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4.26 The Representation of Flavor in the Brain

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Glossary

flavor A sensation produced by the combination of the taste, smell, and texture of food. *reward* A stimulus such as food for which an animal will work (see Rolls, E. T., 2005a).

sensory-specific satiety A reduction in the pleasantness of and appetite for a food that has been eaten to satiety in a meal which is partly specific to the food eaten in a meal.

umami The fifth taste, produced by the stimuli monosodium glutamate and 5′-ribonucleotides such as inosine monophosphate and guanosine monophosphate.

4.26.1 Taste Processing in the Primate Cortex

4.26.1.1 Pathways

A diagram of the taste and related olfactory, somatosensory, and visual pathways in primates is shown in Figure 1. Of particular interest is that in primates there is a direct projection from the rostral part of the nucleus of the solitary tract (NTS) to the taste thalamus and thus to the primary taste cortex in the frontal operculum and adjoining insula, with no pontine taste area and associated subcortical projections as in rodents (Norgren, R., 1984; Pritchard, T. C. *et al.*, 1986).This emphasis on cortical processing of taste in primates may be related to the great development of the cerebral cortex in primates, and the advantage of using extensive and similar cortical analysis of inputs from every sensory modality before the analyzed representations from each modality are brought together in multimodal regions to form representations of flavor.

4.26.1.2 The Primary and Secondary Taste Cortex

The primary taste cortex is in the rostral insula and adjacent frontal operculum (Pritchard, T. C. *et al.*, 1986). A secondary cortical taste area in primates was discovered by Rolls E. T. *et al.* (1990) in the caudolateral orbitofrontal cortex, extending several millimeters in front of the primary taste cortex, and also extending to more medial parts of the orbitofrontal cortex (Rolls, E. T. and Baylis, L. L., 1994).

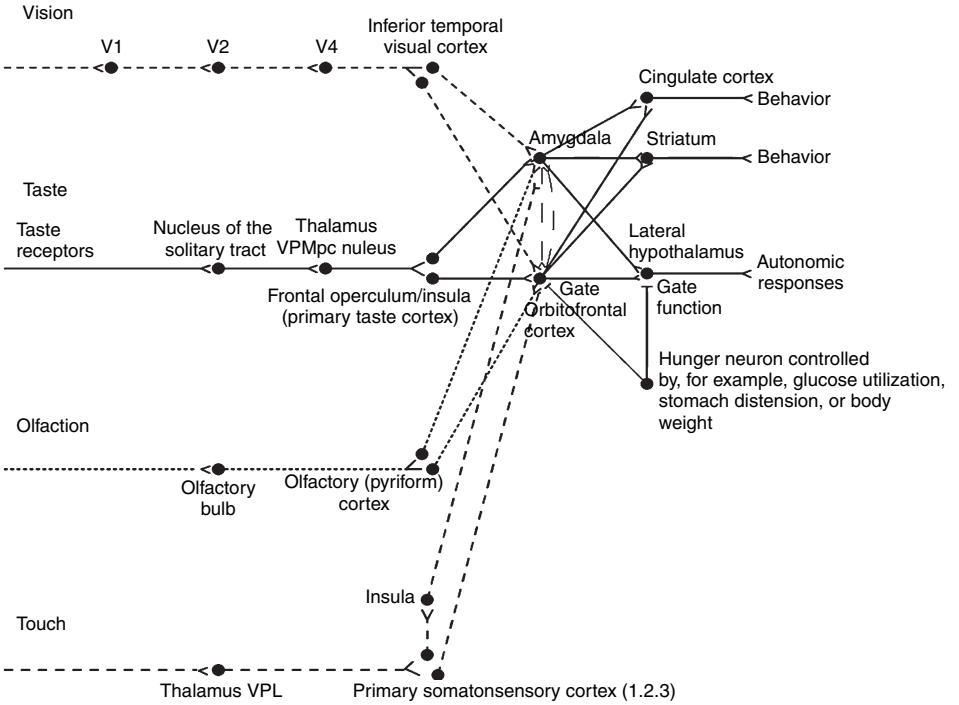

Figure 1 Schematic diagram of the taste and olfactory pathways in primates showing how they converge with each other and with visual pathways. The gate functions shown refer to the finding that the responses of taste neurons in the orbitofrontal cortex and the lateral hypothalamus are modulated by hunger. VPMpc, ventralposteromedial thalamic nucleus; V1, V2, V4, visual cortical areas.

