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INVITED REVIEW

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The texture and taste of food in the brain

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Abstract

Oral texture is represented in the brain areas that represent taste, including the primary taste cortex, the orbitofrontal cortex, and the amygdala. Some neurons represent viscosity, and their responses correlate with the subjective thickness of a food. Other neurons represent fat in the mouth, and represent it by its texture not by its chemical composition, in that they also respond to paraffin oil and silicone in the mouth. The discovery has been made that these fat-responsive neurons encode the coefficient of sliding friction and not viscosity, and this opens the way for the development of new foods with the pleasant mouth feel of fat and with health-promoting designed nutritional properties. A few other neurons respond to free fatty acids (such as linoleic acid), do not respond to fat in the mouth, and may contribute to some "off" tastes in the mouth. Some other neurons code for astringency. Others neurons respond to other aspects of texture such as the crisp fresh texture of a slice of apple versus the same apple after blending. Different neurons respond to different combinations of these texture properties, oral temperature, taste, and in the orbitofrontal cortex to olfactory and visual properties of food. In the orbitofrontal cortex, the pleasantness and reward value of the food is represented, but the primary taste cortex represents taste and texture independently of value. These discoveries were made in macaques that have similar cortical brain areas for taste and texture processing as humans, and complementary human functional neuroimaging studies are described.

KEYWORDS

brain, fat texture, food texture, obesity, olfaction, sensory-specific satiety, sliding friction, taste, viscosity

1 | INTRODUCTION

The aims of this paper are to describe how oral texture including fat is represented in the brain. Part of the importance of understanding this is that the evidence reviewed here shows that neurons in the brain encode fat in the mouth by its coefficient of sliding friction, and not by its viscosity or by its chemical properties (Rolls, Mills, Norton, Lazidis, & Norton et al., 2018). In contrast, the subjective thickness of a food is related to viscosity, represented by different neurons in the brain, and not by the coefficient of sliding friction. Fat in a food may help to make the food pleasant, but the intake of fat may need to be controlled, so understanding how fat is sensed in the mouth is likely to help with the development of new foods with a similar mouth feel and healthy nutritional content. Further, the representation in the brain of oral fat is frequently in terms of particular combinations of fat texture with other sensory aspects of food, including taste, other textures, and olfactory inputs, and these combinations are important for understanding the full impact of a food in the mouth on the pleasantness of that food. A key concept is that different neurons respond to different combinations of these oral texture and other signals produced by food, and understanding these signals helps both to design very pleasant new foods, and to understand how to help with appetite control, using for example sensory-specific satiety, which is based on combinations of these texture and other signals sent to the brain by food in the mouth.

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Oral texture representations in the brain are found in brain areas involved in taste. This enables some neurons to respond to texture only. Some respond to taste only, and some to combinations of oral texture and taste, thus providing across a population of neurons a very information-rich representation of what is in the mouth. For this reason, the taste pathways in the primate including human brain, which are similar, are described first. The taste pathways in primates including humans are quite different from those in rodents, and so the focus here is on studies in primates including humans (Norgren, 1984; Rolls, 2005, 2016c, 2016d, 2019b; Rolls & Grabenhorst, 2008; Rolls & Scott, 2003; Small & Scott, 2009). The studies in primates, macaques, are very important for understanding taste and oral texture processing, because it is possible to examine the responses of individual neurons, each of which is tuned different to combinations of stimuli, thus providing the information-rich representation of stimuli (Rolls & Treves, 2011). The signal recorded in neuroimaging studies in humans is from tens of thousands of neurons, and so cannot provide precise evidence on how information is encoded in each brain region (Rolls, Critchley, Verhagen, & Kadohisa, 2010; Rolls, 2016b; Rolls, Grabenhorst, & Franco, 2009). However, neuroimaging studies in humans can provide complementary evidence, and can address somewhat different questions more easily, such as the role of cognition at the word level on sensory including oral texture and taste processing (Grabenhorst, Rolls, & Bilderbeck, 2008; Rolls, 2016a; Rolls, 2016c, 2016d, 2019b). Because of the importance of the reward value and pleasantness of taste and oral texture in the control of food intake, I also consider here where sensory representations of what the stimulus is are converted into representations of the reward value and pleasantness of the taste and oral texture that are important in the control of appetite and food intake (Rolls, 2014, 2016d, 2019b, 2020). This is very different in primates and humans compared to rodents (Rolls, 2015, 2016c, 2019b). Oral texture refers to somatosensory signals produced by stimuli in the mouth. Oral fat texture refers to the oral texture produced by fat in the mouth. The subjective qualities of these stimuli have been measured by Kadohisa, Rolls, and Verhagen (2005a).

2 | TASTE PROCESSING IN THE PRIMATE BRAIN

2.1 | Pathways

The taste and related somatosensory, olfactory, and visual pathways in primates are illustrated in Figure 1. The multimodal convergence enables single neurons to each have different responses to different

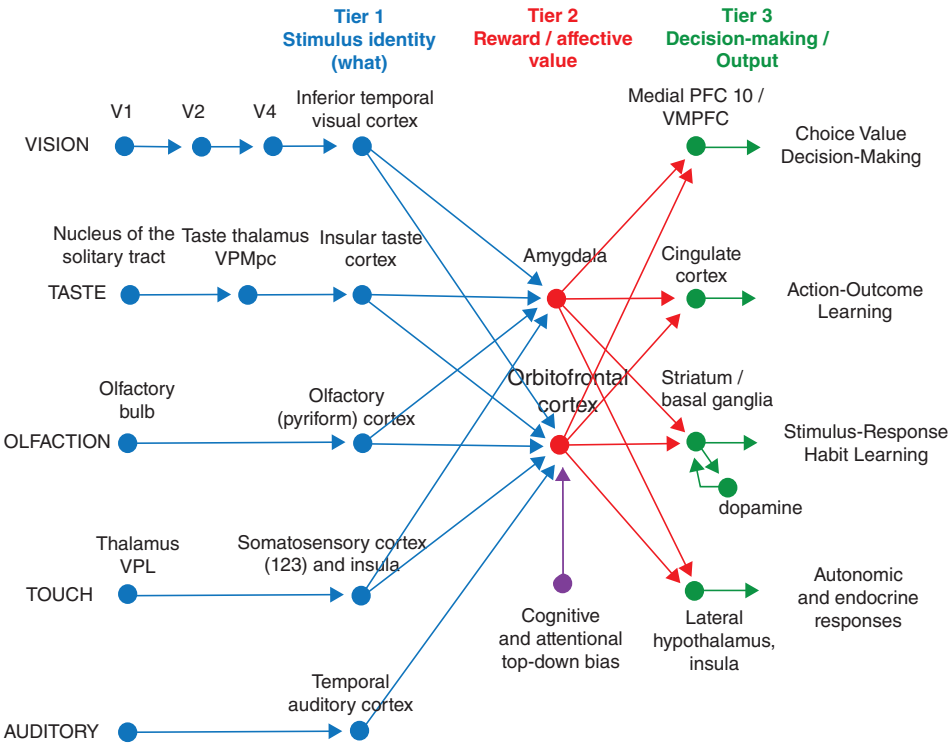

FIGURE 1 Schematic diagram of the taste and olfactory pathways in primates including humans showing how they converge with each other and with visual and other sensory pathways. Hunger modulates the responsiveness of the representations in the orbitofrontal cortex of the taste, smell, texture and sight of food, and the orbitofrontal cortex is where the palatability and pleasantness of food, and its reward value, is represented. VPMpc—ventralposteromedial thalamic nucleus; V1, V2, V4—visual cortical areas. Pregen Cing, pregenual cingulate cortex. For purposes of description, the stages can be described as Tier 1, representing what object is present independently of reward value; Tier 2 in which reward value is represented; and Tier 3 in which decisions between stimuli of different value are taken, and in which value is interfaced to behavioral output systems. A pathway for top-down attentional and cognitive modulation of emotion is shown in purple. Auditory inputs also reach the amygdala

combinations of taste, oral texture, temperature, olfactory, and visual inputs to encode different flavors in brain regions such as the orbitofrontal cortex (Rolls, 2014, 2019b, 2019c). The description provided here refers to primates including humans, as the taste pathways and principles of operation of the taste system are so different in rodents (Rolls, 2016c, 2019b; Small & Scott, 2009).

2.2 | The primary taste cortex

The primary taste cortex is in the primate anterior insula and adjoining frontal operculum and has not only taste neurons tuned to salt, sweet, bitter, sour (Rolls, 2016c; Rolls & Scott, 2003; Scott & Plata-Salaman, 1999; Scott, Yaxley, Sienkiewicz, & Rolls, 1986; Yaxley, Rolls, & Sienkiewicz, 1990), and umami (typically monosodium glutamate) (Baylis & Rolls, 1991; Rolls, Critchley, Wakeman, & Mason, 1996), but also other neurons that encode oral somatosensory stimuli including viscosity, fat texture, temperature, and capsaicin (Verhagen, Kadohisa, & Rolls, 2004). Some neurons respond to particular combinations of taste and oral texture stimuli, but do not respond to visual or olfactory stimuli such as the sight and smell of food (Verhagen et al., 2004). In the primary taste cortex neurons do not encode the reward value of taste, that is the appetite for a food, in that their responses are not decreased to zero by feeding the taste to satiety (Rolls, Scott, Sienkiewicz, & Yaxley, 1988; Yaxley, Rolls, & Sienkiewicz, 1988).

