

Brain processing of reward for touch, temperature, and oral texture

Edmund T. Rolls
Oxford Centre for Computational Neuroscience, Oxford, UK.

Email: Edmund.Rolls@oxcns.org web: www.oxcns.org

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SUMMARY

Some of the principles of the representation of affective touch in the brain are described. Positively affective touch and temperature are represented in parts of the orbitofrontal and pregenual cingulate cortex in which other neurons represent the reward value of taste, olfactory, and/or visual stimuli. The orbitofrontal cortex is implicated in some of the affective aspects of touch that may be mediated through C fibre Touch afferents, in that it is activated more by light touch to the forearm (a source of CT afferents) than by light touch to the glabrous skin of the hand. Oral somatosensory afferents implicated in sensing the texture of food including fat in the mouth also activate the orbitofrontal and pregenual cingulate cortex, as well as the insular taste cortex. Top-down cognitive modulation of the representation of affective touch produced by word labels is found in parietal cortex area 7, the insula and ventral striatum. The cognitive labels also influence activations to the sight of touch and also the correlations with pleasantness in the pregenual cingulate / orbitofrontal cortex and ventral striatum.

The aim of this paper is to consider the principles of the representation of positively affective touch, temperature and oral texture in the brain, and the ways in which cognitive factors influence the representation of touch in the brain. Touch can be a primary (unlearned) reinforcer for actions, and as a goal for action, is one of the foundations of emotion and motivation (Rolls 2005, 2014). By positively affective touch is meant touch that is a reward, i.e. it will be worked for, and is rated as pleasant by humans. By negatively affective touch is meant touch that is a punisher, i.e. work will be performed to avoid or escape from it, and it is rated as unpleasant by humans (Rolls 2014). Touch can be negatively affective without being painful, and an example is a cool surface applied to the hand, which is just unpleasant. Much social and affiliative behavior, as well as behavior directed towards comfort and a feeling of well-being, is directed towards pleasant touch.

First, the representation in the brain of the affective value of somatosensory stimuli including touch and temperature is described (Rolls 2010). Representations in the brain produced by light pleasant touch that activates C-tactile (CT) afferent fibres are included. Then cognitive modulation of the affective value of touch by word-level descriptions is considered, and the brain regions in which the affective modulation is evident are described. Then the brain regions that respond to the sight of touch being applied are described, and how these representations can be modulated by cognitive inputs that alter the affective interpretation of the sight of the touch. This evidence about the affective representations of somatosensory stimuli and their cognitive modulation comes mainly from neuroimaging with functional magnetic resonance imaging (fMRI). This evidence is complemented single neuron studies that show how another set of somatosensory and temperature inputs, from the oral cavity, provides information about the texture and temperature of stimuli in the mouth, which are important in the palatability and affective value of food, and thus in appetite control.

The representation of positively affective touch and temperature in the brain

While there have been many investigations of the neural representations of pain (Hunt 2008; Kobayashi 2012; Wiech, Tracey 2013; Brodersen et al. 2012), there have been fewer investigations of the representation of pleasant touch in the brain.

In one study, the cortical areas that represent affectively positive and negative aspects of touch were investigated using fMRI by comparing activations produced by pleasant touch, painful touch produced by a stylus, and neutral touch, to the left hand (Rolls et al. 2003b). It was found that regions of the orbitofrontal cortex were activated more by pleasant touch and by painful stimuli than by neutral touch, and that different areas of the orbitofrontal cortex were activated by the pleasant and painful touches (see Fig. 1). The orbitofrontal cortex activation was

related to the affective aspects of the touch, in that the somatosensory cortex (S1) was less activated by the pleasant and painful stimuli than by the neutral stimuli (as shown by a two-way analysis of variance performed on the percentage change of the BOLD signals under the different stimulation conditions in the different areas). Further, it was found that a rostral part of the anterior cingulate cortex was activated by the pleasant stimulus and that a more posterior and dorsal part was activated by the painful stimulus. Regions of the somatosensory cortex, including S1, and part of S2 in the superior temporal plane at the mid-insula level, were activated more by the neutral touch than by the pleasant and painful stimuli. Part of the posterior insula was activated only in the pain condition, and different parts of the brainstem, including the central grey, were activated in the pain, pleasant and neutral touch conditions. The results provide evidence that different areas of the human orbitofrontal cortex are involved in representing both pleasant touch and pain, and that dissociable parts of the cingulate cortex are involved in representing pleasant touch and pain (Rolls et al. 2003b).

Warm and cold stimuli have affective components such as feeling pleasant or unpleasant, and these components may have survival value, for approach to warmth and avoidance of cold may be reinforcers or goals for action built into us during evolution to direct our behaviour to stimuli that are appropriate for survival (Rolls 2014). Understanding the brain processing that underlies these prototypical reinforcers provides a direct approach to understanding the brain mechanisms of emotion. In an fMRI investigation in humans, we showed that the mid-orbitofrontal and pregenual cingulate cortex and the ventral striatum have activations that are correlated with the subjective pleasantness ratings made to warm (41°C, rated as pleasant) and cold (12°C, rated as unpleasant) stimuli, and combinations of warm and cold stimuli, applied to the hand (Rolls et al. 2008). Activations in the lateral and some more anterior parts of the orbitofrontal cortex were correlated with the unpleasantness of the stimuli. In contrast, activations in the somatosensory cortex and ventral posterior insula were correlated with the intensity but not the pleasantness of the thermal stimuli (Rolls et al. 2008). Temperature may also be important for social touch, in that slow soft touch that activated CT afferents produced the best responses when the touch stimulus was at a typical skin temperature (32°C), rather than colder or warmer (Ackerley et al. 2014).

A principle thus appears to be that processing related to the affective value and associated subjective emotional experience of somatosensory and thermal stimuli that are important for survival is performed in different brain areas to those where activations are related to sensory properties of the stimuli such as their intensity. This conclusion appears to be the case for processing in a number of sensory modalities, and the finding with such prototypical stimuli as

pleasant and painful touch, and warm (pleasant) and cold (unpleasant) thermal stimuli, provides strong support for this principle (Rolls, Grabenhorst 2008; Grabenhorst, Rolls 2011; Rolls 2012, 2014, 2015). An implication of the principle is that by having a system specialized for the affective or reward aspects of stimuli it is possible to modify goal oriented behaviour, and to do this independently of being able to know what the stimulus is (its intensity, physical characteristics etc). Thus even if a stimulus has lost its pleasantness because of for example a change of core body temperature, it is still possible to represent the stimulus, recognize it, and learn about where it is in the environment for future use (Rolls 2014). This is a fundamental aspect of brain design (Rolls 2005, 2008b, 2014).

Decision-making about whether to select an affective stimulus may involve a further tier of representation beyond that involved in representing the affective value of the stimulus. Indeed, representing the affective value of a reward on a continuous scale may occur before and separately from making a binary, for example yes-no, decision about whether to choose the reward (Rolls, Grabenhorst 2008; Grabenhorst, Rolls 2011; Rolls 2014). To investigate whether these are separable processes, we used fMRI to measure activations produced by pleasant warm, unpleasant cold, and affectively complex combinations of these stimuli applied to the hand (Grabenhorst et al. 2008b). On some trials the affective value was rated on a continuous scale, and on different trials a Yes-No decision was made about whether the stimulus should be repeated in future. Decision-making contrasted with just rating the affective stimuli revealed activations in the medial prefrontal cortex area 10 implicating this area in binary decision making. Activations related to the pleasantness ratings and which were not influenced when a binary decision was made were found in the pregenual cingulate and parts of the orbitofrontal cortex implicating these regions in the continuous representation of affective value. When a decision was yes vs no, effects were found in the dorsal cingulate cortex, agranular (anterior) insula, and ventral tegmental area, implicating these areas in initiating actions to obtain goals (Grabenhorst et al. 2008b).