4.26.1.3 Five Prototypical Tastes, Including Umami

In the primary and secondary taste cortex, there are many neurons that respond best to each of the four classical prototypical tastes sweet, salt, bitter and sour (Scott, T. R. *et al.*, 1986; Yaxley, S. *et al.*, 1988; Rolls, E. T. *et al.*, 1990; Rolls, E. T., 1997; Rolls, E. T. and Scott, T. R., 2003), but also there are many neurons that respond best to umami tastants such as glutamate (which is present in many natural foods such as tomatoes, mushrooms and milk; Baylis, L. L. and Rolls, E. T., 1991) and inosine monophosphate (which is present in meat and some fish such as tuna; Rolls, E. T. *et al.*, 1996a).

4.26.2 The Pleasantness of the Taste of Food

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 (Rolls, E. T., 2005a). The subjective correlate of this modulation is that food tastes pleasant when hungry, and tastes hedonically neutral when it has been eaten to satiety. We have found that the modulation of taste-evoked signals by motivation is not a property found in early stages of the primate gustatory system including the nucleus of the solitary tract (Yaxley, S. *et al.*, 1985) and the primary taste cortex (frontal opercular, Rolls, E. T. *et al.*, 1988; insular, Yaxley, S. *et al.*, 1988). In contrast, in the secondary taste cortex, in the caudolateral part of the orbitofrontal cortex, the responses of neurons to the taste of glucose decreases to zero while the monkey is fed glucose to satiety (Rolls, E. T. *et al.*, 1989). It is an important principle that the identity of a taste, and its intensity, are represented separately (in the primary taste cortex) from its pleasantness (in the secondary taste cortex) (Rolls, E. T., 2005a). Thus it is possible to represent what a taste is, and to learn about it, even when we are not hungry.

4.26.3 The Representation of Flavor: Convergence of Olfactory and Taste Inputs

Neuronal responses in the primate primary taste cortex are not driven by olfactory inputs during normal taste/smell tests (Verhagen, J. V. *et al.*, 2004).

However, we found (Rolls, E. T. and Baylis, L. L., 1994) that in the orbitofrontal cortex taste areas, of 112 single neurons which responded to any of these modalities, many were unimodal (taste 34%, olfactory 13%, visual 21%), but were found in close proximity to each other. Some single neurons showed convergence, responding for example to taste and visual inputs (13%), taste and olfactory inputs (13%), and olfactory and visual inputs (5%). Some of these multimodal single neurons had corresponding sensitivities in the two modalities, in that they responded best to sweet tastes (e.g., 1M glucose), and responded more in a visual discrimination task to the visual stimulus which signified sweet fruit juice than to that which signified saline; or responded to sweet taste, and in an olfactory discrimination task to fruit odor (see Figure 2). The different types of neurons (unimodal in different modalities, and multimodal) were frequently found close to one another in tracks made into this region, consistent with the hypothesis that the multimodal representations are actually being formed from unimodal inputs to this region.

It thus appears to be in these orbitofrontal cortex areas that flavor representations are built, where flavor is taken to mean a representation which is evoked best by a combination of gustatory and olfactory input.

The primate amygdala has neurons that combine representations of taste and oral texture (Kadohisa, M. *et al.*, 2005b), and visual stimuli (Wilson, F. A. W. and Rolls, E. T., 2005), and olfactory inputs also reach the amygdala, but less is known about olfactory-taste association learning in the primate amygdala.

4.26.4 The Rules Underlying the Formation of Flavor Representations in the Primate Cortex

Critchley H. D. and Rolls E. T. (1996c) showed that 35% of orbitofrontal cortex olfactory neurons categorized odors based on their taste association in an olfactory-to-taste discrimination task. Rolls E. T. *et al.* (1996a) found that 68% of orbitofrontal cortex odor-responsive neurons modified their responses in some way following changes in the taste reward associations of the odorants during olfactory-taste discrimination learning and its reversal. (In an olfactory discrimination experiment, if a lick response to one odor, the S+, is made a drop of glucose taste reward is obtained; if incorrectly a lick response is made to another odor, the S−, a drop of aversive saline is obtained. At some time in the experiment, the contingency between the odor and the taste is reversed, and when the meaning of the two odors alters, so does the behavior. It is of interest to investigate in which parts of the olfactory system the neurons show reversal, for where they do, it can be concluded that the neuronal response to the odor depends on the taste with which it is associated, and does not depend primarily on the physicochemical structure of the odor). An example of a neuron showing olfactory-to-taste reversal is shown in Figure 3. These findings demonstrate directly a coding principle in primate olfaction whereby the responses of some orbitofrontal cortex olfactory neurons are modified by and depend upon the taste with which the