2.3 | The secondary taste cortex in the orbitofrontal cortex

A secondary taste cortical area in primates was discovered by Rolls, Yaxley, and Sienkiewicz (1990) in the orbitofrontal cortex, extending several mm anterior to the primary taste cortex, and proved to be secondary taste cortex by its anatomically shown inputs from the primary taste cortex (Baylis, Rolls, & Baylis, 1995). The region that corresponds to this in humans is the caudal orbitofrontal cortex, as shown by its cytoarchitectonics (Carmichael & Price, 1994; Öngür, Ferry, & Price, 2003; Price, 2006), and by its activations in neuroimaging studies (see below), with further discussion of the topology by Rolls (2019b, 2019c). One principle of taste analysis is that by the secondary taste cortex, the neuronal tuning can be selective, with some neurons responding for example only to sweet taste. The selective responses of these neurons helps, especially when combined with texture, olfactory, and visual inputs, to provide a basis for changes in appetite for some but not other foods eaten during a meal, that is, for sensory-specific satiety (Rolls, 2014, 2016d; Rolls, Sienkiewicz, & Yaxley, 1989).

2.4 | Five prototypical tastes, including umami

In the primary and secondary taste cortices, many neurons have their best responses to each of the four classical prototypical tastes: salt, sweet, bitter and sour (Rolls, 2015, 2016c; Scott & Plata-Salaman, 1999), but also many neurons have their best responses to umami tastants such as glutamate (which is present in many natural foods such as tomatoes, mushrooms and milk) (Baylis & Rolls, 1991) and inosine monophosphate (which is present in meat and some fish such as tuna) (Rolls, Critchley, Wakeman, & Mason, 1996). These findings, and the identification of possible glutamate taste receptors (Chandrashekar, Hoon, Ryba, & Zuker, 2006; Roper & Chaudhari, 2017), provides evidence that there are five prototypical types of taste information channels, with umami contributing, often in combination with corresponding olfactory inputs (McCabe & Rolls, 2007; Rolls, Critchley, Browning, & Hernadi, 1998), to the flavor of protein. Other neurons respond to water, and others to somatosensory texture-related stimuli including astringency (e.g., revealed by responses to tannic acid) (Critchley & Rolls, 1996c), and capsaicin (Kadohisa, Rolls, & Verhagen, 2004; Rolls, Verhagen, & Kadohisa, 2003).

2.5 | The pleasantness of the taste of food

The reward value of a stimulus such as the taste of food is modulated by motivational state, for example hunger, and this is an important way in which appetite and motivational behavior is controlled (Rolls, 2014). The subjective correlate is that food tastes pleasant when hungry, and tastes neutral hedonically after it has been eaten to satiety. This modulation of taste-evoked signals by hunger is not a property found in early stages of the primate gustatory system, including the nucleus of the solitary tract (Yaxley, Rolls, Sienkiewicz, & Scott, 1985) and the primary taste cortex (Rolls et al., 1988; Yaxley et al., 1988). On the other hand, in the orbitofrontal secondary taste cortex, taste neurons decrease their responses to zero during feed to satiety, and sensory-specific satiety is represented here (Rolls et al., 1989). This is very different to what happens in rodents, in which some reduction in neuronal responses to food does occur in early stages of taste (and olfactory) processing, making the relevance to humans of food-related brain processing in rodents (Rolls, 2015, 2016c).

2.6 | Sensory-specific satiety

The responses of neurons in the secondary taste cortex in the orbitofrontal cortex to the taste, sight, and odor of food decrease to the particular food eaten to satiety, and this implement sensory-specific satiety (Critchley & Rolls, 1996a; Rolls et al., 1989). This is a devaluation procedure, and shows that reward value is represented in the orbitofrontal cortex (Rolls, 2019b, 2019c). The discovery of sensory-specific satiety by neuronal recordings in the macaque lateral hypothalamus, which receives inputs from the orbitofrontal cortex (Rolls, 1981; Rolls, Murzi, Yaxley, Thorpe, & Simpson, 1986) led to studies showing that this applies in humans (B. J. Rolls, E. T. Rolls, & E. A. Rowe, 1983; Rolls, Rowe, & Rolls, 1982; Rolls et al., 1981; Rolls & Rolls, 1977, 1982; Rolls & Rolls, 1997, Rolls, 1981 #440). The reduced reward value and pleasantness of food is computed in the orbitofrontal cortex, in that it is not found in the responses of neurons in the nucleus of the solitary tract or frontal opercular or insular gustatory cortices to gustatory stimuli (Rolls et al., 1988; Yaxley et al., 1985; Yaxley et al., 1988), or in the inferior temporal cortex to visual stimuli (Rolls, Judge, & Sanghera, 1977). Consistently, humans

report that the food on which they have been satiated tastes almost as intense as when they were hungry, but is much less pleasant (E. T. Rolls, B, J. Rolls, & E. A. Rowe, 1983). The same principle applies to oral texture, in that the responses of orbitofrontal cortex neurons show satiety effects after feeding to satiety with fat (cream) (Critchley & Rolls, 1996a; Rolls, Critchley, Browning, Hernadi, & Lenard, 1999). Further evidence on sensory-specific satiety, and on appetite control, is provided elsewhere (Critchley & Rolls, 1996b; Rolls, 1996; Rolls, 1999, 2000b; Rolls, 2000c, 2015, 2016d, 2018; Rolls & Scott, 2003; Scott, Yan, & Rolls, 1995).

It is an important principle that the identity of a taste, and its intensity, are represented separately from its pleasantness (Grabenhorst et al., 2008; Grabenhorst & Rolls, 2008; Grabenhorst & Rolls, 2011; Rolls, 2014, 2016b; Rolls & Grabenhorst, 2008). Thus it is possible to represent what a taste is, and to learn about it, even when we are not hungry.

3 | THE REPRESENTATION OF FLAVOR: CONVERGENCE OF OLFACTORY AND TASTE INPUTS

Taste representations are combined with olfactory representations in the orbitofrontal cortex to produce a representation of flavor (Rolls & Baylis, 1994). Before the orbitofrontal cortex, neurons have mainly unimodal responses, for example, to taste and not to odor or sight in the primary taste cortex (Rolls & Baylis, 1994; Verhagen et al., 2004), and not to taste or odor in the inferior temporal visual cortex (Rolls et al., 1977). The bimodal neurons are formed by learning of odor-taste associations in the orbitofrontal cortex (Critchley & Rolls, 1996b; Rolls, 2014, 2015).

4 | THE REPRESENTATION OF THE PLEASANTNESS OF ODOR IN THE BRAIN: OLFACTORY AND VISUAL SENSORY-SPECIFIC SATIETY, THEIR REPRESENTATION IN THE PRIMATE ORBITOFRONTAL CORTEX, AND THE ROLE OF SENSORY-SPECIFIC SATIETY IN APPETITE

The pleasantness of odor is represented in the orbitofrontal cortex, in that the responses of some olfactory neurons to a food odor are decreased during feeding to satiety with a food (e.g., fruit juice, or cream) containing that odor, and produces sensory-specific satiety (Critchley & Rolls, 1996a).

5 | THE RESPONSES OF ORBITOFRONTAL CORTEX NEURONS TO THE TEXTURE AND TEMPERATURE OF FOOD

The orbitofrontal cortex (OFC) of primates is also important in receiving somatosensory inputs, including inputs produced by the texture of food including fat in the mouth (Rolls, 2016a). In one series of experiments, the texture of foods were altered by the addition of gelatine or methyl cellulose, or by puréeing a semisolid food (Rolls, 1998, 1999). Some examples of how taste neurons that respond to taste in the OFC also respond to the texture of foods are shown in Figure 2. A neuron with high responses to the texture of a crisp dry expanded rice cereal, and smaller responses when water was added to make it soft is illustrated in Figure 2a. A neuron with higher responses to a crisp slice of fresh apple than to a puree made from the apple, and with lower responses to the apple juice made from the filtered puree is shown in Figure 2b.

Some neurons with responses to texture parametrically encode the viscosity of food in the mouth (shown with a carboxymethyl cellulose series in the range 1–10,000 centiPoise). Other neurons encode the particulate quality of food in the mouth, shown quantitatively by, for example, adding 20–100 μm microspheres to 1,000 cP methyl cellulose ("Gritty") (Rolls, Verhagen, & Kadohisa, 2003; Rolls, 2020). Two OFC neurons are shown in Figure 3 to illustrate these properties. Neuron bk244 responded with a graded increase of firing rate to viscosity in the range 10–1,000 cP, had no taste responses, did respond to oils, and did not respond to capsaicin. The responses of these viscosity-sensitive neurons parallel that of humans' subjective ratings of the thickness of the same methyl cellulose viscosity series: the human subjective ratings of thickness were linearly related to the log of the measured viscosity of the stimuli (Kadohisa et al., 2005a). Neuron bo34 shown in Figure 3 also had a graded increase of firing rate to viscosity in the range 10–10,000 cP; also respond to some tastes (glucose: sweet; HCl: sour; and quinine: bitter) but not to others (NaCl and monosodium glutamate), had no responses to oils, and did respond to capsaicin. These neurons illustrate that taste, viscosity, fatty oils, and capsaicin can be coded for independently by a population of neurons of which these are examples. The independence arises from the fact that different neurons respond to different combinations of these stimuli. The oils used included vegetable oil, coconut oil, and safflower oil, mineral oil, and silicone oil (see Table 1) (Rolls, Verhagen, & Kadohisa, 2003).