Thus decision-making about whether to select a stimulus may be a process implemented in the brain separately from the representation of the continuous affective value of a stimulus (Rolls 2008b; Grabenhorst et al. 2008b; Rolls et al. 2010; Deco et al. 2009; Rolls, Deco 2010; Rolls, Grabenhorst 2008; Grabenhorst, Rolls 2011; Rolls 2014, 2015). It is important to be able to represent the current affective value of a stimulus on a continuum, and indeed the exact affective value on a continuum is an important input to the decision-making mechanism. However, the implication of the findings is that the decision-making mechanism is separate, for on a given trial, a binary decision, such as 'yes' vs 'no' must be taken, and the outcome must be represented in a

binary way. Indeed, decision-making is probabilistic, so that for two stimuli that are equally pleasant on a continuous scale, the decision on each trial will be different on a probabilistic basis. The understanding we have of this process is that each decision is represented in an attractor network by a separate attractor state, and that on an individual trial, the continuous value of the evidence biases the two attractors, and which attractor wins the competition depends on the probabilistic spiking of the neurons in the network (Wang 2002; Deco, Rolls 2006; Rolls 2008b; Rolls, Deco 2010; Deco et al. 2013; Rolls 2014)..

C-Tactile (CT) afferents and light touch

Light touch to hairy skin such as the forearm can activate CT afferents (i.e. C fibres with low mechanical thresholds) and can be pleasant, and such afferents are thought not to be present in glabrous skin such as the palm of the hand (Olausson et al. 2002; McGlone et al. 2007; Bjornsdotter et al. 2010). In an fMRI study, a contrast of the effects of rubbing the forearm vs rubbing the glabrous skin of the hand revealed activation in the mid-orbitofrontal cortex (see Fig. 2) (McCabe et al. 2008). The implication is that the orbitofrontal cortex may be especially activated in relation to CT afferents vs afferents from the glabrous skin. (The activation of the orbitofrontal cortex by this contrast was of significance, in that the effects of rubbing the glabrous skin of the hand were for most somatosensory cortical areas much larger than those produced by rubbing the forearm, which has a smaller cortical representation than the hand.)

In a different study, Olausson et al (2002) showed in a neuropathy patient who specifically lacks A-beta afferents that CT afferent stimulation can activate the insula, and such patients can have feelings of a pleasant touch, and sympathetic responses produced by the touch (Olausson et al. 2008). In our study, the contrast rubbing the arm vs rubbing the hand also showed a region of activation in the insula ([-30 26 0]), though this was not significant ($Z=2.04$) (McCabe et al. 2008).

An implication of these findings is that the pleasantness of CT stimulation may be related to activation of the medial/mid orbitofrontal cortex, a region in which many other pleasant sensory stimuli are represented (Rolls, Grabenhorst 2008; Grabenhorst, Rolls 2011; Rolls 2014), and that CT stimulation can also produce activation of the insula (Olausson et al. 2002). It will be of interest to explore the role of CT afferents in pleasant touch further, though I note that they cannot have an exclusive role in affective touch, in that touch to the glabrous skin of the hand can be pleasant (McCabe et al. 2008). Indeed, it has been suggested that the pleasantness produced by stimulation of the glabrous skin of the hand is mediated by A-beta afferent fibres (McGlone et al. 2012).

Cognitive modulation of affective touch processing

There have been many studies of the top-down attentional modulation (Rolls 2008b, 2013) of touch, with effects typically larger in secondary somatosensory and association cortical areas (e.g. parietal area 7), and smaller in S1 (Johansen-Berg, Lloyd 2000), and seeing unpleasant pictures can influence somatosensory evoked responses (Montoya, Sitges 2006). However, there has been little investigation of where high-level cognition influences the representation of affective touch in the brain.

To investigate where cognitive influences from the very high level of language might influence the affective representation of touch, we performed a fMRI study in which the forearm was rubbed with a typical skin lotion, but this could be accompanied by a word label that indicated that it was a rich moisturizing cream (pleasant to most people) vs a basic cream (McCabe et al. 2008).

We found that cognitive modulation by a label at the word level indicating pleasantness / richness (“rich moisturising cream” vs “basic cream”) influenced the representation of tactile inputs in the orbitofrontal cortex (McCabe et al. 2008). (The cream was identical in all conditions in the study: it was only the word labels that were changed. The cream was rubbed onto the ventral, volar, surface of the arm, as illustrated in Fig. 4.) For example, a negative correlation with the pleasantness ratings of the touch as influenced by the word labels was found in the lateral orbitofrontal cortex, a region shown in other studies to be activated by less pleasant stimuli including unpleasant odors, and losing money (O’Doherty et al. 2001; Rolls et al. 2003a; Rolls et al. 2003b). A positive correlation with the pleasantness of touch as influenced by the word labels was found in the pregenual cingulate cortex (McCabe et al. 2008). Convergent evidence on the functions of this region is that the pregenual cingulate region is close to (with peaks mm apart, and frequently with overlapping activations) where in different studies another somatosensory stimulus, oral texture, is represented (de Araujo, Rolls 2004), correlations with pleasantness ratings are found to food and olfactory stimuli (Kringelbach et al. 2003; de Araujo et al. 2005), and pleasant touch produces activation (Rolls et al. 2003b). We also found that activations to touch in the parietal cortex area 7 were influenced by the word labels, in that there was more activation when the rich label than when the thin label was present (as shown by a contrast analysis at the group level) (McCabe et al. 2008).

Activations to the sight of touch, and cognitive modulation

The sight of touch can influence some areas involved in somatosensory processing including S1, S2, the inferior frontal gyrus and the parietal cortex (Blakemore et al. 2005; Schaefer et al. 2006). Indeed, it has been shown that somatosensory perception can be activated without actual touch but by imagery or empathy (Yoo et al. 2003; Singer et al. 2004; Bufalari et al. 2007) and also by the intention/anticipation of a touch (Carlsson et al. 2000).

We found that S1 was activated by the sight of the arm being rubbed with cream, in a region that overlapped with that activated by actually rubbing the arm. However, interestingly, activations were not produced by the sight of the arm being rubbed in the insular somatosensory areas in the mid insula activated by the arm actually being rubbed (see Fig. 3) (McCabe et al. 2008). In the rubbing condition the stimulation will be related to one's own body, whereas in the sight condition it is less likely to be related to one's own body. The implication is that the insular activation is more closely related to body ownership, that is to the fact that one's own body is being rubbed, than is activation of S1. (However, under conditions of slow and social touch being seen to the arm, some insular activation has been found (Morrison et al. 2011).) It might be particularly interesting to follow up the finding of McCabe et al (2008) in patients: are denials of ownership of a part of the body particularly related to damage to the insula as compared with damage to S1? Evidence using a rubber hand also suggests that insular activation may be related to body ownership (Tsakiris et al. 2007), whereas somatosensory cortex areas 1,2,3 was activated when the touch was not attributed to the self. Moreover, the study by Blakemore et al. (2005) showed that a synesthetic subject who felt touch whilst just observing touch had anterior insula activation whereas the control non-synesthetic subjects who did not feel touch as they observed touch did not have insular activation, again evidence for the insula being involved in recognition of touch to one's own body. The insula has also been described as a system involved in interoception (Craig 2002), but in our study the insular activation was produced by a thoroughly exteroceptive input, touch to the arm or hand. There was also activation in the lateral orbitofrontal cortex (area 47/12) which extended into the inferior frontal gyrus bilaterally (McCabe et al. 2008).