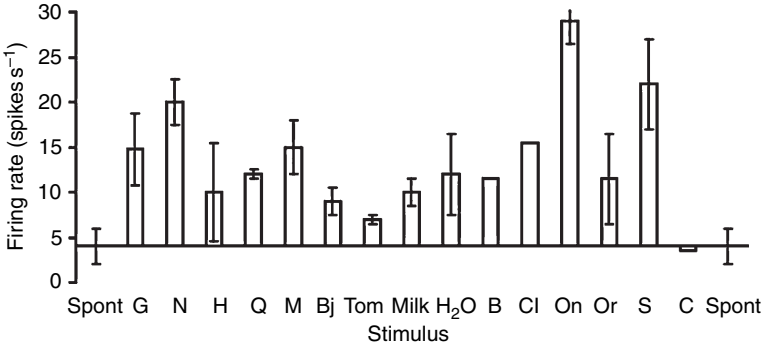

Figure 2 Olfactory to taste convergence on to a single neuron in the macaque orbitofrontal cortex. Spont, spontaneous; G, 1 M glucose; N, 0.1 M NaCl; H, 0.01 M hycrochloride; Q, 0.001 M quinine hycrochloride; M, 0.1 M monosodium glutamate; Bj, 20% blackcurrant juice; Tom, tomato juice; B, banana odor; Cl, clove oil odor; On, onion odor; Or, orange odor; S, salmon odor; C, control no-odor presentation. The mean responses ± standard error of the means are shown. The neuron responded best to the savory tastes of NaCl and monosodium glutamate and to the consonant odors of onion and salmon. Adapted from Rolls, E. T. and Baylis, L. L. 1994. Gustatory, olfactory, and visual convergence within the primate orbitofrontal cortex. J. Neurosci. 14, 5437–5452.

