Taste and Smell, Psychology of

Edmund T Rolls, Oxford Centre for Computational Neuroscience, Oxford, UK; and University of Warwick, Coventry, UK

In International Encyclopedia of the Social & Behavioral Sciences, 2nd edition, Vol 24. Oxford: Elsevier. pp. 26–31, James D. Wright (editor-in-chief),.ISBN: 9780080970868. Copyright © 2015 Elsevier Ltd.

Abstract

There are five types of taste receptor cell, sweet, salt, bitter, sour, and umami (protein taste). There are 1000 olfactory receptor genes each specifying a different type of receptor each for a set of odors. Tastes are primary, unlearned, rewards and punishers, and are important in emotion. Pheromones and some other olfactory stimuli are primary reinforcers, but for many odors the reward value is learned by stimulus–reinforcer association learning. The primary taste cortex in the anterior insula provides separate and combined representations of the taste, temperature, and texture (including fat texture) of food in the mouth independently of hunger and thus of reward value and pleasantness. One synapse on, in the orbitofrontal cortex, these sensory inputs are for some neurons combined by learning with olfactory and visual inputs, and these neurons encode food reward value in that they only respond to food when hungry, and in that activations correlate with subjective pleasantness. Cognitive factors, including word-level descriptions, and attention, modulate the representation of the reward value of taste, odor, and flavor in the orbitofrontal cortex and a region to which it projects, the anterior cingulate cortex. Further, there are individual differences in the representation of the reward value of food in the orbitofrontal cortex. Overeating and obesity are related in many cases to an increased reward value of the sensory inputs produced by foods, and their modulation by cognition and attention that override existing satiety signals.

Rapid advances have been made recently in understanding the receptors for taste and smell, the neural systems for taste and smell, the separation of sensory from hedonic processing of taste and smell, and how taste and smell and also the texture of food are important in the palatability of food and appetite control. Emphasis is placed on these advances.

Taste and Olfactory Receptors

Taste receptors. There are receptors on the tongue for sweet, salt, bitter, sour, and the fifth taste, umami as exemplified by monosodium glutamate (Chandrashekar et al., 2006; Chaudhari and Roper, 2010). Umami taste is found in a diversity of foods rich in glutamate like fish, meat, human mothers' milk, tomatoes and some vegetables, and is enhanced by some ribonucleotides (including inosine and guanosine nucleotides), which are present in, for example, meat and some fish. The mixture of these umami components, which act synergistically at the receptor, underlies the rich taste characteristic of many cuisines (Rolls, 2009).

Olfactory receptors. There are approximately 1000 different types of odor receptor each coded for by a different gene (Buck and Bargmann, 2013). This is a significant proportion of the total number of genes in humans, which is in the order of 30 000. This is a simple but genetically expensive way to build specificity into a sensory system. In humans, only approximately one-third of these receptor types are used, with stop codes in the majority of the olfactory receptor genes. This may reflect the greater reliance of primates including humans on stimuli in other sensory modalities, especially vision and hearing.

In addition to this main olfactory system using the main olfactory epithelium and its connections to the main olfactory bulb, there is an accessory olfactory system with its peripheral receptors located in the vomeronasal organ (VNO), which projects to the accessory olfactory bulb. This system is involved in the detection of pheromones, present, for example, in urinary volatiles, which are used for mate attraction, territory marking, etc (Wyatt, 2014). The VNOs of humans and Old World monkeys are nonfunctional, although pheromones or pheromone-like substances acting through the main olfactory system may be involved in social and reproductive behavior in these species.

Taste, Smell, Reward, and Emotion

Emotions can be defined as states elicited by rewards and punishers (Rolls, 2014). A reward is any stimulus or event for which an animal (and that includes humans) will work for (i.e., learn and perform an action instrumental in obtaining the reward), and a punisher is any stimulus or event that an animal to work to escape from or avoid. All tastes are primary, unlearned, reinforcers. For example, animals show that a sweet taste (if hungry) and a salt taste (if salt deprived) are rewards the first time that taste is made available. Animals will similarly reject bitter tastes (which are generally produced by plants for exactly that function). Taste is thus very important in emotion, for it serves as an unlearned reward or punisher. Other primary reinforcers include soft pleasant touch, and pain, with many other examples provided in *Emotion and Decision-Making Explained* (Rolls, 2014).