We may consider here the functions of some different parts of the insula. There are somatosensory areas that represent parts of the body in the mid- to posterior insula, as illustrated in Fig. 3 (McCabe et al. 2008; Baumgartner et al. 2010). The anterior and dorsal part of the primate including human insula includes the primary taste cortex (Pritchard et al. 1986; Yaxley et al. 1990; de Araujo et al. 2003; Kadohisa et al. 2005a; Rolls 2007a, 2015), but it also includes a representation of oral texture (Verhagen et al. 2004; de Araujo, Rolls 2004), so this might be

thought of as an insular somatosensory area for the mouth which also contains the primary taste cortex. Having these taste and somatosensory oral representations in the same anterior insular cortex enables neurons to respond to combinations of oral texture and taste, which is important for enabling effects related to particular foods to be computed (Rolls 2005, 2007a, 2008b, 2012, 2014, 2015). The anterior more ventral part of the insula may be a visceral cortical area, and consistent with this, this part of the insula has activations related to autonomic functions (Critchley et al. 2004; Critchley, Harrison 2013). Painful somatosensory stimuli, because they produce autonomic activity, may activate this anterior insular area.

To investigate how specific the sight of touch needs to be to evoke activity in somatosensory areas, we compared the sight of rubbing the forearm by a finger that was applying cream, with a close visual control condition which showed the finger moving 1 cm above the arm and clearly not touching the arm. This contrast showed effects in parietal area 7, the lateral orbitofrontal cortex perhaps continuing into the inferior frontal gyrus (see Fig. 4), and S1 (McCabe et al. 2008). This is of considerable interest, for it shows that these areas are activated particularly when the intention to touch is made clear in the stimulus, that is when the fingers are seen to be intentionally rubbing the arm, and not just moving facing upwards 1 cm above the arm clearly not intending to touch it. The close visual control we use provides evidence that these systems are very sensitive to whether intentionality to touch is implied by what is seen. Indeed, in our study the difference between the conditions indicated whether physical interpersonal contact was going to occur or not, and this could influence activations in all these areas. Because the moving stimuli were so similar, yet only one implied that touch was occurring, we interpret the effects as being related to the sight of touch, and not to the sight of the movement (McCabe et al. 2008).

Although other studies did not address so directly the issue of interpersonal touch, some investigations support our finding that intentionality can be important, by showing in the movement system that a movement seen in a context that implies an intention (to drink tea from a cup or clean the cup) produced more activation in the inferior frontal gyrus and premotor cortex than did seeing the same movement without a context-setting background (Iacoboni et al. 2005). A relation to intentionality is also implied by grasp-related mirror neurons in the macaque F5 that respond when a hand is reaching behind a screen to grasp a hidden object (Umiltà et al. 2001), and by activation in the human inferior frontal gyrus occurring when there is a visible goal for a movement (Koski et al. 2002).

Interestingly, in our investigation this contrast, the sight of a finger rubbing an arm - the sight of a finger moving in a similar way but clearly not touching the arm - produced some

activation in S1 (McCabe et al. 2008), implying that back projections from higher cortical areas (in e.g. the parietal cortex) can influence S1 when there is an evident intentionality to touch and touch is therefore being imagined. In another study without such a close visual control condition (because the contrast was between the sight of a body and the sight of an object being touched), S1 activations were found when touch to a body but not touch to an object was being seen (Blakemore et al. 2005). Consistent with the hypothesis that activation of S1 can be produced by imagining touch in our sight of touch condition, a neuroimaging study by Carlsson et al., (2000) showed that anticipation of tickling activated the primary somatosensory cortex. The visual input to the primary somatosensory cortex may have some useful functions, in that for example TMS of the primary somatosensory cortex impairs the usual visual enhancement of tactile acuity (Fiorio, Haggard 2005).

Positive correlations with pleasantness ratings to the sight of touch, which were being influenced by the cognitive word labels, revealed significant effects in the medial orbitofrontal cortex and the ventral striatum (see Fig. 5) (McCabe et al. 2008). Further evidence for cognitive modulation of affective representations of touch was found in a related area, the pregenual cingulate cortex, as shown by the contrast of the effects of the sight of touch when the label was “rich moisturising cream” vs “basic cream”. A negative correlation with the pleasantness of the sight of touch in the lateral orbitofrontal cortex bilaterally and extensively, and in the dorsal anterior cingulate cortex, was found (McCabe et al. 2008).

Interesting implications of these findings are that cognitive input produced by word-level descriptions can modulate the representations of the affective value of touch and of the sight of touch in areas such as the orbitofrontal cortex, anterior cingulate cortex, and ventral striatum (McCabe et al. 2008), where the pleasantness of many stimuli are represented. A similar modulation by cognitive labels that influence affective value is found for taste (Grabenhorst et al. 2008a), flavour (Grabenhorst et al. 2008a), and olfaction (de Araujo et al. 2005). What is fascinating here is that the cognitive modulation can reach right down into these sensory systems to modulate the activations at the first stage of processing that for several of these systems is the first stage at which the pleasantness is represented. Thus the cognitive modulation appears to have a direct influence on the brain’s representation of the affective value of stimuli, and these interactions are not left until purely cognitive or language-related processing systems in the brain, that is, there is a top-down effect of cognition on areas where the pleasantness of stimuli is represented (Rolls 2008b, 2014; Ge et al. 2012; Grabenhorst, Rolls 2010; Rolls 2013). The mechanism may be implemented by top-down biased competition in a way similar to that which appears to be involved in top-down attention (Rolls 2008b), though whole cortical processing

streams may be biased by attention to affect vs intensity (Rolls 2013; Ge et al. 2012; Grabenhorst, Rolls 2010; Rolls 2014). Further, affective cognitive modulation of sight of touch representations may help in processes such as empathy.

Oral texture

Another somatosensory stimulus, the texture of food in the mouth, is also very important in perceived pleasantness. Neurophysiological studies have shown that the orbitofrontal cortex of primates is also important as an area of convergence for somatosensory inputs, related for example to the texture of food including fat in the mouth, with other sensory inputs. We have shown for example that single neurons influenced by taste in the lateral and medial macaque orbitofrontal cortex (Rolls et al. 1990; Rolls, Baylis 1994; Rolls et al. 1996; Critchley, Rolls 1996; Pritchard et al. 2005; Pritchard et al. 2007; Rolls 2008a; Rolls 2015) can in some cases have responses produced by the texture of the food. This was shown in experiments in which the texture of food was manipulated by the addition of methyl cellulose or gelatine, or by puréeing a semi-solid food (Rolls 1998, 1999), or by the astringent stimulus tannic acid (Critchley, Rolls 1996). It has been shown that some of these neurons with texture-related responses encode parametrically the viscosity of food in the mouth (using a methyl cellulose series in the range 1 – 10,000 centiPoise), and that 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 et al. 2003c).