Further, some neurons in the OFC encode the temperature of substances in the mouth, and this information about temperature is represented independently of other sensory inputs by some neurons, and in combination with oral texture or taste by other neurons (Kadohisa et al., 2004).

Neurons in the insular primary taste cortex (Verhagen et al., 2004), and in the amygdala (Kadohisa, Rolls, & Verhagen, 2005b), also respond to these oral texture signals including viscosity and fat texture, and to temperature. One difference is that neurons in the insular primary taste cortex have these taste and oral texture responses, but are little affected by olfactory stimuli, or by the sight of food (Kadohisa et al., 2005a; Verhagen et al., 2004). These olfactory and visual inputs are added to the representation in the orbitofrontal cortex (Critchley & Rolls, 1996a, 1996b; Rolls & Baylis, 1994; Rolls, Critchley, Mason, & Wakeman, 1996; Rolls, Critchley, & Treves, 1996). Other differences between these areas are that in the primary

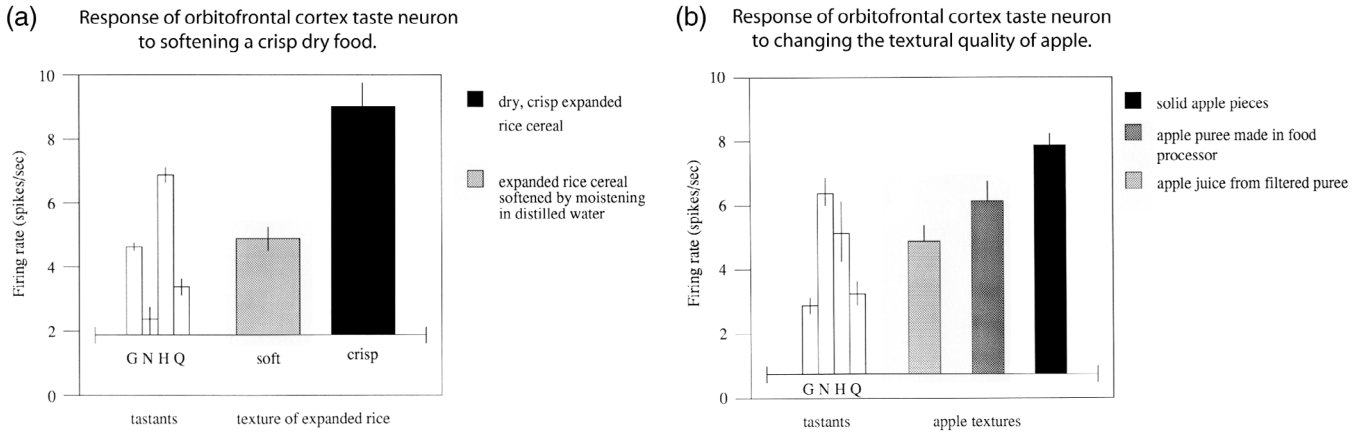

FIGURE 2 Examples of the effects on orbitofrontal cortex taste-responsive neurons of altering the textural properties of foods. (a) A neuron that responded more to the texture of a crisp dry expanded rice cereal than when it was made soft with water. (b) A neuron that responded more to a crisp slice of fresh apple than to a puree made from the apple, which in turn produced a larger response than the apple juice from the filtered puree. The response measured is the firing rate of the single neuron in spikes/s with the mean and *SEM* over 4–10 trials shown. The responses of the neurons to 1 M glucose (G), 0.1 M NaCl (N), 0.01 M hydrochloric acid (H), and 0.001 M quinine are also shown. The responses are shown as changes from the baseline spontaneous firing rate of the neurons. *Source:* Previously unpublished experiments of H.D. Critchley and E.T. Rolls (1995)

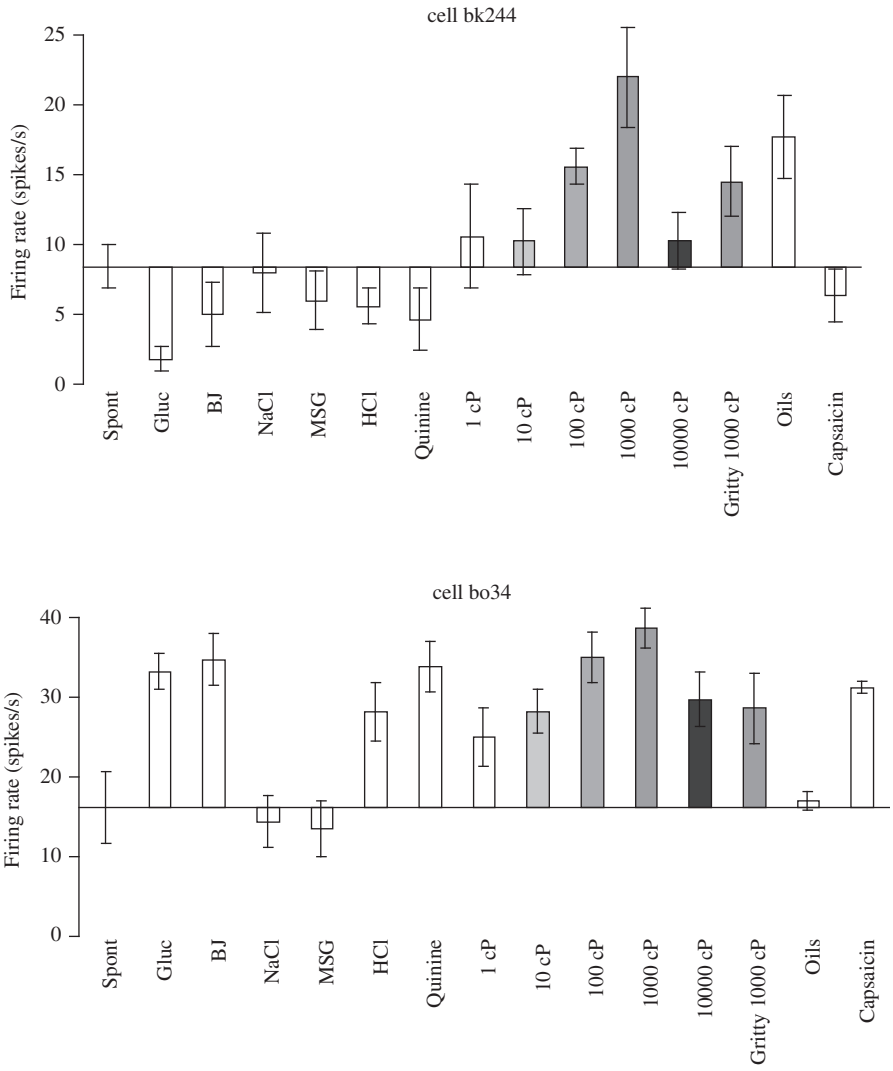

FIGURE 3 Oral somatosensory and taste inputs to orbitofrontal cortex neurons. Above. Firing rates (mean ± *SEM*) of viscosity-sensitive neuron bk244 which did not have taste responses, in that it did not respond differentially to the different taste stimuli. The firing rates are shown to the viscosity series (carboxymethyl cellulose 1–10,000 centiPoise, to the gritty stimulus (1,000 cP carboxymethyl cellulose with Fillite microspheres), to the taste stimuli 1 M glucose (Gluc), 0.1 M NaCl, 0.1 M MSG, 0.01 M HCl and 0.001 M QuinineHCl, and to fruit juice (BJ). Spont = spontaneous firing rate. Below. Firing rates (mean ± *SEM*) of viscosity-sensitive neuron bo34 which had no response to the oils (mineral oil, vegetable oil, safflower oil and coconut oil, which have viscosities that are all close to 50 cP). The neuron did not respond to the gritty stimulus in a way that was unexpected given the viscosity of the stimulus, was taste tuned, and did respond to capsaicin. *Source:* After Rolls, Verhagen, and Kadohisa (2003)

TABLE 1 Stimuli

Stimulus	Abbreviation	Concentration	MWt	Approx. viscosity (cP)[b]	Chemical group	CSF[c] 25 mm/s
Glucose	G	1 M	180	1	Monosaccharide aldohexose	
Black currant juice	BJ	20%		1	Mixture	
Monosodium glutamate	M	0.1 M	187	1	Amino acid salt	
NaCl	N	0.1 M	58	1	Inorganic salt	
HCl	H	0.01 M	36	1	Inorganic acid	
Quinine HCl	Q	0.001 M	387	1	Alkaloid	
Water	V1 or 1 cP	5 mM NaCl		1		0.169
CMC[a]	C10 or 10 cP	0.2 g + 1 L V1	70,000	5	Polysaccharide	0.110
CMC[a]	C100 or 100 cP	4.0 g + 1 L V1	70,000	108	Polysaccharide	0.076
CMC[a]	C1000 or 1,000 cP	11.0 g + 1 L V1	70,000	945	Polysaccharide	0.057
CMC[a]	C10000 or 10,000 cP	24.0 g + 1 L V1	70,000	8,550	Polysaccharide	0.035
Mineral oil	MO	100%		26	Hydrocarbon mixture	0.031
Silicone oil	SiO or SilO	100%		10,100, and 1,000 or 280	Silicon-oxygen polymer	0.007 for Si280
Vegetable oil	VOo or VOf	100%		56	Fat	0.029
Coconut oil	CO	100%		118	Fat	0.032
Safflower oil	SaO or SafO	100%		50	Fat	0.035
Single cream	SC	100%		250	Emulsion	0.031
Lauric acid C12:0	LaA	100 μM		1	FFA	0.11
Linoleic acid C18:2	LiA	100 μM		1	FFA	0.11

[a]CMC, carboxymethyl cellulose.
[b]The values given for the viscosity are those measured with the Kinexus rheometer, rather than the nominal values measured previously with a Brookfield rheometer.
[c]CSF, coefficient of sliding friction.

taste cortex, taste and viscosity are more likely to activate different neurons, with more convergence onto single neurons particularly in the OFC and amygdala. This reflects the hierarchical organization shown in Figure 1.