Emotions, as states elicited by instrumental reinforcers (e.g., a warm pleasant feeling produced by a soft caressing touch), can thus be seen to provide an evolutionary adaptive value account of why genes, for example, taste receptor genes, code for the reward or punisher value of some stimuli. Genes do this in their own selfish interests, and making a particular taste such as sweet rewarding is very adaptive, for this is much simpler and more flexible than a gene that tries to specify a response such as climbing a tree, picking an apple, and placing it in the mouth. By specifying rewards and punishers, the genes that provide a foundation for emotion are thus acting in their own selfish interests (Rolls, 2014). Tastes are thus important in many emotional and related states, such as the pleasantness of the taste of sweet.

Some olfactory stimuli are primary reinforcers, including pheromones, and some odors such as perhaps the smell of ripe fruit, and the smell of rotting food. An interesting example is that the odors of some individuals may be pleasant because of major histocompatibility complex genes, which specify olfactory receptors that signal reward produced be the smell of another individual with different immune system. The adaptive value is that offspring produced with an individual with a different immune system may have more diverse immune systems, and thereby greater resistance to disease. However, many odors only become reinforcers by a learned, stimulus–reinforcer association. An example is that the odor of the cheese brie may be initially unpleasant, but may become pleasant after learned association with its taste and fatty texture. (Fatty texture may be a primary reinforcer because it is an indicator of a high-energy value food.)

These concepts help to show how taste and smell are closely linked to reward value and emotion. A broad perspective on emotion and the pleasantness of sensory stimuli including taste and smell is provided in *Emotion and Decision-Making Explained* (Rolls, 2014).

We now turn to consider how taste and smell, and their functions related to reward value and subjective pleasantness, are implemented in the brain, again an area in which rapid progress is being made.

Taste Processing in the Brain

Pathways

A diagram of the taste and related olfactory, somatosensory, and visual pathways in primates is shown in Figure 1, as the focus of this article is on processing relevant to humans. (The pathways involved in taste in rodents are quite different, with subcortical connections to a pontine taste area, with no granular orbitofrontal cortex so that other areas are more involved in the processing, and with hunger modulating taste processing even in the brain stem (Rolls, 2014).) The multimodal convergence that enables single neurons to respond to different combinations of taste, olfactory, texture, temperature, and visual inputs to represent different flavors produced often by new combinations of sensory input is a theme of recent research that will be described, as is the separation in primates including humans of processing of what the taste is (in the primary taste cortex) from its reward value and pleasantness (in the orbitofrontal cortex and anterior cingulate cortex).

The Primary Taste Cortex

Rolls and colleagues have shown that the primary taste cortex in the primate anterior insula and adjoining frontal operculum contains not only taste neurons tuned to sweet, salt, bitter, sour, and umami as exemplified by monosodium glutamate, but also other neurons that encode oral somatosensory stimuli including viscosity, fat texture, temperature, and capsaicin. Some neurons in the primary taste cortex respond to particular combinations of taste and oral texture stimuli, but do not respond to olfactory stimuli or visual stimuli such as the sight of food. Neurons in the primary taste cortex do not represent the reward value of taste, that is the appetite for a food, in that their firing is not decreased to zero by feeding the taste to satiety (Rolls, 2012, 2014).