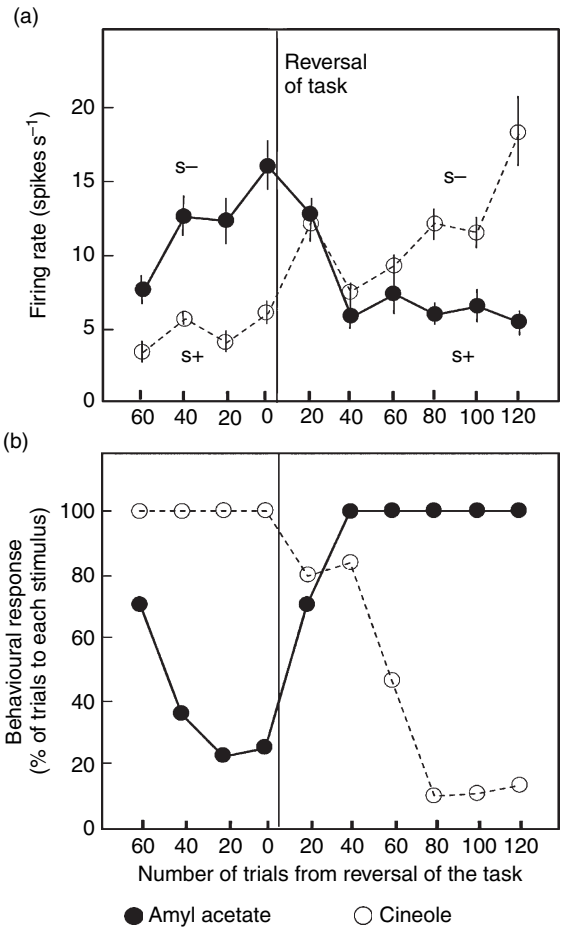

Figure 3 Flavor learning: olfactory to taste association reversal by an orbitofrontal cortex neuron. (a) The activity of a single orbitofrontal olfactory neuron during the performance of a two-odor olfactory discrimination task and its reversal is shown. Each point represents the mean poststimulus activity of the neuron in a 500 ms period on approximately 10 trials of the different odorants. The standard errors of these responses are shown. The odorants were amyl acetate (closed circle; initially s–) and cineole (open circles; initially s+). After 80 trials of the task the reward associations of the stimuli were reversed. This neuron reversed its responses to the odorants following the task reversal. (b) The behavioral responses of the monkey during the performance of the olfactory discrimination task. The number of lick responses to each odorant is plotted as a percentage of the number of trials to that odorant in a block of 20 trials of the task. Adapted from Rolls, E. T., Critchley, H., Mason, R., and Wakeman, E. A. 1996. Orbitofrontal cortex neurons: role in olfactory and visual association learning. J. Neurophysiol. 75, 1970–1981.

odor is associated (Rolls, E. T., 2001; 2002a; 2002b; Deco, G. and Rolls, E. T., 2005b).

Some neurons in the same orbitofrontal cortex region are influenced by the sight as well as by the taste of food, and this is a learned convergence (Thorpe, S. J. *et al.*, 1983; Rolls, E. T. *et al.*, 1996b). As a result of this learning, food choice based on the visual–taste association can be made, and potentially the sight of food can influence its perceived taste. It is of interest that the olfactory-taste association learning is less complete, and much slower, than the modifications found for orbitofrontal visual neurons during visual–taste learning and its reversal (Rolls, E. T. *et al.*, 1996b). This relative inflexibility of olfactory responses is consistent with the need for some stability in odor–taste associations to facilitate the formation and perception of flavors.

Some orbitofrontal cortex olfactory neurons do not code in relation to the taste with which the odor is associated (Critchley, H. D. and Rolls, E. T., 1996c) so that there is also a taste-independent representation of odor in this region.

4.26.5 The Responses of Orbitofrontal Cortex Taste and Olfactory Neurons to the Texture, and Temperature of Food

The texture of food may be considered as a component of the flavor of food. The texture of food, including its viscosity, influences some neurons in the primary taste cortex that have taste responses (Verhagen, J. V. *et al.*, 2004). These texture inputs also thereby influence neurons in the primate orbitofrontal cortex (Rolls, E. T. *et al.*, 2003b), which thus becomes a region where flavor representations can be influenced by the taste, smell, sight and texture of food. Some of the orbitofrontal cortex neurons with texture-related responses encode parametrically the viscosity of food in the mouth (shown using a methyl cellulose series in the range 1–10 000 centiPoise) (see Figure 3), and others independently encode the particulate quality of food in the mouth, produced quantitatively for example by adding 20–100 μm microspheres to methyl cellulose (Rolls, E. T. *et al.*, 2003b). Other neurons respond to water, and others to the somatosensory stimuli astringency as exemplified by tannic acid (Critchley, H. D. and Rolls, E. T., 1996a), and to capsaicin (Rolls, E. T. *et al.*, 2003b; Kadohisa, M. *et al.*, 2004; 2005a).

Texture in the mouth is an important indicator of whether fat is present in a food, which is important not only as a high value energy source, but also as a potential source of essential fatty acids. In the orbitofrontal cortex, Rolls E. T. *et al.* (1999) have found a

population of neurons that responds when fat is in the mouth. The fat-related responses of these neurons are produced at least in part by the texture of the food rather than by chemical receptors sensitive to certain chemicals, in that such neurons typically respond not only to foods such as cream and milk containing fat, but also to paraffin oil (which is a pure hydrocarbon) and to silicone oil ($Si(CH_3)O_2)_n$). Moreover, the texture channel through which these fat-sensitive neurons are activated are separate from viscosity sensitive channels, in that the responses of these neurons cannot be predicted by the viscosity of the oral stimuli (Verhagen, J. V. *et al.*, 2003). Some of the fat-related neurons do though have convergent inputs from the chemical senses, in that in addition to taste inputs, some of these neurons respond to the odor associated with a fat, such as the odor of cream (Rolls, E. T. *et al.*, 1999). Feeding to satiety with fat (e.g., cream) decreases the responses of these neurons to zero on the food eaten to satiety, but if the neuron receives a taste input from for example glucose taste, that is not decreased by feeding to satiety with cream. Thus there is a representation of the macronutrient fat in this brain area, and the activation produced by fat is reduced by eating fat to satiety.