The different responses of different orbitofrontal cortex neurons to different combinations of these oral sensory stimuli provides a basis for different behavioral responses and subjective experiences. Consistently, the mean correlations between the representations of the different stimuli provided by the population of orbitofrontal cortex neurons were lower (0.71) than for the insula (0.81) and amygdala (0.89). Further, the representation was more sparse in the OFC (0.67) than in the insula (0.74) and amygdala (0.79) (Kadohisa et al., 2005a). (In a sparse representation, each neuron is more specifically tuned to the stimuli, and the proportion of neurons responding to any one stimulus is low (Rolls, 2016b; Rolls & Treves, 2011). Sparse representations in the orbitofrontal cortex help in the computation of sensory-specific satiety that probably involves synaptic adaptation in the OFC (Rolls, 2016b)). Multidimensional scaling (MDS) provides evidence that the insular primary taste cortex and amygdala emphasize the representation of oral viscosity, and that the orbitofrontal cortex emphasizes the representation of pleasant tastes such as glucose and fruit juice (see Fig. 2 of Kadohisa et al., 2005a). (The distances between stimuli in a MDS space reflects how closely correlated the responses of a set of neurons are to the different stimuli.)

6 | FAT TEXTURE IN THE MOUTH IS ENCODED BY NEURONS IN THE ORBITOFRONTAL CORTEX, PRIMARY TASTE CORTEX, AND AMYGDALA BY THE COEFFICIENT OF SLIDING FRICTION. FOOD THICKNESS IS ENCODED BY VISCOSITY

The texture of food in the mouth provides an important indication of whether fat is present in a food, as described next. Fat is important as a food with a high energy value, and as a source of essential fatty acids. Rolls et al. (1999) discovered a population of neurons in the orbitofrontal cortex that responds to the texture of fat in the mouth. Figure 4 shows an example of one such neuron. The neuron increased its firing rate to cream (double and single cream, which have different proportions of fat as an emulsion), to the oils, and responded to oral texture rather than the chemical properties of the fat in that it also responded to 0.5 ml of silicone oil $(Si(CH_3)_2O)_n$ and paraffin oil

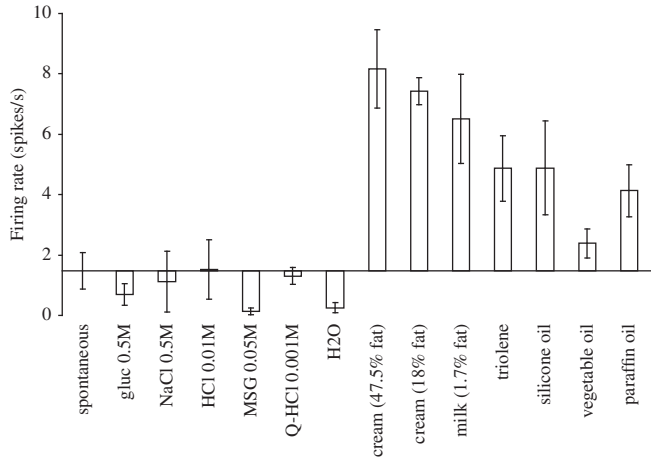

FIGURE 4 A neuron in the primate orbitofrontal cortex responding to the texture of fat in the mouth. The neuron increased its firing rate to cream (double and single cream, with the fat proportions shown), and responded to texture rather than the chemical structure of the fat in that it also responded to 0.5 ml of silicone oil $(Si(CH_3)_2O)_n$ or paraffin oil (hydrocarbon). The neuron did not have a taste input. Gluc, glucose; NaCl, salt; HCl, sour; Q-HCl, quinine, bitter. The spontaneous firing rate of the cell is also shown. *Source:* After Rolls et al. (1999)

(hydrocarbon). The neuron did not have a taste input. The firing rate responses are shown against the baseline spontaneous firing rate of the neuron.

6.1 | Fat texture responsive neurons

In a series of investigations, populations of single neurons have been shown to respond selectively to fat texture in the mouth (Kadohisa et al., 2005a). This has been shown for macaque single neurons in the anterior insular primary taste cortex (Verhagen et al., 2004), in the orbitofrontal cortex (secondary taste cortex) (Rolls et al., 1999; Verhagen, Rolls, & Kadohisa, 2003), and in the amygdala (Kadohisa et al., 2005b). These neurons respond to the texture of fat in that they respond to food oils such as coconut oil, safflower oil, and vegetable oil, to emulsions such as dairy cream, and also to mineral oil (a pure hydrocarbon), and to silicone oil. These neurons do not respond to fatty acids such as linoleic acid or lauric acid, and their responses are not correlated with taste properties such as sweet, salt, bitter, sour, and umami, nor with oral temperature (Kadohisa et al., 2005a; Rolls et al., 1999).

Until recently, the texture property encoded by fat-sensitive neurons was unknown, although it was evident that it is not viscosity (Kadohisa et al., 2005a; Verhagen, Rolls, & Kadohisa, 2003). Indeed, different neurons encode oral viscosity (Rolls, Verhagen, & Kadohisa, 2003). However, the hypothesis that has been tested recently (Rolls, Mills, et al., 2018) is that the neurons with selectivity for fat and nonfat oils in previous neurophysiological investigations (Kadohisa et al., 2005a; Kadohisa et al., 2005b; Verhagen et al., 2004; Verhagen, Rolls, & Kadohisa, 2003) have responses that are correlated with the coefficient of sliding friction. The coefficient of sliding friction is the force required to slide two surfaces divided by the force normal to the surfaces (Ludema, 1996). This is also known as kinetic or dynamic friction. The aim of the recent investigation (Rolls, Mills, et al., 2018) was to analyze whether the responses of the previously recorded fat-sensitive neurons (Kadohisa et al., 2005a; Kadohisa et al., 2005b; Verhagen et al., 2004; Verhagen, Rolls, & Kadohisa, 2003) were correlated with the coefficient of sliding friction.

The stimuli used in the neurophysiological investigations (Kadohisa et al., 2005a; Kadohisa et al., 2005b; Verhagen et al., 2004; Verhagen, Rolls, & Kadohisa, 2003) are shown in Table 1, and included a viscosity series of the food thickening agent carboxymethyl cellulose with nominal viscosities measured with a Brookfield rheometer in the original experiments of 10, 100, 1,000 and 10,000 centiPoise (1 Pa.s = 1,000 cP); safflower, coconut and vegetable oil, and single cream (18% fat); silicone oil (either 10, 100, and 1,000 cP or 280 cP); mineral oil; and distilled water. The carboxymethyl cellulose series was included in the investigations to assess whether any neurons had responses to the thickness of the food, which is subjectively linearly related to the log of the viscosity of the carboxymethyl cellulose (Kadohisa et al., 2005a). The nonfat oils, mineral (paraffin) oil which is a pure hydrocarbon, and silicone oil $(Si(CH_3)_2O)_n$, were included to investigate whether neurons categorized as responding to fat also responded to nonfat oils (Kadohisa et al., 2005a; Kadohisa et al., 2005b; Verhagen et al., 2004; Verhagen, Rolls, & Kadohisa, 2003).

In the new analyses (Rolls, Mills, et al., 2018), the tribology of the stimuli was measured with a MTM2 Mini Traction Machine (PCS Instruments) using a Stribeck series with a 2 N normal force, a rolling stainless steel ball with a silicone disk rotating with a slide roll ratio of 50%, and average of 1–1,500 mm/s (Malone, Appelqvist, & Norton, 2003). From multiple measurements with increasing and decreasing speed sweeps values at 10, 25, and 80 mm/s were taken, as 40–250 mm/s is considered representative of conditions in the mouth from previous work with a mixed lubrication regime (Malone et al., 2003). The results were presented for 25 mm/s as the correlations between the friction measures at these different speeds were very high ($r \geq 0.985$) for this set of stimuli.