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, Critchley 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 ($\text{Si}(\text{CH}_3)_2\text{O}_n$). Moreover, the texture channels 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 et al. 2003; Rolls 2011). Behavioral evidence consistent with this comes from a study in rats (Ramirez 1994). 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 odour associated with a fat, such as the odour of cream (Rolls 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, the response to the taste of glucose is not decreased by feeding to satiety with cream (Rolls et al. 1999; Rolls 2014). Thus there is a representation of the macronutrient fat in this brain area, and the activation produced by fat is specifically reduced by eating fat to satiety.

The pleasantness of oral fat texture is represented in the orbitofrontal cortex and anterior cingulate cortex, as shown in an fMRI investigation using high and low fat dairy products (Grabenhorst et al. 2010). The soft pleasant feel of fat in the mouth is reminiscent of the soft pleasant feel produced by gentle rubbing of the forearm that is associated with the activation of CT fibre afferents. It is an interesting hypothesis that the texture of fat in the mouth might involve CT afferents.

Fat texture, oral viscosity, and temperature, for some neurons in combination with taste, are represented in the macaque primary taste cortex in the rostral insula and adjoining frontal operculum (Verhagen et al. 2004).

These oral sensory properties of food, and also the sight and smell of food, are also represented in the primate amygdala (Kadohisa et al. 2005b; Kadohisa et al. 2005a; Rolls 2000; Rolls, Scott 2003). Interestingly, the responses of these amygdala neurons do not correlate well with the preferences of the macaques for the oral stimuli (Kadohisa et al. 2005a), and feeding to satiety does not produce the large reduction in the responses of amygdala neurons to food (Rolls 2000; Rolls, Scott 2003) that is typical of orbitofrontal cortex neurons (Rolls 2006, 2007a). Multidimensional scaling analyses of the spaces encoded by neurons suggest that the amygdala emphasises texture (oral viscosity), and the orbitofrontal cortex sweet taste stimuli (Kadohisa et al. 2005a).

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 which represents oral somatosensory stimuli (de Araujo, Rolls 2004). In these regions, the fMRI BOLD activations are proportional to the log of the viscosity of carboxymethyl cellulose in the mouth. 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).

Oral temperature representations in the brain

It has been discovered 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 (Kadohisa et al. 2004).

Until recently, no neuroimaging study had investigated whether changes in oral temperature activate these areas in humans, or the activity of middle or posterior insular cortex, the areas most frequently identified in neuroimaging studies for the encoding of temperature information from the human hand. To analyze the representation of oral temperature in the human brain, we conducted an fMRI study to identify areas of activation in response to temperature-controlled (cooled and warmed, 5, 20 and 50°C) liquid introduced into the mouth (Guest et al. 2007). The results showed that the oral temperature stimuli activated the insular taste cortex (identified by glucose taste stimuli), a part of the somatosensory cortex, the orbitofrontal cortex, the anterior cingulate cortex, and the ventral striatum. Brain regions where activations correlated with the pleasantness ratings of the oral temperature stimuli included the orbitofrontal cortex and pregenual cingulate cortex. We conclude that a network of taste- and reward-responsive regions of the human brain are activated by intra-oral thermal stimulation, and that the pleasant subjective states elicited by oral thermal stimuli are correlated with the activations in the orbitofrontal cortex and pregenual cingulate cortex.

Thus somatosensory and temperature inputs from the oral cavity provide information about the texture and temperature of stimuli in the mouth in a number of brain regions, and in regions such as the orbitofrontal cortex represent the palatability and affective value of the food, and are thus important in appetite control (Rolls 2005, 2007a, b).

In conclusion, exciting discoveries are being made at present about the affective representations of touch, and their cognitive modulation. The affective value of touch is represented particularly in brain regions such as the orbitofrontal and anterior cingulate cortices. In these regions, cognitive inputs from as high as the word level can influence the affective representations, showing that cognition can influence the pleasantness or unpleasantness of touch by modulating activations to touch in some of the first cortical regions where the affective value of touch is represented. The same regions can be influenced by the sight of touch, emphasizing the contribution of the visual as well as the somatosensory modality to the affective value of touch and how this is represented in the brain. Multimodal inputs have been shown too to be very important for oral aspects of touch, with somatosensory inputs that contribute to the texture and mouth feel of food including fat being combined in these orbitofrontal and anterior cingulate cortical areas, and also the insular taste cortex, with taste and oral temperature inputs (Rolls 2007a; Rolls 2008a). All of these somatosensory and taste inputs combine further with visual and olfactory inputs in the orbitofrontal cortex to produce a multimodal representation of the affective value (pleasantness) of the sensory properties of food. These representations of affective value are in turn important in

decision-making (Rolls 2008b, 2014).

Figure Legends

Fig. 1. Brain activation to painful, pleasant and neutral touch of the human hand. The top row shows strongest activation of the somatosensory cortex S1/insula by the neutral touch, on parasagittal sections (parallel to the midline). The middle row shows activation of the most anterior part of the anterior cingulate cortex by the pleasant touch, and of a more posterior part by the painful touch, on parasagittal sections. The bottom row shows activation of the orbitofrontal cortex by the pleasant and by the painful touch, on axial sections (in the horizontal plane). The activations were thresholded at $p < 0.0001$ to show the extent of the activations. (After Rolls, O'Doherty et al., 2003b.) (painpleas2E.eps)

Fig. 2. A region of the mid-orbitofrontal cortex ([26 50 -8] $Z=3.18$, $p=0.035$ svc) was activated more by light touch to the forearm, which has CT afferents, than by light touch to the glabrous skin of the hand, which does not. The right of the brain is on the right of the coronal sections in this and subsequent Figures. (After McCabe, Rolls, Bilderbeck and McGlone, 2008.) (fig8mOFCrev.eps)

Fig. 3. Activations were produced by touch to the arm (rubarm condition) in the contralateral insula with peak at [44 -16 14] $Z=3.83$ $p=0.003$ fc. Activations were not produced in this region by the sight of the arm being rubbed. (After McCabe, Rolls, Bilderbeck and McGlone, 2008.) (Fig2armINSrev.eps)

Fig. 4. The contrast Sight-Sightnotouch: a comparison of the effects of the sight of the arm being touched by an experimenter's finger vs the sight of the arm not being touched in that the experimenter's finger was moved inverted and 1 cm above the image of the arm (as shown in the inset image). Effects were found in the contralateral orbitofrontal cortex area 47 at [42 30 -2] $Z=3.45$ $p < 0.03$ and extended medially through much of the orbitofrontal cortex. (After McCabe, Rolls, Bilderbeck and McGlone, 2008.) (Fig5s-sntOFCrev.eps).

Fig. 5. Cognitive modulation of the affective value of touch. Correlations with the pleasantness of the sight of touch as influenced by the word labels "rich moisturising cream" vs "basic cream" were found in the medial orbitofrontal / pregenual cingulate cortex ([-14 50 -16] $Z=2.97$ $p=0.02$) and ventral striatum ([-4 4 -14] $Z=2.95$ $p \approx 0.05$). (After McCabe, Rolls, Bilderbeck and McGlone, 2008.) (Fig6pleasOFCrev.eps).