In addition, we have shown recently (Kadohisa, M. *et al.*, 2004; 2005a) that some neurons in the orbitofrontal cortex reflect the temperature of substances in the mouth, and that this temperature information is represented independently of other sensory inputs by some neurons, and in combination with taste or texture by other neurons.

4.26.6 The Representation of the Pleasantness of Flavor in the Brain: Olfactory and Visual Sensory-Specific Satiety, and Their Representation in the Primate Orbitofrontal Cortex

In the orbitofrontal cortex, it is found that the decreases in the responsiveness of the neurons are relatively specific to the food with which the monkey has been fed to satiety. For example, in seven experiments in which the monkey was fed glucose solution, neuronal responsiveness decreased to the taste of the glucose but not to the taste of blackcurrant juice. Conversely, in two experiments in which the monkey was fed to satiety with fruit juice, the responses of the neurons decreased to fruit juice but not to glucose (Rolls, E. T. *et al.*, 1989).

It has also been possible to investigate whether the olfactory representation in the orbitofrontal cortex is affected by hunger, and thus whether the pleasantness of odor is represented in the orbitofrontal cortex. In satiety experiments, Critchley H. D. and Rolls E. T. (1996b) showed that the responses of some olfactory neurons to a food odor are decreased during feeding to satiety with a food (e.g., fruit juice) containing that odor. In particular, seven of nine olfactory neurons that were responsive to the odors of foods, such as blackcurrant juice, were found to decrease their responses to the odor of the satiating food. The decrease was typically at least partly specific to the odor of the food that had been eaten to satiety, potentially providing part of the basis for sensory-specific satiety. It was also found for eight of nine neurons that had selective responses to the sight of food that they demonstrated a sensory-specific reduction in their visual responses to foods following satiation. These findings show that the olfactory and visual representations of food, as well as the taste representation of food, in the primate orbitofrontal cortex are modulated by hunger. Usually a component related to sensory-specific satiety can be demonstrated. It is thus the orbitofrontal cortex which computes sensory-specific satiety, and it is in areas such as this and the areas that receive from it that neuronal activity may be related to whether a food tastes pleasant, and to whether the food should be eaten (see Scott, T. R. *et al.*, 1995; Critchley, H. D. and Rolls, E. T., 1996c; Rolls, E. T. and Rolls, J. H., 1997; Rolls, E. T., 1999; 2000a; 2000b; Rolls, E. T. and Scott, T. R., 2003; Rolls, E. T., 2005a; 2005b; 2006).

The enhanced eating when a variety of foods is available, as a result of the operation of sensory-specific satiety, may have been advantageous in evolution in ensuring that different foods with important different nutrients were consumed, but today in humans, when a wide variety of foods is readily available, it may be a factor that can lead to overeating and obesity (Rolls, E. T., 2005a).

4.26.7 Functional Neuroimaging Studies in Humans

4.26.7.1 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 (Francis, S. *et al.*, 1999; Small, D. M. *et al.*, 1999; O'Doherty, J. *et al.*, 2001; de Araujo, I. E. T. *et al.*, 2003b; Faurion, A. *et al.*, 2005). Another study has recently shown that umami taste stimuli, including monosodium glutamate, activate similar cortical regions of the human taste system to those activated by a prototypical taste stimulus, glucose (de Araujo, I. E. T. *et al.*, 2003a). A part of the rostral anterior cingulate cortex (ACC) was also activated in this study, as it is in many studies by taste, odor, flavor, and oral texture (Rolls, E. T., 2007). O'Doherty J. *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.