The rheology of the stimuli was measured (Rolls, Mills, et al., 2018) with a Kinexus Rheometer (Malvern Instruments, UK) using a set of shear rates at values between 0.1 and 100 s^{-1} after a steady state was reached. The values at 12 s^{-1} were used, as this is thought to be representative of conditions in the mouth (Shama & Sherman, 1973), but the values for this set of stimuli were very highly correlated ($r = 0.995$ for the logs of the viscosities) for 50 s^{-1} (Wood, 1968). An additional reason for this choice is that for the carboxymethyl cellulose used here, there is a high correlation between the log of the viscosity measured at the shear rate of 12 s^{-1} and subjective thickness ratings (Kadohisa et al., 2005a).

Correlations between the firing rates of 164 neurons and the two physical measures, the coefficient of sliding friction, and the viscosity, were calculated (Rolls, Mills, et al., 2018). Sixty-eight of the macaque neurons analyzed were in the insular primary taste cortex (with the recording sites shown in Fig. 10 of Verhagen et al. (2004)), 51 in the orbitofrontal secondary taste cortex (with the recording sites shown in Fig. 11 of Verhagen et al. (2003)), and 45 in the amygdala (with the recording sites shown in Fig. 7 of Kadohisa et al. (2005b)). Three types of fat-sensitive neuron were found in the analysis (Rolls, Mills, et al., 2018), as follows.

6.1.1 | Neurons with responses linearly correlated with decreases in the coefficient of sliding friction: Linear fat texture neurons

A neuron with its firing rate responses linearly correlated with decreases in the coefficient of sliding friction is shown in Figure 5 (left). Low coefficients of sliding friction indicate lubricity produced for example by the oils. The relation to viscosity (right) is much weaker, with the oils producing a larger neuronal response than is predicted linearly.

Seven neurons were recorded with similar properties (4/68 in the insular primary taste cortex, 1/51 in the orbitofrontal secondary taste cortex, and 2/45 in the amygdala), with details of their coefficients provided in the original report (Rolls, Mills, et al., 2018).

6.1.2 | Neurons with responses nonlinearly correlated with decreases in the coefficient of sliding friction: Nonlinear fat texture neurons

A neuron with its firing rate responses nonlinearly correlated with decreases in the coefficient of sliding friction is illustrated in Figure 6 (left). The neuron responded only to very low coefficients of sliding friction, that is, its responses were supra-linearly related to decreases in the coefficient of sliding friction. This resulted in it being a highly selective fat-encoding neuron. There was a much weaker relation to viscosity (right), with the oils producing a larger response than predicted linearly. Further, a regression line through the nonoil stimuli would have a much lower slope.

Eight neurons with similar properties were recorded (2/68 in the insular primary taste cortex, 5/51 in the orbitofrontal secondary taste cortex, and 1/45 in the amygdala), with details of their coefficients provided in the original paper (Rolls, Mills, et al., 2018).

A neuronal population analysis showed that the mean information available from these 8 single cells was 1 bit (the maximum possible) about the coefficient of sliding friction (whether its value was less than or greater than 0.35), and the mean percentage correct for the population of 8 single cells was 100% correct. This showed that when combined together, these neurons convey accurate information about the coefficient of sliding friction. They encoded little information about the viscosity of the stimuli (Rolls, Mills, et al., 2018). The population of 7 neurons with firing rates linearly related to decreases in the coefficient of sliding friction encoded 0.41 bits of information and provided for 87.5% correct discrimination between fat and nonfat. This population of 7 neurons again had no information about viscosity (0.0 bits and 54% correct). The information from the 8 neurons

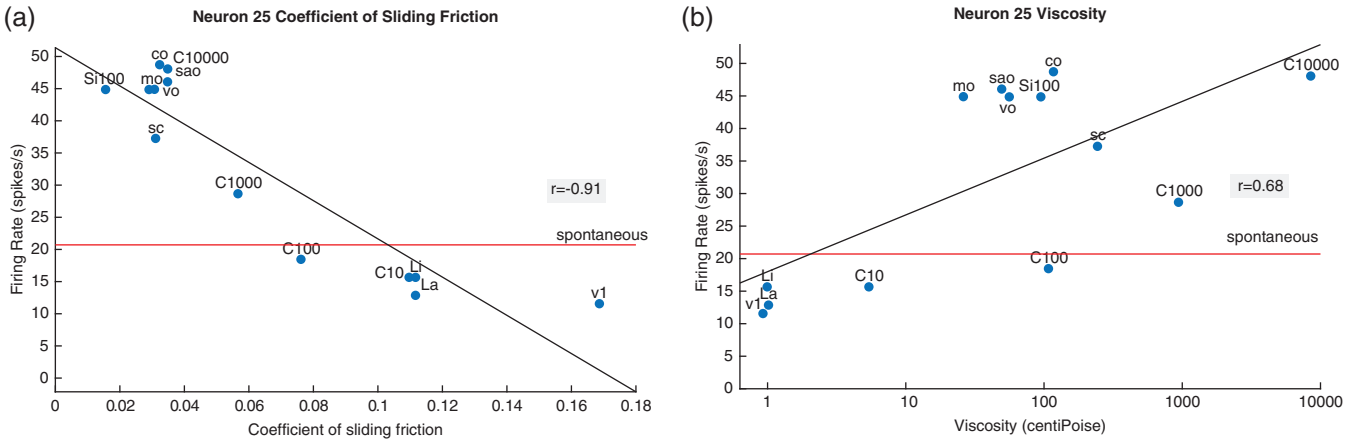

FIGURE 5 An orbitofrontal taste cortex neuron with responses linearly correlated with decreases in the coefficient of sliding friction (a). Low coefficients of sliding friction indicate lubricity produced for example by the oils. The linear regression line shown has a correlation of $r = -0.91$ ($p = 1.2 \times 10^{-5}$) between the firing rate of the neuron and the coefficient of sliding friction. The closeness of the data points to this regression line, and the value of the correlation coefficient, indicate how well the data fit a linear function of the coefficient of sliding friction. (b): There is a much weaker relation to viscosity ($r = 0.68$, $p = .01$), with the oils producing a larger response than predicted linearly. Further, a regression line through the nonoil stimuli would have a much lower slope. C10-C10000: carboxymethyl cellulose with the nominal viscosity of 10, 100, 1,000 and 10,000 cP. v1: water (1 cP). co: coconut oil; mo: mineral oil; sao: safflower oil; vo: vegetable oil; sc: single cream. Si10, Si100, Si1000: silicone oil with the viscosity indicated. Li: linoleic acid; La; lauric acid. The horizontal line indicates the spontaneous firing rate. The Pearson correlation between the firing rate of each neuron and (a) the coefficient of sliding friction, and (b) the viscosity, was calculated to show to what extent the firing of a neuron reflected one or other of these measures. Linear regression lines are shown in the figures for how the firing rates were related to the coefficient of sliding friction, or to the log of the viscosity. (The log of the viscosity was used because human psychophysical measures of the thickness of these stimuli were linearly related to the log of the viscosity (Kadohisa et al., 2005a).) Each firing rate value shown in the figure and used in the statistical analyses is the mean of four or more firing rate measurements taken in random permuted sequence across the set of stimuli, with standard errors shown in the original publications (Kadohisa et al., 2005a; Kadohisa et al., 2005b; Verhagen et al., 2004; Verhagen, Rolls, & Kadohisa, 2003). Moreover, it has been established that some cortical neurons respond to water in the mouth; and that some neurons can respond to oral stimuli by decreasing their firing rates below the spontaneous level of firing (Kadohisa et al., 2005a; Kadohisa et al., 2005b; Rolls et al., 1990; Scott et al., 1986; Verhagen et al., 2004; Verhagen, Rolls, & Kadohisa, 2003; Yaxley et al., 1990)

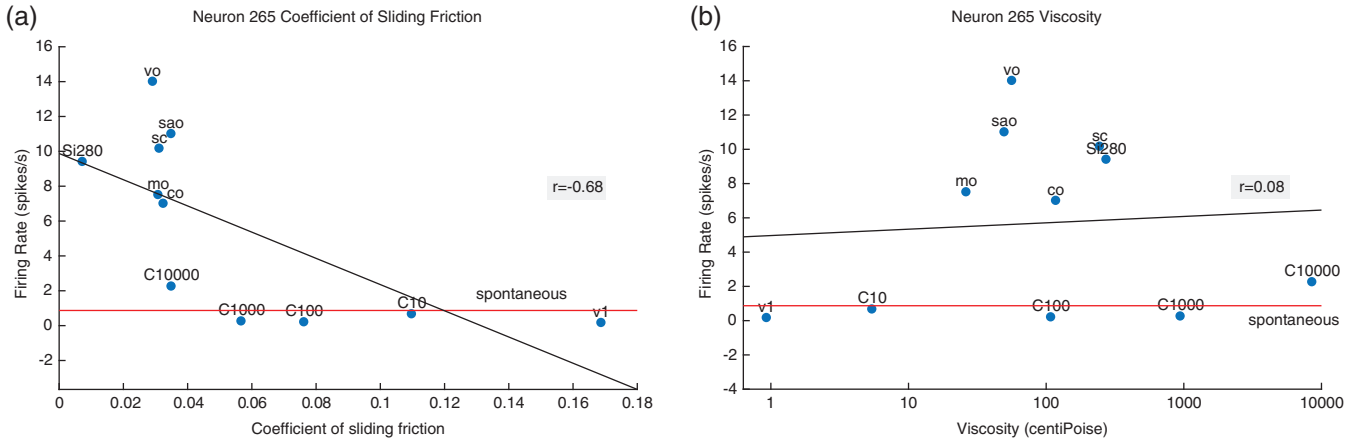

FIGURE 6 An orbitofrontal cortex (secondary taste cortex) neuron with responses nonlinearly correlated with decreases in the coefficient of sliding friction (a). The neuron responds almost not at all until the coefficient of sliding friction falls below 0.04. The neuron is thus very selective for fat texture, because of its nonlinear response in relation to the coefficient of sliding friction. The linear regression line has a correlation of $r = -0.68$ ($p = .02$). (b): There is a much weaker relation to viscosity ($r = 0.08$, $p = .82$), with the oils producing a larger response than predicted linearly. Further, a regression line through the nonoil stimuli would have a lower slope. Conventions as in Figure 5. Si280: silicone oil with a nominal viscosity of 280 cP. *Source:* Modified from Rolls et al. (2018)

inhibited by fat (described next) was 0.24 bits and 77% correct. This rigorous information theoretic analysis provides evidence with a quantitative metric that can also be applied to behavioral and other neuroscience measures such as fMRI. This enables what is signaled by these fat-responsive neurons to be compared to the information available to the whole organism, or by other measures such as fMRI (Rolls et al., 2009).