The Secondary Taste Cortex

A secondary cortical taste area in primates was discovered by Rolls et al. (1990) in the orbitofrontal cortex, extending several mm in front of the primary taste cortex. Different neurons in this region respond not only to each of the four classical prototypical tastes sweet, salt, bitter, and sour, but also to umami tastants such as glutamate (which is present in many natural foods such as tomatoes, mushrooms, milk) and inosine monophosphate (which is present in meat and some fish such as tuna). This evidence, taken together with the identification of glutamate taste receptors (Zhao et al., 2003; Maruyama et al., 2006), leads to the view that there are five prototypical types of taste information channels, with umami contributing, often in combination with corresponding olfactory inputs, to the flavor of protein. In addition, some neurons respond to water and others to somatosensory stimuli including astringency as exemplified by tannic acid, and capsaicin (Rolls, 2012, 2014).

The Pleasantness of the Taste of Food, Sensory-Specific Satiety, and the Effects of Variety on Food Intake

The modulation of the reward value of a sensory stimulus such as the taste of food by motivational state, for example, hunger is one important way in which motivational behavior is controlled. The subjective correlate of this modulation is that food tastes pleasant when hungry, and tastes hedonically neutral when it has been eaten to satiety. Following Edmund Rolls' discovery of sensory-specific satiety revealed by the selective reduction in the responses of lateral hypothalamic neurons to a food eaten to satiety (Rolls, 1981; Rolls et al., 1986), it has been shown that this is implemented in a region that projects to the hypothalamus, the orbitofrontal (secondary taste) cortex, for the taste, odor, and sight of food (Rolls et al., 1989; Critchley and Rolls, 1996).

This evidence shows that the reduced acceptance of food that occurs when food is eaten to satiety, the reduction in the pleasantness of its taste and flavor, and the effects of variety to increase food intake, are produced in the orbito-frontal cortex, but not at earlier stages of processing where the responses reflect factors such as the intensity of the taste, which is little affected by satiety (Rolls and Grabenhorst, 2008; Rolls, 2012, 2014). In addition to providing an implementation of sensory-specific satiety (probably by habituation of the synaptic afferents to orbitofrontal