4.26.7.2 Odor

In humans, in addition to activation of the pyriform (olfactory) cortex (Zald, D. H. and Pardo, J. V., 1997; Sobel, N. *et al.*, 2000; Poellinger, A. *et al.*, 2001), there is strong and consistent activation of the orbitofrontal cortex by olfactory stimuli (Zatorre, R. J. *et al.*, 1992; Francis, S. *et al.*, 1999). In an investigation of where the pleasantness of olfactory stimuli might be represented in humans, O'Doherty J. *et al* (2000) showed that the activation of an area of the orbitofrontal cortex to banana odor was decreased (relative to a control vanilla odor) after bananas were eaten to satiety. Thus activity in a part of the human orbitofrontal cortex olfactory area is related to sensory-specific satiety, and this is one brain region where the pleasantness of odor is represented. Flavor sensory-specific satiety is also represented in the human orbitofrontal cortex, in that when a whole food (either chocolate milk, or tomato juice) is eaten to satiety activation to the flavor of the food eaten to satiety, but not to the other flavor, decreases in the orbitofrontal cortex but not in the primary taste cortex (Kringelbach, M. L. *et al.*, 2003; see Figure 4).

An important issue is whether there are separate regions of the brain discriminable with fMRI that represent pleasant and unpleasant odors. To investigate this, we measured the brain activations produced by three pleasant and three unpleasant odors. The pleasant odors chosen were linalyl acetate (floral, sweet), geranyl acetate (floral), and alpha-ionone (woody, slightly food-related). (Chiral substances were used as racemates.) The unpleasant odors chosen were hexanoic acid, octanol, and isovaleric acid. We found that they activated dissociable parts of the human brain (Rolls, E. T. *et al.*, 2003a). Pleasant but not unpleasant odors were found to activate a medial region of the rostral orbitofrontal cortex. Further, there was a correlation between the subjective pleasantness ratings of the six odors given during the investigation with activation of a medial region of the rostral orbitofrontal cortex. In contrast, a correlation between the subjective unpleasantness ratings of the six odors was found in regions of the left and more lateral orbitofrontal cortex. Activation was also found in the ACC, with a middle part of the anterior cingulate activated by both pleasant and unpleasant odors, and a more anterior part of the ACC showing a correlation with the subjective pleasantness ratings of the odors. Activation in primary olfactory cortical areas was not correlated with the pleasantness of the odor, but was correlated with the intensity (Rolls, E. T. *et al.*, 2003a).

4.26.7.3 Olfactory-Taste Convergence to Represent Flavor

To investigate where in the human brain interactions between taste and odor stimuli may be realized to implement flavor, we performed an event-related fMRI study with sucrose and monosodium glutamate taste, and strawberry and methional (chicken) odors, delivered unimodally or in different combinations (de Araujo, I. E. T. *et al.*, 2003c). The brain regions that were activated by both taste and smell included parts of the caudal orbitofrontal cortex, amygdala, insular cortex and adjoining areas, and ACC. It was shown that a small part of the anterior (putatively agranular) insula responds to unimodal taste and to unimodal olfactory stimuli; and that a part of the anterior frontal operculum is a unimodal taste area (putatively primary taste cortex) not activated by olfactory stimuli. Activations to combined olfactory and taste stimuli where there was little or no activation to either alone (providing positive evidence for interactions between the olfactory and taste inputs) were found in a lateral anterior part of the orbitofrontal cortex. Correlations with consonance ratings for the smell and taste combinations, and for their pleasantness, were found in a medial anterior part of the orbitofrontal cortex (see Figure 5). 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 (de Araujo, I. E. T. *et al.*, 2003c).