6.1.3 | Neurons with responses positively correlated with increases in the coefficient of sliding friction: neurons that are inhibited by fat

Another population of neurons had low firing rates to fats and oils, and higher firing rates to other stimuli. It was discovered that these neurons had firing rates that were positively correlated with the coefficient of sliding friction. One such neuron is shown in Figure 7 (left). The neuron did not respond to any stimulus with a coefficient of sliding friction less than 0.06. This made it not respond to fats and oils. This neuron had nonlinear properties, and was inhibited by any stimulus with a coefficient of sliding friction less than 0.06, including C1000 and C10000. Some neurons had more linear responses, and therefore had some response to stimuli with a coefficient of sliding friction of 0.06, such as C1000. This neuron had a much weaker relation to viscosity (Figure 7, right), with the oils producing no response. This neuron responded to the linoleic acid and lauric acid as predicted by their coefficients, showing that inhibition by fats and oils in this class of neuron is not produced by (at least these) fatty acids, consistent with other evidence (Rolls, 2011a).

32 neurons with similar properties were recorded (18/68 in the insular primary taste cortex, 6/51 in the orbitofrontal secondary taste cortex, and 8/45 in the amygdala), with details of their coefficients provided in the original report (Rolls, Mills, et al., 2018).

6.2 | Viscosity-sensitive neurons

In the same investigation, other neurons responsive to viscosity were also analyzed (Rolls, Mills, et al., 2018).

To highlight the difference of the fat-encoding and fat-inhibited neurons described above from other neurons encoding of the thickness of stimuli in the mouth as reflected in viscosity, Figure 8 shows the responses of a viscosity-encoding neuron as functions of the coefficient of sliding friction and the viscosity. This orbitofrontal cortex (secondary taste cortex) neuron had firing rates that were linearly positively correlated with increases in the log of the viscosity of the stimuli (right). The linear regression line has a correlation of $r = 0.94$ ($p = 2 \times 10^{-5}$). The firing rate of the neuron is not well predicted by the coefficient of sliding friction (left) ($r = -0.74$, $p = 0.01$).

11 neurons with responses linearly related to the log of the viscosity were recorded (6/68 in the insular primary taste cortex, 2/51 in the orbitofrontal secondary taste cortex, and 3/45 in the amygdala). Of these neurons, 2 had responses that were inversely linearly related to viscosity, and one neuron had responses linearly related to viscosity provided that the stimulus was not an oil. Other neurons had tuned response functions to viscosity, that is, they respond optimally to a range of viscosities and not to other viscosities in the carboxymethyl cellulose series (Kadohisa et al., 2005a; Kadohisa et al., 2005b; Rolls, Verhagen, & Kadohisa, 2003; Verhagen et al., 2004). None of these neurons responded to the fat or fat-related oils. This analysis emphasizes the point that the fat-related neurons have firing rates that are strongly correlated as a population with the coefficient of sliding friction; and that other neurons that respond to viscosity do not respond

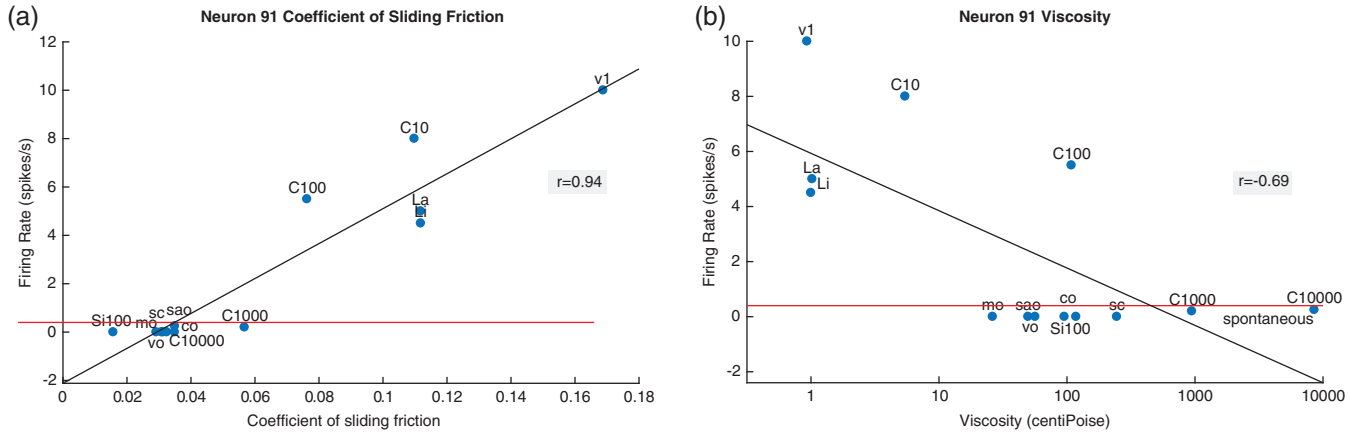

FIGURE 7 An orbitofrontal cortex (secondary taste cortex) neuron with responses correlated with increases in the coefficient of sliding friction (a). The neuron responds almost not at all until the coefficient of linear friction is above 0.06. The linear regression line has a correlation of $r = 0.94$ ($p = 1 \times 10^{-6}$). There is thus no response to the fats or oils. (b) There is a weaker relation to viscosity ($r = -0.69$, $p = .01$), with all the oils eliciting no response. Conventions as in Figure 5. *Source:* Modified from Rolls et al. (2018)

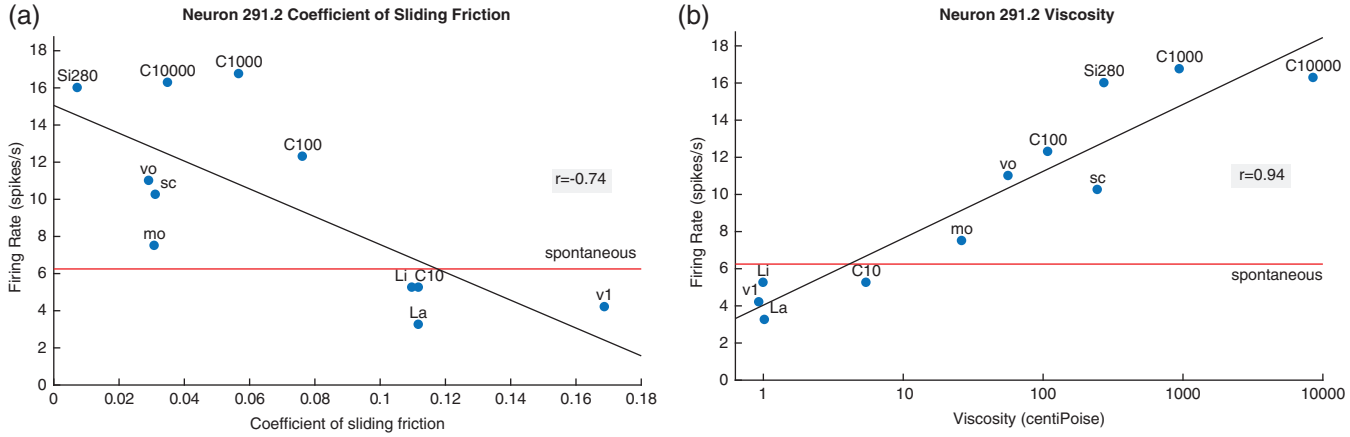

FIGURE 8 An orbitofrontal cortex (secondary taste cortex) neuron with responses correlated with increases in the viscosity of stimuli (b). The linear regression line has a correlation of $r = 0.94$ ($p = 2 \times 10^{-5}$). The firing rate of the neuron is less well predicted by the coefficient of sliding friction (a) ($r = -0.74$, $p = .01$). Conventions as in Figure 5. *Source:* Modified from Rolls et al. (2018)

to fat or fat-related oils. This dissociation of responsiveness helps to show that the fat-related neurons respond in relation to the coefficient of sliding friction, but not in relation to viscosity.

Very interestingly, the subjective thickness rating of the carboxymethyl cellulose stimuli was linearly related to the log of the viscosity (Kadohisa et al., 2005a) (Figure 9).