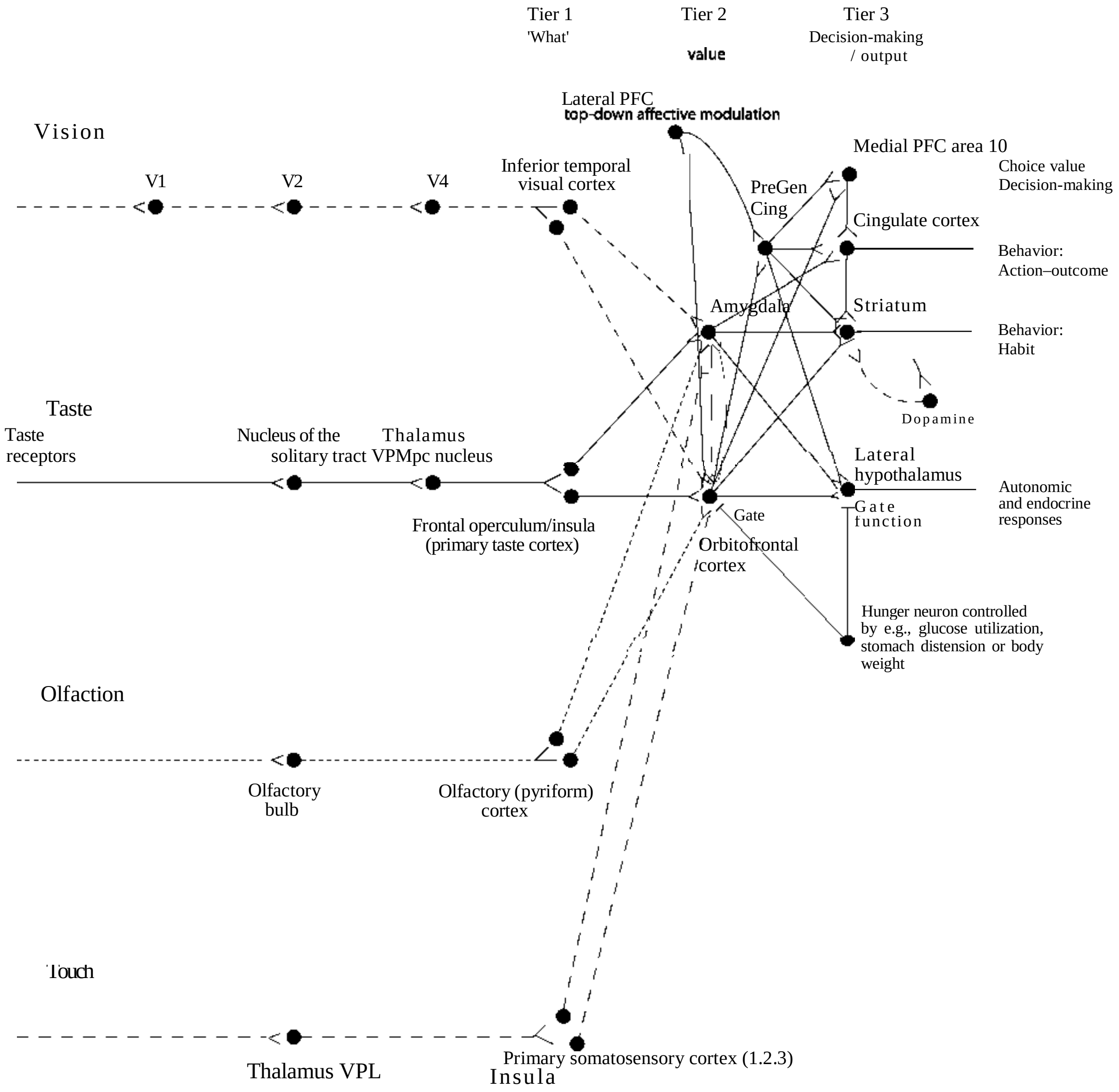

Figure 1 Schematic diagram showing some of the gustatory, olfactory, visual, and somatosensory pathways to the orbitofrontal cortex, and some of the outputs of the orbitofrontal cortex, in primates. The secondary taste cortex and the secondary olfactory cortex are within the orbitofrontal cortex. V1 - 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, E.T., 2005. Emotion Explained. Oxford University Press, Oxford.). 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, which are represented in the next tier of brain regions, the orbitofrontal cortex and amygdala, and in the anterior cingulate cortex. In areas beyond these such as medial prefrontal cortex area 10, choices or decisions about reward value are taken, with the mechanisms described elsewhere (Rolls, E.T., 2008. Memory, Attention, and Decision-making: A Unifying Computational Neuroscience Approach. Oxford University Press, Oxford; Rolls, E.T., Deco, G., 2010. The Noisy Brain: Stochastic Dynamics as a Principle of Brain Function. Oxford University Press, Oxford; Rolls, E.T., 2014. Emotion and Decision-making Explained. Oxford University Press, Oxford.). Medial PFC area 10 - medial prefrontal cortex area 10; VPMpc - ventralposteromedial thalamic nucleus (tasolfpaths6i.eps).

neurons with a time course of the order of the length of a course of a meal), it is likely that visceral and other satiety-related signals reach the orbitofrontal cortex (as indicated in **Figure 1**) (from the nucleus of the solitary tract, via thalamic and possibly hypothalamic nuclei) and there modulate the representation of food, resulting in an output that reflects the reward (or appetitive) value of each food.

The Representation of Flavor: Convergence of Olfactory, Taste, and Visual Inputs in the Orbitofrontal Cortex

Taste and olfactory pathways are brought together in the orbitofrontal cortex where flavor is formed by learned associations at the neuronal level between these inputs (see Figure 1). Visual inputs also become associated by learning in the orbitofrontal cortex with the taste of food to represent the sight of food and contribute to flavor. The visual and olfactory as well as the taste inputs represent the reward value of the food, as shown by sensory-specific satiety effects (Rolls, 2012, 2014).