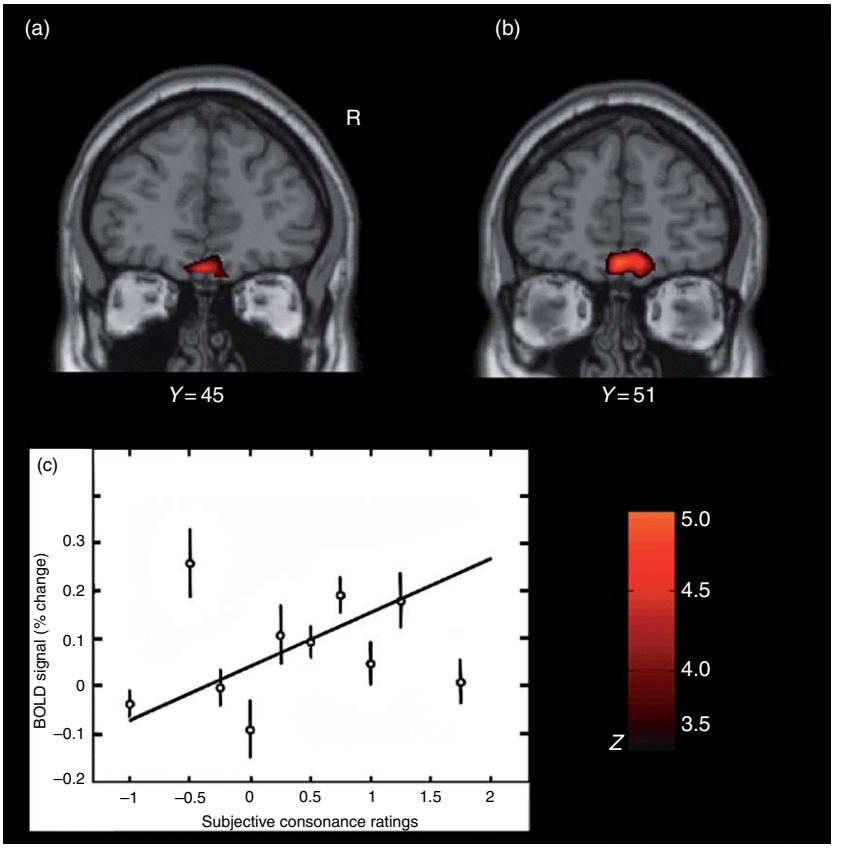

Figure 4 Flavor formation in the human brain, shown by cross-modal olfactory–taste convergence. Brain areas where activations were correlated with the subjective ratings for stimulus (taste–odor) consonance and pleasantness. (a) A second-level, random effects analysis based on individual contrasts (the consonance ratings being the only effect of interest) revealed a significant activation in a medial part of the anterior orbitofrontal cortex. (b) Random effects analysis based on the pleasantness ratings showed a significant cluster of activation located in a (nearby) medial part of the anterior orbitofrontal cortex. The images were thresholded at $P < 0.0001$ for illustration. (c) The relation between the blood oxygen level-dependent (BOLD) signal from the cluster of voxels in the medial orbitofrontal cortex shown in (a) and the subjective consonance ratings. The analyses shown included all the stimuli included in this investigation. The means and standard errors of the mean across subjects are shown, together with the regression line, for which $r = 0.52$. Adapted from de Araujo, I. E. T., Rolls, E. T., Kringelbach, M. L., McGlone, F., and Phillips, N. 2003c. Taste-olfactory convergence, and the representation of the pleasantness of flavour, in the human brain. Eur. J. Neurosci. 18, 2374–2390.

We have also investigated how the flavor of savory foods is produced. Umami taste is produced by glutamate acting on a fifth taste system. However, glutamate presented alone as a taste stimulus is not highly pleasant, and does not act synergistically with other tastes (sweet, salt, bitter and sour). McCabe C. and Rolls E. T. (2007) showed that when glutamate is given in combination with a consonant, savory, odor (vegetable), the resulting flavor can be much more pleasant. Moreover, we showed using functional brain imaging with fMRI that the glutamate and savory odor combination produced much greater activation of the medial orbitofrontal cortex and pregenual cingulate cortex than the sum of the activations by the taste and olfactory components presented separately. Supralinear effects were much less (and significantly less) evident for sodium chloride and vegetable odor. Further, activations in these brain regions were correlated with the pleasantness, consonance of the taste and olfactory components, and the fullness of the flavor, of the stimuli. We thus proposed that glutamate acts by the nonlinear effects it can produce when combined with a consonant odor (McCabe, C. and Rolls, E. T., 2007). I therefore propose the concept that umami can be thought of as a rich and delicious flavor that is produced by a combination of glutamate taste and a consonant savory odor. Glutamate is thus a flavor enhancer because of the way that it can combine supralinearly with consonant odors.