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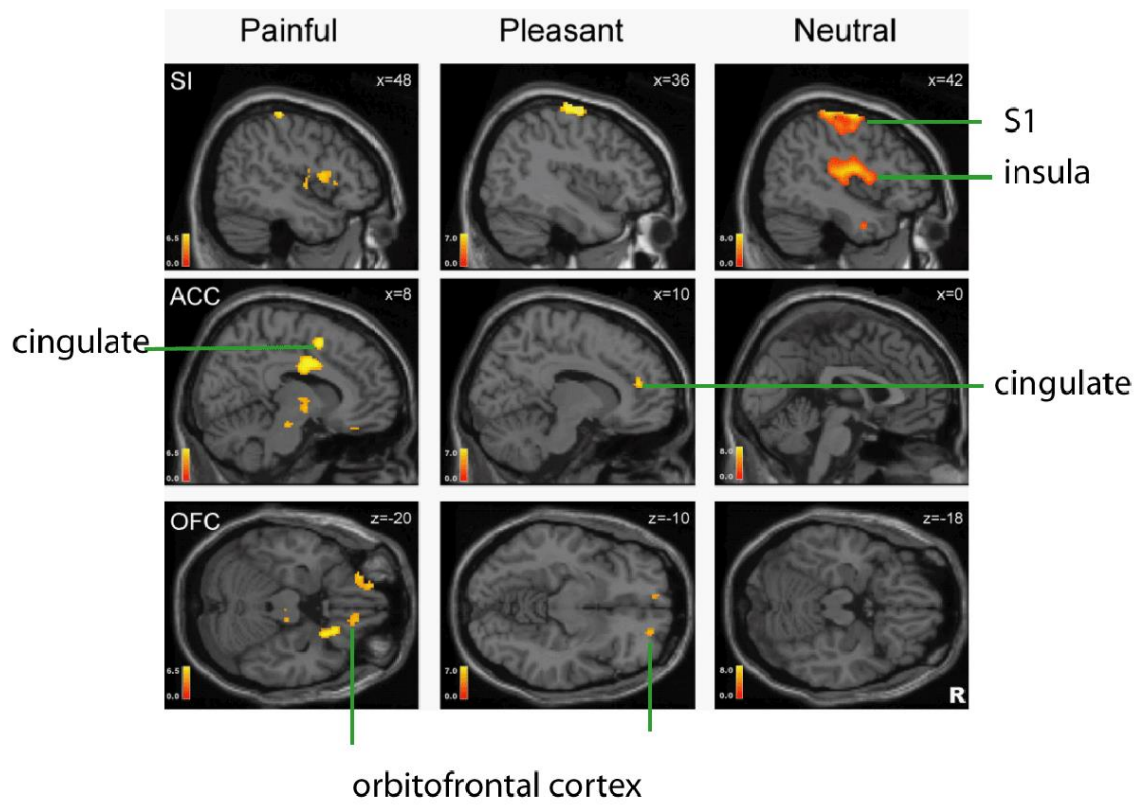


Fig 1.

**Activation of the mid-orbitofrontal cortex
by a contrast of rubbing the arm (with CT afferents)
- rubbing the hand (without CT afferents)**

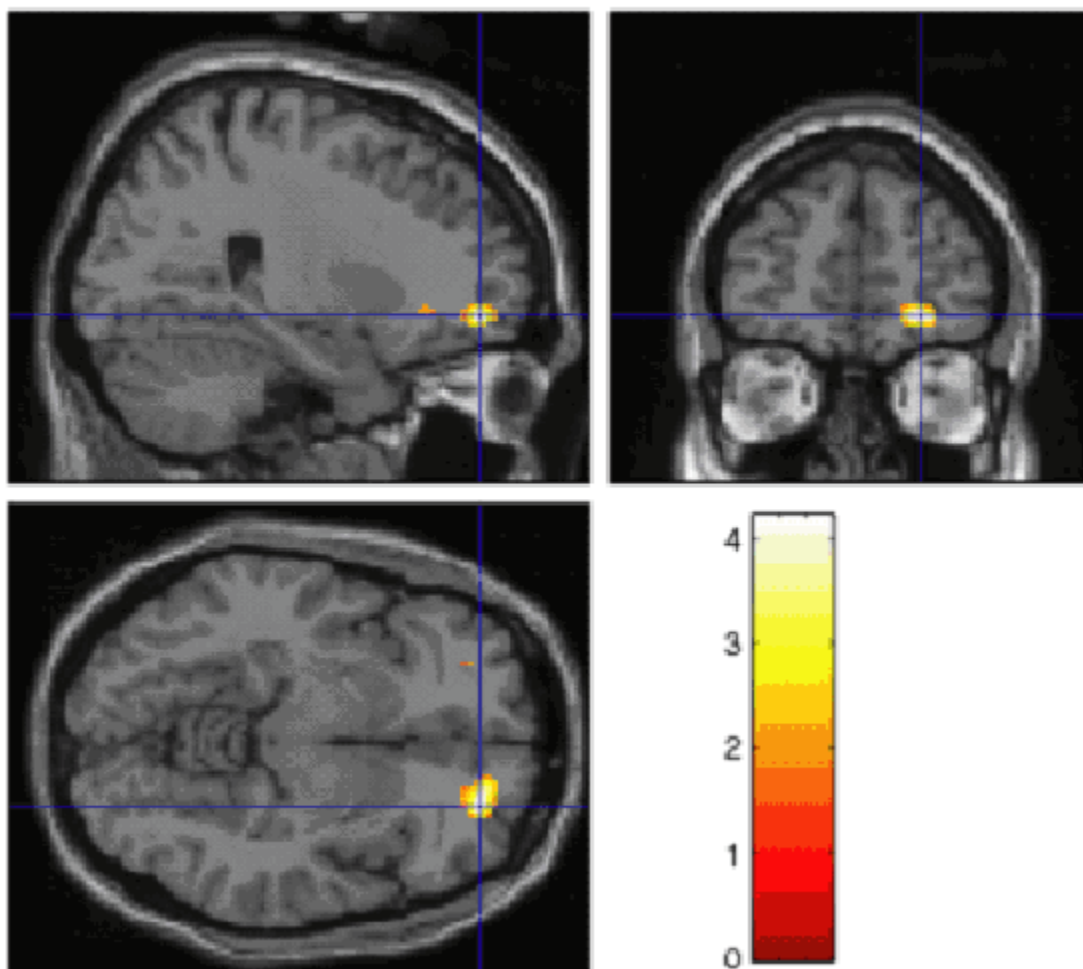


Fig 2.