The Texture of Food, Including Fat Texture

Some orbitofrontal cortex neurons have oral texture-related responses that encode parametrically the viscosity of food in the mouth (shown using a methyl cellulose series in the range 1-10 000 cP), others independently encode the particulate quality of food in the mouth, produced quantitatively, for example, by adding 20-100 mm microspheres to methyl cellulose (Rolls et al., 2003a), and others encode the oral texture of fat. Somatosensory signals that transmit information about capsaicin (chili) and astringency are also reflected in neuronal activity in these cortical areas.

Imaging Studies in Humans

Taste

In humans, it has been shown 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, and part of the orbitofrontal cortex, which is probably the secondary taste cortex. 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 orbitofrontal and anterior cingulate cortex represents the reward value of taste, in that activations there correlate with the subjective pleasantness of taste (Grabenhorst and Rolls, 2008; Grabenhorst et al., 2008).

We also found activation of the human amygdala by the taste of glucose. Indeed, the human amygdala is 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.

Odor

In humans, in addition to activation of the pyriform (olfactory) cortex, there is strong and consistent activation of the orbito-frontal cortex by olfactory stimuli, and this region appears to represent the pleasantness of odor. Further, pleasant odors tend to activate the medial, and unpleasant odors the more lateral, orbi-tofrontal cortex (Rolls et al., 2003b), adding to the evidence that it is a principle that there is a hedonic map in the orbitofrontal cortex, and also in the anterior cingulate cortex, which receives inputs from the orbitofrontal cortex (Rolls and Grabenhorst, 2008; Grabenhorst and Rolls, 2011). 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 orbitofrontal and anterior cingulate cortex represents the reward value of odor, in that activations there correlate with the subjective pleasantness of odor (Grabenhorstetal., 2007; Rolls and Grabenhorst, 2008; Grabenhorst and Rolls, 2011).

Olfactory-Taste Convergence to Represent Flavor, and the Influence of Satiety

Supradditive effects indicating convergence and interactions were found for taste (sucrose) and odor (strawberry) in the orbitofrontal and anterior cingulate cortex, and activations in these regions were correlated with the pleasantness ratings given by the participants (de Araujo et al., 2003). These results provide evidence on the neural substrate for the convergence of taste and olfactory stimuli to produce flavor in humans, and where the pleasantness of flavor is represented in the human brain.

McCabe and Rolls (2007) have 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 orbitofrontal cortex. 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, which produces taste, olfactory, and texture stimulation, we measured brain activation by whole foods before and after the food is eaten to satiety. The foods eaten to satiety were either chocolate milk, or tomato juice. A decrease in activation by the food eaten to satiety relative to the otherfood was found in the orbitofrontal cortex (Kringelbach et al., 2003) but not in the primary taste cortex. This study provided evidence that the pleasantness of the flavor of food and sensory-specific satiety, are represented in the orbitofrontal cortex.

Cognitive and Selective Attentional Effects on Representations of Smell, Taste, and Flavor

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 a 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 orbitofrontal cortex/rostral anterior cingulate cortex that had correlations with the pleasantness ratings (de Araujo et al., 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 processing, 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 orbitofrontal cortex and regions to which it projects including the pregenual 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 et al., 2008).

In addition, we have found that with taste, flavor, and olfactory food-related stimuli, selective attention to pleasantness modulates representations in the orbitofrontal cortex, whereas selective attention to intensity modulates activations in areas such as the primary taste cortex (Grabenhorst and 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 taste and odor 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. This differential biasing by prefrontal cortex attentional mechanisms (Grabenhorst and Rolls, 2010; Ge et al., 2012) 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, which have implications for how strongly the reward system is driven by food, and thus for eating and the control of appetite (Grabenhorst and Rolls, 2008, 2011; Rolls et al., 2008).

There are individual differences in the representation of the reward value of food, for example of chocolate, in the orbitofrontal cortex (Rolls and McCabe, 2007). Overeating and obesity may be related in many cases to an increased reward value of the sensory inputs produced by foods, and their modulation by cognition and attention, that override existing satiety signals. The findings described here thus have implications for understanding what causes obesity (Rolls, 2012, 2014).