6.3 | The coefficient of sliding friction and the representation of fat content with a semisolid food

The evidence considered so far shows that with liquid foods, the coefficient of sliding friction is a measure that reflects fat in the mouth and that is sensed and provided as information about fat content to the brain. To investigate whether the coefficient of sliding friction may also be what is being sensed and can be applied to semisolid food, we (E.T. Rolls, E. Everson, T. Egan, & B. Lawlor in new research) measured the coefficient of sliding friction and the viscosity of a wide range of yogurts. The fat content ranged from 0 to 9.9%, the coefficient of sliding friction from 0.773 to 0.208, and the viscosity from 662 to 3,176 mPa.s. First, we found that for these semisolid foods, the coefficient of sliding friction usefully reflected the fat content of the food, and the viscosity did not. This is an important extension of this research, for it shows that for semisolid foods, sensing of the coefficient of sliding friction in the mouth by the fat selective neurons is likely to provide a reliable guide to the fat content of semisolid as well as liquid foods. Second, it was found that there was a reported subjective sensation that correlated with the coefficient of sliding friction measures of the semisolid foods. (That subjective measure is the subject of future research.) Third, it was found, as previously, that the subjectively reported thickness of the food reflected the measured viscosity of the food (Kadohisa et al., 2005a), and further, not the measured coefficient of sliding friction. These findings provide

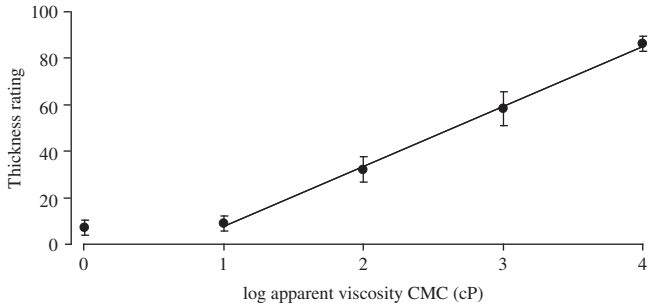

FIGURE 9 Human psychophysical ratings (mean ± *SEM*) of the thickness of the carboxymethyl cellulose viscosity series 1–10,000 cP in 12 participants. The regression line is calculated across all points apart from 1 cP, as this viscosity is below that of human saliva, and a clear relation no longer holds. *Source:* Modified from Kadohisa, Rolls, and Verhagen (2005a)

evidence that the coefficient of sliding friction is used by the brain to provide an indication of the fat content of semisolid as well as liquid foods. This further supports my proposal that the coefficient of sliding friction is what is being sensed by the mouth and transmitted to the brain to provide an indication of the pleasant texture of fat in the mouth. This reinforces my proposal that the coefficient of sliding friction is likely to be a useful measure in the development of new foods with an ideal nutritional content and the pleasant mouth feel of fat, even when no or little fat is present in the food.

6.4 | Discussion of neuronal encoding of the texture of food in the mouth, including fat texture

6.4.1 | The coefficient of sliding friction is sensed to encode oral fat

It is a completely new discovery that fat-responsive neurons in two primate taste cortical areas and the amygdala encode the coefficient of sliding friction of what is in the mouth (Rolls, Mills, et al., 2018). Some do so with linearly increasing firing rates, and others with supra-linearly increasing firing rates as a function of the decrease of the coefficient of sliding friction. Another new discovery is that there is also a population of neurons that has firing rates that are reduced according to the coefficient of sliding friction, that is, they respond less to oils and emulsions (Rolls, Mills, et al., 2018). Again, some are linear, and some are nonlinear, making them very selective in the reduction of their firing rate produced by fats, oils and emulsions such as cream. These two classes of neuron, one responding to fat with firing rates increasing as the coefficient of sliding friction decreases (Figures 5 and 6), and the second class which is inhibited by fat and has increasing firing rates as the coefficient of sliding friction increases (Figure 7), reveal an opponent process type of encoding that enables precise encoding of the coefficient of sliding friction, and thus whether there is the texture of fat in the mouth. These findings have I suggest important implications, for they open the way for the systematic development of foods with the pleasant mouth feel of fat, but low energy, and health-promoting, content.

6.4.2 | Fat sensing is by the coefficient of sliding friction and not by viscosity

The neuronal population analyses confirmed that there are different populations of neurons that encode the coefficient of sliding friction and viscosity (Rolls, Mills, et al., 2018). This is very interesting, for the coefficient of sliding friction and the viscosity of the set of stimuli used here were correlated with $r = -0.74$. Especially interesting were the neurons with responses nonlinearly related to the CSF, as illustrated in Figure 6, for these neurons as a consequence were very selective for the fats and fat-related oils, even showing little response to the carboxymethyl cellulose food thickener at 1,000 and 10,000 cP, even though their CSF was a little lower than the other nonfat-related stimuli. Neuronal processes that can produce such nonlinear responses include competitive networks, as described elsewhere (Rolls, 2016b). It may be biologically adaptive to also have neurons with responses linearly related to the CSF, for such neurons provide a flexible foundation for building other representations potentially useful in different and evolving environments, without the restricted potential of very highly selective neurons. A key discovery is that different individual neurons have different tuning to the coefficient of sliding friction (Rolls, Mills, et al., 2018), and it is this difference in the response of neurons that enables them to code for the specific details and indeed information about a wide range of stimuli (Rolls, 2016b), and that this important information about what is represented in the brain cannot be captured by fMRI, which averages together the activity of very many thousands of neurons. Finally, the point is made that there are many other types of viscosity neurons than the set with responses linearly related to viscosity described here, and these other viscosity neurons make the encoding of viscosity very selective (Kadohisa et al., 2005a; Kadohisa et al., 2005b; Rolls, Verhagen, & Kadohisa, 2003; Verhagen et al., 2004).

6.4.3 | The sensing of oral fat is by its texture and not chemical constituents

The results of the studies on insular, orbitofrontal cortex, and amygdala neurons (Kadohisa et al., 2005b; Rolls et al., 1999; Rolls, Verhagen, & Kadohisa, 2003; Verhagen et al., 2004) show that fat-sensitive neurons respond not only to fats such as vegetable oil and other fatty oils in the mouth, and to substances rich in fat such as cream and chocolate, but also to chemically different substances that have a similar slick or oily texture such as mineral oil (pure hydrocarbon), and silicone oil ($(Si(CH_3)_2O)_n$). This evidence thus indicates that the mechanisms that sense fat and to which these neurons respond are sensing a physical rather than a chemical property of the stimuli. The results described here also provide evidence that the responses of fat-sensitive neurons are not based on a texture information channel that is tuned to viscosity. The results presented here show that their responses are based on a texture information channel that is tuned to the coefficient of sliding friction. Many nonfat substances can produce low coefficients of sliding friction, including

polysaccharides (Mills, Koay, & Norton, 2013), and such substances provide possible foods that mimic the mouth feel of fat.

6.4.4 | Fat is sensed by its oral texture; there is a separate system for fatty acids

Gustatory mechanisms have been revealed in rat oral taste cells that may mediate a possible fat taste: the modulation of Ca^{2+} and K^{+} channels by long-chain free fatty acids such as linoleic acid (Gilbertson, 1998; Gilbertson, Fontenot, Liu, Zhang, & Monroe, 1997; Gilbertson & Khan, 2014). However, salivary lipase which could release fatty acid from fat in rats to activate such a mechanism, is hardly present in humans (Gilbertson, 1998; Gilbertson et al., 1997), so that this mechanism may not be important in humans. Further evidence that this chemical sensing mechanism may not be important in primates including humans is that the time course of the activation of the K-channel mechanism is very slow (Gilbertson, 1998; Gilbertson et al., 1997), and does not match the rapidly developing subjective sensation of fat in the mouth. However, to test this possibility, in our studies in primates responses by the population of orbitofrontal cortex neurons to the free fatty acids (FFA) linoleic acid (LiA) and lauric acid (LaA) were measured, and for most neurons responses were not found, that is for most neurons the activity evoked by these stimuli was indistinguishable to that evoked by water (Verhagen, Rolls, & Kadohisa, 2003). In particular, of 37 neurons tested with lauric and linoleic acid, 34 had no significant responses compared to water. Of the three neurons that had statistically significant responses in this comparison, all three consisted of a smaller response than was obtained to water, and in two cases the statistical significance was marginal, that is, $p \approx .05$. The responses of the neuron shown in Figure 5 to linoleic and lauric acid were slightly below the spontaneous firing rate, in contrast to the robust excitatory responses to safflower oil (45 spikes/s) and coconut oil (50 spikes/s), which are rich in linoleic and lauric acid bound into triglycerides, providing evidence that the neurons did not respond to fats based on gustatory sensitivity to the fatty acids. To further assess whether the firing rates obtained to lauric and linoleic acid could predict the responses of the neurons to coconut oil (high in lauric conjugated to glycerol) and to safflower (high in linoleic conjugated to glycerol), linear regression analysis was performed across the sample of 14 fat-sensitive neurons in the orbitofrontal cortex (Verhagen, Rolls, & Kadohisa, 2003). There was no significant correlation between the responses to the fatty acids and these two fat stimuli. (For lauric acid, $r = 0.45$, $p = .20$; for linoleic, $r = 0.61$, $p = .06$). Thus, the responses to fats by this population of neurons cannot be accounted for by sensitivity to lauric acid and linoleic acid. By contrast, the responses to fats could be predicted by their response to the texture of silicone oil. (For silicone oil, vs. coconut oil $r = 0.99$, $p < .001$; while for silicone oil vs. safflower oil $r = 0.99$, $p < .001$.) Together, these points of evidence (Verhagen, Rolls, & Kadohisa, 2003) suggest that fat in the mouth can be sensed in primates independently of any oral gustatory mechanism for free fatty acids (the latter mechanism suggested by Gilbertson (1998) in rodents (Gilbertson & Khan, 2014)). These data suggest that different sensing mechanisms and percepts are evoked by FFA as compared to fatty oils. Perceptual responses to FFA, if large enough not to also taste sour (Forss, 1972), depend at least partly on the trigeminal-nociceptive pathway and may be associated with the percept of oral irritation. To the extent that fatty acid taste may occur in humans, it may tend to make food unpleasant, with a rancid flavor, and consistent with this, food manufacturers minimize the content of free fatty acids in foods (Mattes, 2009). The oils, whether triglyceride-based or not, are sensed by a somatosensory-textural pathway and may be associated with the mouth feel of fatty/slickness. It is the fat texture component that may impart pleasant sensory attributes to fat, as shown by the evidence that orbitofrontal cortex fat texture neurons in macaques respond less to fat texture after feeding to satiety with a high fat food (Rolls et al., 1999), with the pleasantness of oral fat represented in humans in the orbitofrontal and pregenual cingulate cortex (Grabenhorst, Rolls, Parris, & D'Souza, 2010).