Activation of the mid-insula by rubbing the arm

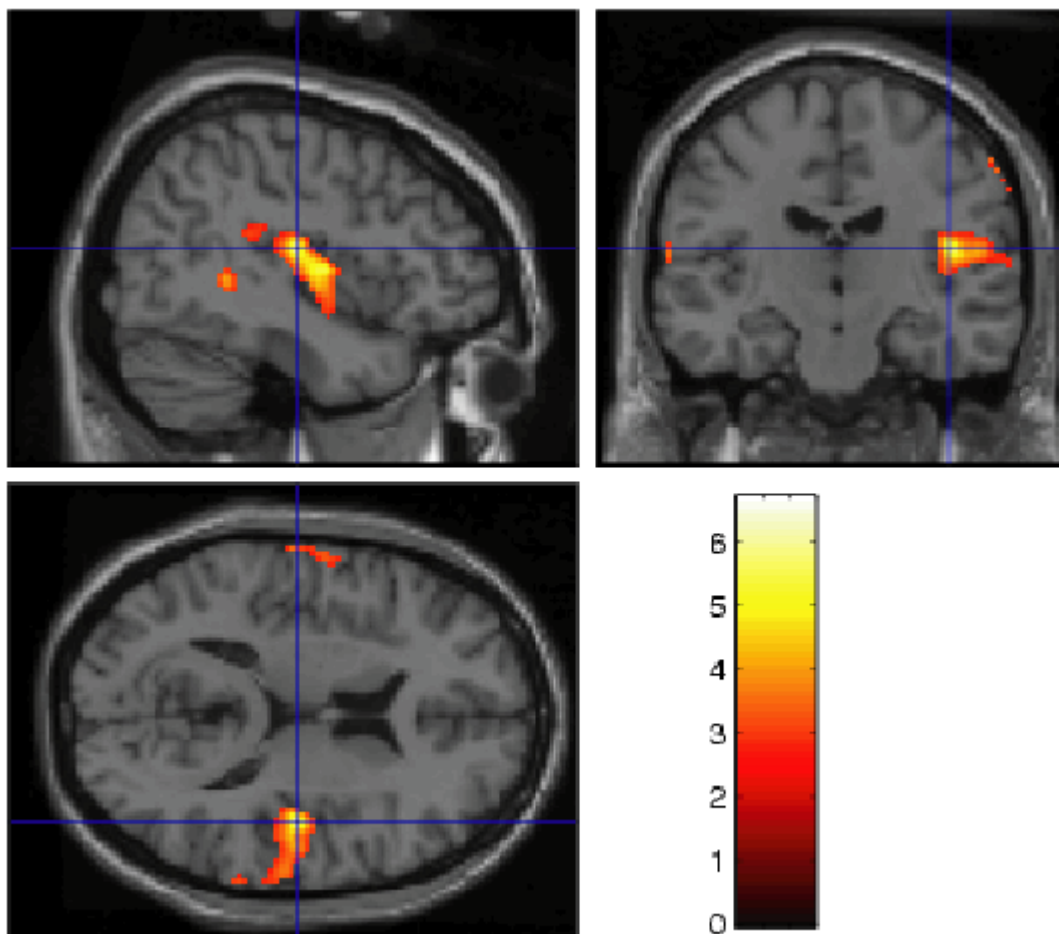


Fig 3.

**Activation of the orbitofrontal cortex
by seeing the arm being touched
- seeing the arm not being touched**

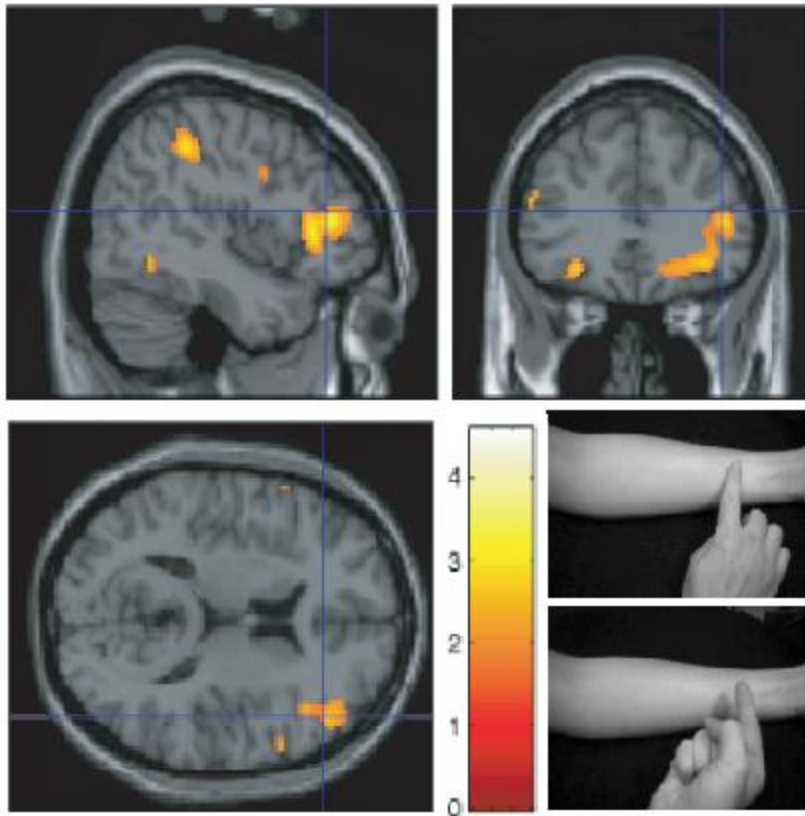


Fig 4.