Acknowledgments

This research was supported by the Medical Research Council. The participation of many colleagues in the studies cited is sincerely acknowledged.

See also: Emotion, Neural Basis of; Food Preferences, Psychology and Physiology of; Hunger and Eating, Neural Basis of; Olfactory System.

Bibliography

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.

Buck, L., Bargmann, C.I., 2013. Smell and taste: the chemical senses. In: Kandel, E.R., Schwartz, J.H., Jessell, T.H., Siegelbaum, S.A., Hudspeth, A.J. (Eds.), Principles of Neural Science, fifth ed. McGraw-Hill, New York, pp. 712-742.

Chandrashekar, J., Hoon, M.A., Ryba, N.J., Zuker, C.S., 2006. The receptors and cells for mammalian taste. Nature 444, 288-294.

Chaudhari, N., Roper, S.D., 2010. The cell biology of taste. The Journal of Cell Biology 190, 285-296.

Critchley, H.D., Rolls, E.T., 1996. Hunger and satiety modify the responses of olfactory and visual neurons in the primate orbitofrontal cortex. Journal of Neurophysiology 75, 1673-1686.

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.

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., 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.

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.

Maruyama, Y., Pereira, E., Margolskee, R.F., Chaudhari, N., Roper, S.D., 2006. Umami responses in mouse taste cells indicate more than one receptor. Journal of Neuroscience 26, 2227-2234.

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.

Rolls, E.T., 1981. Central nervous mechanisms related to feeding and appetite. British Medical Bulletin 37, 131-134.

Rolls, E.T., 2005. Emotion Explained. Oxford University Press, Oxford.

Rolls, E.T., 2008. Memory, Attention, and Decision-Making: A Unifying Computational Neuroscience Approach. Oxford University Press, Oxford.

Rolls, E.T., 2009. Functional neuroimaging of umami taste: what makes umami pleasant. American Journal of Clinical Nutrition 90, 803S-814S.

Rolls, E.T., 2012. 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., 2014. Emotion and Decision-Making Explained. Oxford University Press, Oxford.

Rolls, E.T., McCabe, C., 2007. Enhanced affective brain representations of chocolate in cravers vs non-cravers. European Journal of Neuroscience 26, 1067-1076.

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., Deco, G., 2010. The Noisy Brain: Stochastic Dynamics as a Principle of Brain Function. Oxford University Press, Oxford.

Rolls, E.T., Sienkiewicz, Z.J., Yaxley, S., 1989. Hunger modulates the responses to gustatory stimuli of single neurons in the caudolateral orbitofrontal cortex of the macaque monkey. European Journal of Neuroscience 1, 53-60.

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 Neuro-physiology 64, 1055-1066.

Rolls, E.T., Verhagen, J.V., Kadohisa, M., 2003a. Representations of the texture of food in the primate orbitofrontal cortex: neurons responding to viscosity, grittiness and capsaicin. Journal of Neurophysiology 90, 3711-3724.

Rolls, E.T., Kringelbach, M.L., de Araujo, I.E.T., 2003b. Different representations of pleasant and unpleasant odors in the human brain. European Journal of Neuroscience 18, 695-703.

Rolls, E.T., Murzi, E., Yaxley, S., Thorpe, S.J., Simpson, S.J., 1986. Sensory-specific satiety: food-specific reduction in responsiveness of ventral forebrain neurons after feeding in the monkey. Brain Research 368, 79–86.

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.

Wyatt, T.D., 2014. Pheromones and Animal Behavior, second ed. Cambridge University Press, Cambridge.

Zhao, G.Q., Zhang, Y., Hoon, M.A., Chandrashekar, J., Erlenbach, I., Ryba, N.J., Zuker, C.S., 2003. The receptors for mammalian sweet and umami taste. Cell 115, 255–266.