N. D., Telang, F., Jayne, M., Ma, J., Rao, M., et al. (2004). Exposure to appetitive food stimuli markedly activates the human brain. *NeuroImage*, 21, 1790–1797.
- Wise, S. P. (2008). Forward frontal fields: Phylogeny and fundamental function. *Trends in Neurosciences*, 31, 599–608.
- Zald, D. H., Hagen, M. C., & Pardo, J. V. (2002). Neural correlates of tasting concentrated quinine and sugar solutions. *Journal of Neurophysiology*, 87, 1068–1075.
- Zald, D. H., Lee, J. T., Fluegel, K. W., & Pardo, J. V. (1998). Aversive gustatory stimulation activates limbic circuits in humans. *Brain*, 121, 1143–1154.
- Zald, D. H., & Pardo, J. V. (1997). Emotion, olfaction, and the human amygdala: Amygdala activation during aversive olfactory stimulation. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 4119–4124.
- Zatorre, R. J., Jones-Gotman, M., Evans, A. C., & Meyer, E. (1992). Functional localization of human olfactory cortex. *Nature*, 360, 339–340.