**Activations correlated with the pleasantness ratings
of the sight of touch
when they were modulated by word labels**

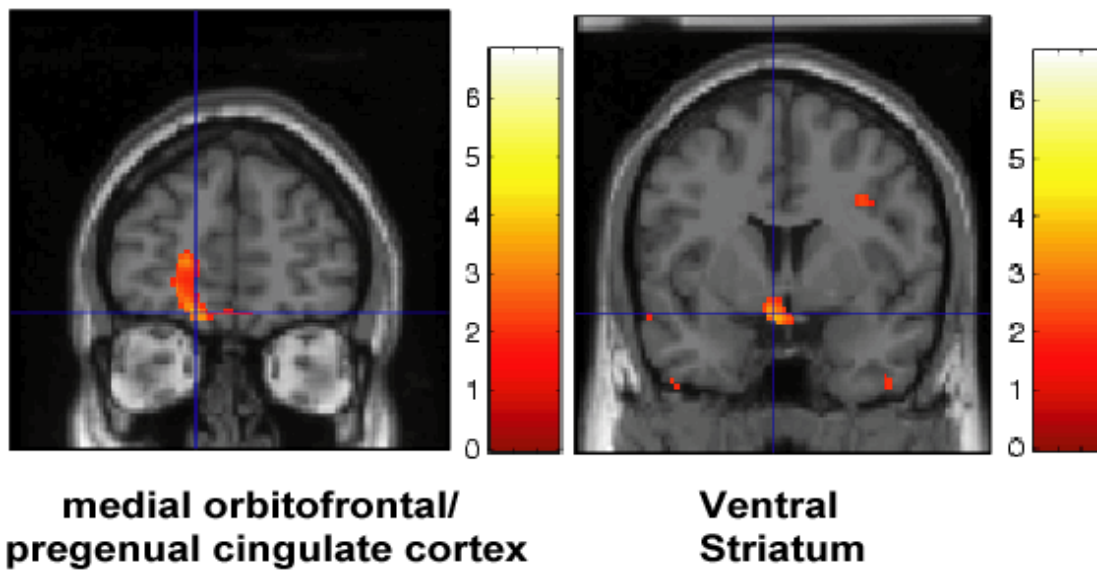


Fig.5

References

- Ackerley R, Backlund Wasling H, Liljencrantz J, Olausson H, Johnson RD, Wessberg J. Human C-tactile afferents are tuned to the temperature of a skin-stroking caress. *J Neurosci*. 2014;34(8):2879-83. doi:10.1523/JNEUROSCI.2847-13.2014.
- Baumgartner U, Iannetti GD, Zambreanu L, Stoeter P, Treede RD, Tracey I. Multiple somatotopic representations of heat and mechanical pain in the operculo-insular cortex: a high-resolution fMRI study. *Journal of neurophysiology*. 2010;104(5):2863-72. doi:10.1152/jn.00253.2010.
- Bjornsdotter M, Morrison I, Olausson H. Feeling good: on the role of C fiber mediated touch in interoception. *Experimental brain research Experimentelle Hirnforschung*. 2010;207(3-4):149-55. doi:10.1007/s00221-010-2408-y.
- Blakemore SJ, Bristow D, Bird G, Frith C, Ward J. Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. *Brain*. 2005;128(Pt 7):1571-83.
- Brodersen KH, Wiech K, Lomakina EI, Lin CS, Buhmann JM, Bingel U et al. Decoding the perception of pain from fMRI using multivariate pattern analysis. *NeuroImage*. 2012;63(3):1162-70. doi:10.1016/j.neuroimage.2012.08.035.
- Bufalari I, Aprile T, Avenanti A, Di Russo F, Aglioti SM. Empathy for pain and touch in the human somatosensory cortex. *Cerebral Cortex*. 2007;17:2553-61.
- Carlsson K, Petrovic P, Skare S, Petersson KM, Ingvar M. Tickling expectations: neural processing in anticipation of a sensory stimulus. *Journal of cognitive neuroscience*. 2000;12(4):691-703.
- Craig AD. How do you feel? Interoception: the sense of the physiological condition of the body. *Nature reviews*. 2002;3(8):655-66.
- Critchley HD, Harrison NA. Visceral influences on brain and behavior. *Neuron*. 2013;77(4):624-38. doi:10.1016/j.neuron.2013.02.008.
- Critchley HD, Rolls ET. Responses of primate taste cortex neurons to the astringent tastant tannic acid. *Chemical Senses*. 1996;21:135-45.
- Critchley HD, Wiens S, Rotshtein P, Ohman A, Dolan RJ. Neural systems supporting interoceptive awareness. *Nature neuroscience*. 2004;7(2):189-95.
- de Araujo IET, Kringelbach ML, Rolls ET, Hobden P. The representation of umami taste in the human brain. *Journal of neurophysiology*. 2003;90:313-9.
- de Araujo IET, Rolls ET. The representation in the human brain of food texture and oral fat. *Journal of Neuroscience*. 2004;24:3086-93.
- de Araujo IET, Rolls ET, Velazco MI, Margot C, Cayeux I. Cognitive modulation of olfactory processing. *Neuron*. 2005;46:671-9.
- Deco G, Rolls ET. Decision-making and Weber's Law: a neurophysiological model. *European Journal of Neuroscience*. 2006;24:901-16.
- Deco G, Rolls ET, Albantakis L, Romo R. Brain mechanisms for perceptual and reward-related decision-making. *Progress in neurobiology*. 2013;103:194-213.
- Deco G, Rolls ET, Romo R. Stochastic dynamics as a principle of brain function. *Progress in neurobiology*. 2009;88:1-16.
- Fiorio M, Haggard P. Viewing the body prepares the brain for touch: effects of TMS over somatosensory cortex. *The European journal of neuroscience*. 2005;22(3):773-7.
- Ge T, Feng J, Grabenhorst F, Rolls ET. 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*. 2012;59:1846-58.
- Grabenhorst F, Rolls ET. Attentional modulation of affective vs sensory processing: functional connectivity and a top-down biased activation theory of selective attention. *Journal of neurophysiology*. 2010;104:1649-60.
- Grabenhorst F, Rolls ET. Value, pleasure, and choice in the ventral prefrontal cortex. *Trends in Cognitive Sciences*. 2011;15:56-67.
- Grabenhorst F, Rolls ET, Bilderbeck A. How cognition modulates affective responses to taste and flavor: top down influences on the orbitofrontal and pregenual cingulate cortices. *Cerebral Cortex*. 2008a;18:1549-59.
- Grabenhorst F, Rolls ET, Parris BA. From affective value to decision-making in the prefrontal cortex. *European Journal of Neuroscience*. 2008b;28:1930-9.
- Grabenhorst F, Rolls ET, Parris BA, D'Souza A. How the brain represents the reward value of fat in the mouth. *Cerebral Cortex*. 2010;20:1082-91.
- Guest S, Grabenhorst F, Essick G, Chen Y, Young M, McGlone F et al. Human cortical representation of oral temperature. *Physiology and Behavior*. 2007;92:975-84.
- Hunt S. The peripheral and central processing of pain. *Neuroscience and biobehavioral reviews*. 2008;in press.
- Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G. Grasping the intentions of others with one's own mirror neuron system. *PLoS biology*. 2005;3(3):e79.
- Johansen-Berg H, Lloyd DM. The physiology and psychology of selective attention to touch. *Front Biosci*. 2000;5:D894-904.
- Kadohisa M, Rolls ET, Verhagen JV. Orbitofrontal cortex neuronal representation of temperature and capsaicin in the mouth. *Neuroscience*. 2004;127:207-21.
- Kadohisa M, Rolls ET, Verhagen JV. Neuronal representations of stimuli in the mouth: the primate insular taste cortex, orbitofrontal cortex, and amygdala. *Chemical Senses*. 2005a;30:401-19.
- Kadohisa M, Rolls ET, Verhagen JV. The primate amygdala: neuronal representations of the viscosity, fat texture, temperature, grittiness and taste of foods. *Neuroscience*. 2005b;132:33-48.
- Kobayashi S. Organization of neural systems for aversive information processing: pain, error, and punishment. *Frontiers in neuroscience*. 2012;6:136. doi:10.3389/fnins.2012.00136.
- Koski L, Wohlschlagel A, Bekkering H, Woods RP, Dubeau MC, Mazziotta JC et al. Modulation of motor and premotor activity during imitation of target-directed actions. *Cereb Cortex*. 2002;12(8):847-55.
- Kringelbach ML, O'Doherty J, Rolls ET, Andrews C. Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness. *Cerebral Cortex*. 2003;13:1064-71.
- McCabe C, Rolls ET, Bilderbeck A, McGlone F. Cognitive influences on the affective representation of touch and the sight of touch in the human brain. *Social, Cognitive and Affective Neuroscience*. 2008;3:97-108.
- McGlone F, Olausson H, Boyle JA, Jones-Gotman M, Dancer C, Guest S et al. Touching and feeling: differences in pleasant touch processing between glabrous and hairy skin in humans. *The European journal of neuroscience*. 2012;35(11):1782-8. doi:10.1111/j.1460-

9568.2012.08092.x.

McGlone F, Vallbo AB, Olausson H, Loken L, Wessberg J. Discriminative touch and emotional touch. *Canadian journal of experimental psychology = Revue canadienne de psychologie experimentale*. 2007;61(3):173-83.

Montoya P, Sitges C. Affective modulation of somatosensory-evoked potentials elicited by tactile stimulation. *Brain Res*. 2006;1068(1):205-12.

Morrison I, Bjornsdotter M, Olausson H. Vicarious responses to social touch in posterior insular cortex are tuned to pleasant caressing speeds. *J Neurosci*. 2011;31(26):9554-62. doi:10.1523/JNEUROSCI.0397-11.2011.

O'Doherty J, Kringelbach ML, Rolls ET, Hornak J, Andrews C. Abstract reward and punishment representations in the human orbitofrontal cortex. *Nature neuroscience*. 2001;4:95-102.

Olausson H, Cole J, Rylander K, McGlone F, Lamarre Y, Wallin BG et al. Functional role of unmyelinated tactile afferents in human hairy skin: sympathetic response and perceptual localization. *Experimental brain research Experimentelle Hirnforschung*. 2008;184(1):135-40.

Olausson H, Lamarre Y, Backlund H, Morin C, Wallin BG, Starck G et al. Unmyelinated tactile afferents signal touch and project to insular cortex. *Nature neuroscience*. 2002;5(9):900-4.