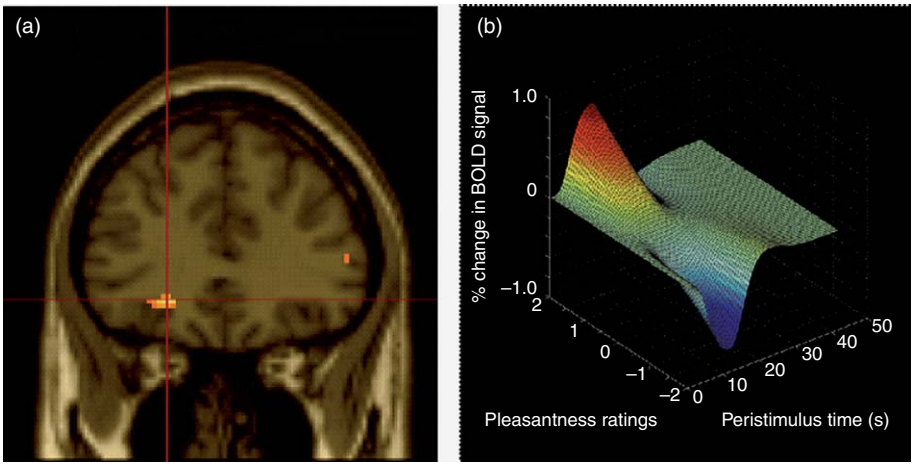

Figure 5 Areas of the human orbitofrontal cortex with activations correlating with pleasantness ratings for flavor in a sensory-specific satiety design. (a) Coronal section through the region of the orbitofrontal cortex from the random effects group analysis showing the peak in the left orbitofrontal cortex (Talairach co-ordinates *X, Y, Z* = −22, 34, −8, z-score = 4.06), in which the blood oxygen level-dependent (BOLD) signal in the voxels shown in yellow was significantly correlated with the subjects' subjective pleasantness ratings of the foods throughout an experiment in which the subjects were hungry and found the food pleasant, and were then fed to satiety with the food, after which the pleasantness of the food decreased to neutral or slightly unpleasant. The design was a sensory-specific satiety design, and the pleasantness of the food not eaten in the meal, and the BOLD activation in the orbitofrontal cortex, were not altered by eating the other food to satiety. The two foods were tomato juice and chocolate milk. (b) Plot of the magnitude of the fitted hemodynamic response from a representative single subject against the subjective pleasantness ratings (on a scale from −2 to +2) and peristimulus time in seconds. Adapted from Kringelbach, M. L., O'Doherty, J., Rolls, E. T., and Andrews, C. 2003. Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness. Cereb. Cortex 13, 1064–1071.

4.26.7.4 Cognitive Influences on Olfactory and Flavor Processing

In line with the neuronal convergence of visual and taste inputs on to single neurons in the orbitofrontal cortex (see above), it is found that the sight of food can influence its perceived flavor, and an fMRI correlate of this has been reported (Osterbauer, R. A. *et al.*, 2005). An example of this interaction is that if a white wine is colored red, then adjectives used to describe the flavor of red wine are used to describe the flavor of the white wine.

To investigate how cognitive this influence could be, de Araujo I. E. T. *et al.* (2005) delivered a standard test odor (isovaleric acid with added cheese flavor), but paired it on some trials with a (visually presented) word label Cheddar cheese, and on other trials with the word label body odor. It was found that the word label produced a large modulation of the olfactory activation in the secondary olfactory cortex in the orbitofrontal cortex (with also some modulation in the amygdala). Moreover, the activations in the orbitofrontal cortex were correlated with the pleasantness ratings given by the subjects of the test odor, which were influenced by the word label. In a control with clean air from the olfactometer, the word labels had much less influence, so that their effect was in particular to modulate the activations being produced in the secondary olfactory cortex by an olfactory stimulus. Thus cognitive influences from the linguistic level, the level of words, can reach down into the secondary olfactory cortex in the orbitofrontal cortex, and modulate their representation of olfactory stimuli (de Araujo, I. E. T. *et al.*, 2005). The mechanism is probably similar to the way in which top-down attentional processes operate, that is by a biased competition mechanism (Rolls, E. T. and Deco, G., 2002; Deco, G. and Rolls, E. T., 2003; 2004; 2005a; 2005c).

It is thus becoming possible to start to understand not only where flavor is represented in the brain, but also how the affective value of smell, taste and flavor are represented, how these representations are influenced by visual stimuli and cognitive states, and how these representations fit into a wider picture of the brain processes underlying the affective or hedonic value of stimuli. This in turn helps to advance understanding of the neural basis of appetite, the control of food intake, and emotion, and their disorders (Rolls, E. T., 2005a).

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