Pritchard TC, Edwards EM, Smith CA, Hilgert KG, Gavlick AM, Maryniak TD et al. Gustatory neural responses in the medial orbitofrontal cortex of the old world monkey. *J Neurosci*. 2005;25:6047-56.

Pritchard TC, Hamilton RB, Morse JR, Norgren R. Projections of thalamic gustatory and lingual areas in the monkey, *Macaca fascicularis*. *Journal of Comparative Neurology*. 1986;244:213-28.

Pritchard TC, Schwartz GJ, Scott TR. Taste in the medial orbitofrontal cortex of the macaque. *Ann N Y Acad Sci*. 2007;1121:121-35. doi:annals.1401.007 [pii] 10.1196/annals.1401.007.

Ramirez I. Chemosensory similarities among oils: does viscosity play a role? *Chemical Senses*. 1994;19:155-68.

Rolls ET. Taste and olfactory processing in the brain, and its relation to the control of eating. *Frontiers of Oral Biology*. 1998;9:40-75.

Rolls ET. *The Brain and Emotion*. Oxford: Oxford University Press; 1999.

Rolls ET. Neurophysiology and functions of the primate amygdala, and the neural basis of emotion. In: Aggleton JP, editor. *The Amygdala: A Functional Analysis*. Second Edition ed. Oxford: Oxford University Press; 2000. p. 447-78.

Rolls ET. *Emotion Explained*. Oxford: Oxford University Press; 2005.

Rolls ET. Brain mechanisms underlying flavour and appetite. *Philosophical Transactions of the Royal Society London B*. 2006;361:1123-36.

Rolls ET. Sensory processing in the brain related to the control of food intake. *Proceedings of the Nutrition Society*. 2007a;66:96-112.

Rolls ET. Understanding the mechanisms of food intake and obesity. *Obesity Reviews*. 2007b;8(Supplement 1):67-72.

Rolls ET. Functions of the orbitofrontal and pregenual cingulate cortex in taste, olfaction, appetite and emotion. *Acta Physiologica Hungarica*. 2008a;95:131-64.

Rolls ET. *Memory, Attention, and Decision-Making: A Unifying Computational*

- Neuroscience Approach. Oxford: Oxford University Press; 2008b.
- Rolls ET. The affective and cognitive processing of touch, oral texture, and temperature in the brain. *Neuroscience and biobehavioral reviews*. 2010;34:237-45.
- Rolls ET. The neural representation of oral texture including fat texture. *Journal of Texture Studies*. 2011;42:137-56.
- Rolls ET. Taste, olfactory, and food texture reward processing in the brain and the control of appetite. *Proceedings of the Nutrition Society*. 2012;71:488-501.
- Rolls ET. A biased activation theory of the cognitive and attentional modulation of emotion. *Frontiers in Human Neuroscience*. 2013;7, 74:1-15.
- Rolls ET. *Emotion and Decision-Making Explained*. Oxford: Oxford University Press; 2014.
- Rolls ET. Taste, olfactory, and food reward value processing in the brain. *Progress in neurobiology*. 2015.
- Rolls ET, Baylis LL. Gustatory, olfactory, and visual convergence within the primate orbitofrontal cortex. *Journal of Neuroscience*. 1994;14:5437-52.
- Rolls ET, Critchley H, Wakeman EA, Mason R. Responses of neurons in the primate taste cortex to the glutamate ion and to inosine 5'-monophosphate. *Physiology and Behavior*. 1996;59:991-1000.
- Rolls ET, Critchley HD, Browning AS, Hernadi A, Lenard L. Responses to the sensory properties of fat of neurons in the primate orbitofrontal cortex. *Journal of Neuroscience*. 1999;19:1532-40.
- Rolls ET, Deco G. *The Noisy Brain: Stochastic Dynamics as a Principle of Brain Function*. Oxford: Oxford University Press; 2010.
- Rolls ET, Grabenhorst F. The orbitofrontal cortex and beyond: from affect to decision-making. *Progress in neurobiology*. 2008;86:216-44.
- Rolls ET, Grabenhorst F, Parris BA. Warm pleasant feelings in the brain. *NeuroImage*. 2008;41:1504-13.
- Rolls ET, Grabenhorst F, Parris BA. Neural systems underlying decisions about affective odors. *Journal of cognitive neuroscience*. 2010;22:1069-82.
- Rolls ET, Kringelbach ML, de Araujo IET. Different representations of pleasant and unpleasant odors in the human brain. *European Journal of Neuroscience*. 2003a;18:695-703.
- Rolls ET, O'Doherty J, Kringelbach ML, Francis S, Bowtell R, McGlone F. Representations of pleasant and painful touch in the human orbitofrontal and cingulate cortices. *Cerebral Cortex*. 2003b;13:308-17.
- Rolls ET, Scott TR. Central taste anatomy and neurophysiology. In: Doty RL, editor. *Handbook of Olfaction and Gustation*. 2nd ed. New York: Dekker; 2003. p. 679-705.
- Rolls ET, Verhagen JV, Kadohisa M. Representations of the texture of food in the primate orbitofrontal cortex: neurons responding to viscosity, grittiness and capsaicin. *Journal of neurophysiology*. 2003c;90:3711-24.
- Rolls ET, Yaxley S, Sienkiewicz ZJ. Gustatory responses of single neurons in the caudolateral orbitofrontal cortex of the macaque monkey. *Journal of neurophysiology*. 1990;64:1055-66.
- Schaefer M, Flor H, Heinze HJ, Rotte M. Dynamic modulation of the primary somatosensory cortex during seeing and feeling a touched hand. *NeuroImage*. 2006;29(2):587-92.

- Singer T, Seymour B, O'Doherty J, Kaube H, Dolan RJ, Frith CD. Empathy for pain involves the affective but not sensory components of pain. *Science*. 2004;303(5661):1157-62.
- Tsakiris M, Hesse MD, Boy C, Haggard P, Fink GR. Neural signatures of body ownership: a sensory network for bodily self-consciousness. *Cereb Cortex*. 2007;17:2235-44.
- Umiltà MA, Kohler E, Gallese V, Fogassi L, Fadiga L, Keysers C et al. I know what you are doing. A neurophysiological study. *Neuron*. 2001;31(1):155-65.
- Verhagen JV, Kadohisa M, Rolls ET. The primate insular/opercular taste cortex: neuronal representations of the viscosity, fat texture, grittiness, temperature and taste of foods. *Journal of neurophysiology*. 2004;92:1685-99.
- Verhagen JV, Rolls ET, Kadohisa M. Neurons in the primate orbitofrontal cortex respond to fat texture independently of viscosity. *Journal of neurophysiology*. 2003;90:1514-25.
- Wang XJ. Probabilistic decision making by slow reverberation in cortical circuits. *Neuron*. 2002;36:955-68.
- Wiech K, Tracey I. Pain, decisions, and actions: a motivational perspective. *Frontiers in neuroscience*. 2013;7:46. doi:10.3389/fnins.2013.00046.
- Yaxley S, Rolls ET, Sienkiewicz ZJ. Gustatory responses of single neurons in the insula of the macaque monkey. *Journal of neurophysiology*. 1990;63:689-700.
- Yoo SS, Freeman DK, McCarthy JJ, 3rd, Jolesz FA. Neural substrates of tactile imagery: a functional MRI study. *Neuroreport*. 2003;14(4):581-5.