6.4.5 | Convergence of oral fat texture and taste

Some of the fat-related neurons described here do receive convergent inputs from the chemical senses, in that some respond to taste (Kadohisa et al., 2005a; Kadohisa et al., 2005b; Rolls et al., 1999; Verhagen et al., 2004; Verhagen, Rolls, & Kadohisa, 2003), and some of these neurons respond to the odor associated with a fat, such as the odor of cream (Rolls et al., 1999). Some of the fat-related neurons also have oral temperature encoding inputs (Kadohisa et al., 2004; Kadohisa et al., 2005b; Verhagen et al., 2004). The principle here is that information is encoded in the firing rates of neurons to different stimuli, that each neuron responds to different combinations of inputs, that the neurons encode information almost independently (up to at least reasonable numbers of neurons), and that this is a very efficient encoding scheme (Rolls, 2016b; Rolls & Treves, 2011). This type of encoding enables the information available to increase almost linearly with the number of neurons (Rolls, 2016b; Rolls et al., 2010; Rolls & Treves, 2011). This type of encoding also provides the basis for sensory-specific satiety, in that the responses of neurons that respond to a combination of taste, smell, oral texture, and so forth can by adaptation implement sensory-specific satiety and thereby the effects of variety on food intake (Rolls, 2014, 2015, 2016b, 2016d, 2018, 2019c). Feeding to satiety with fat (e.g., cream) decreases the responses of these orbitofrontal cortex neurons to zero on the food eaten to satiety (including its odor (Critchley & Rolls, 1996a)), but if the neuron receives a taste input from for example glucose taste, that is not decreased by feeding to satiety with cream (Rolls et al., 1999). Thus there is a representation of the macronutrient fat in the cortical taste and related areas, and the activation produced by fat is reduced by eating fat to satiety. It is thus the reward, affective, or hedonic value of fat that is represented in the orbitofrontal cortex (Rolls, 2014, 2018). In the insular primary taste cortex, the identity of taste and not its reward value are represented, in that feeding to satiety does not reduce the neuronal responses in primates (Rolls, 2016c; Yaxley et al., 1988). We do not have evidence on this for fat texture in the insula. In the pregenual cingulate cortex, where there is a taste

and oral fat representation, the available evidence shows that feeding to satiety does reduce the neuronal responses to fat (Rolls, 2008a).

The dual or opponent process coding scheme revealed in this research (Rolls, Mills, et al., 2018), with some neurons increasing their firing rates to fat, and others having their firing rates reduced by fat, provides a robust way of representing information about the exact fat content of food in the mouth, as well as how fat is combined with other properties including taste, temperature, and viscosity. Further, the firing rates of at least the linear neurons in this investigation were somewhat monotonically related to the coefficient of sliding friction or to viscosity, illustrating that the magnitude of the variable is being represented by the firing rate, which is different to the place coding found in many other parts of the cerebral cortex (Rolls, 2016b, 2017; Rolls et al., 2010; Rolls & Treves, 2011).

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). This could reflect convergence of taste and texture inputs in the insular cortex, or the convergence could be present already at earlier stages of taste processing. It is known that some neurons in the taste thalamus (nucleus VPMpc) have thermal responsiveness in monkeys (Pritchard, Hamilton, & Norgren, 1989) and rats (Verhagen, Giza, & Scott, 2003). In the periphery, it is known that chorda tympani fibers in the monkey (Sato, Ogawa, & Yamashita, 1975) and hamster (Ogawa, Sato, & Yamashita, 1968) show significant correlations between the responses to HCl and those to cooling (20°C), and between the responses to sucrose and warming (to 40°C). Some lingual nerve fibers in monkeys were activated by cooling to 15°C but not by taste (Danilova & Hellekant, 2002). There may be no studies in the periphery of the effects of food-relevant oral stimuli such as viscosity and fat texture. It is also possible that oral somatosensory information reaches the anterior insular / frontal opercular primary taste cortex via cortico-cortical connections, perhaps from areas 3b which contains oral somatosensory representations of for example touch of the tongue, teeth and palate (Jain, Qi, Catania, & Kaas, 2001; Manger, Woods, & Jones, 1996) and which might send afferents to the anterior insular/frontal opercular primary taste cortex (Friedman, Murray, O'Neill, & Mishkin, 1986; Mufson & Mesulam, 1982).

Given that an important input to the orbitofrontal cortex is from the primary taste cortex (Baylis et al., 1995), the responses of orbitofrontal cortex neurons to fat texture, and also oral viscosity, temperature, and taste, are likely to be produced at least in a large part via the primary taste cortex.

These oral sensory properties of food, including viscosity and fat texture, and also the sight and smell of food, are also represented in the primate amygdala (Kadohisa et al., 2005a; Kadohisa et al., 2005b; Rolls, 2000a ; Rolls & Scott, 2003), which also receives inputs from the primary taste cortex (Figure 1). 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, 2000a; Rolls & Scott, 2003) that is typical of orbitofrontal cortex neurons.

7 | ACTIVATION OF THE HUMAN BRAIN BY ORAL SIGNALS, INCLUDING FAT TEXTURE

7.1 | Taste

Humans neuroimaging studies with functional magnetic resonance imaging (fMRI) show that taste activates an area of the anterior insular/frontal opercular cortex, which is probably the primary taste cortex, and part of the orbitofrontal cortex, which is the secondary taste cortex (de Araujo, Kringelbach, Rolls, & McGlone, 2003; Francis et al., 1999; O'Doherty, Rolls, Francis, Bowtell, & McGlone, 2001; Small et al., 1999). Different parts of the orbitofrontal cortex are activated by sweet (pleasant) and salt (unpleasant) tastes (O'Doherty et al., 2001).

The human amygdala is also activated by the taste of glucose (Francis et al., 1999). Addressing the issue of whether the human amygdala is activated by pleasant as well as by unpleasant stimuli, we showed that the human amygdala is as much activated by the affectively pleasant taste of glucose as by the affectively negative taste of NaCl (O'Doherty et al., 2001). Zald, Lee, Fluegel, and Pardo (1998) had shown that the amygdala, as well as the orbitofrontal cortex, respond to aversive (saline) taste stimuli. However, there is nothing special about aversive stimuli in relation to the brain areas activated, for pleasant taste stimuli also activate the human amygdala and orbitofrontal cortex (O'Doherty et al., 2001).

Umami taste stimuli, for example, monosodium glutamate (MSG), and which represent what is described as the taste of protein, activate similar human taste cortical regions as those activated by a prototypical taste stimulus, glucose (de Araujo, Kringelbach, Rolls, & Hobden, 2003). The anterior cingulate cortex, which receives inputs from the orbitofrontal cortex (Du et al., 2019; Rolls, 2019a; Rolls et al., 2018), was also activated. Addition of the nucleotide 0.005 M inosine 5′-monophosphate (IMP) to MSG (0.05 M), produced supralinear additivity in the BOLD (blood oxygenation-level dependent) signal in an anterior part of the orbitofrontal cortex, reflecting the enhancement subjectively that occurs of umami taste that occurs when IMP is added to MSG. These findings show that particular parts of the brain, in this case the orbitofrontal cortex for taste stimuli, can reflect inputs produced by combinations of sensory stimuli with supralinear activations that relate to the subjective experience produced by the combination.

7.2 | Odor

In humans, the pyriform (primary olfactory) cortex (Gottfried, 2010; Poellinger et al., 2001; Rolls, Kringelbach, & de Araujo, 2003; Sobel et al., 2000; Zald & Pardo, 1997) is activated by olfactory stimuli, and in addition there is strong activation of the orbitofrontal cortex (Francis et al., 1999; Rolls, Kringelbach, & de Araujo, 2003; Zatorre, Jones-Gotman, Evans, & Meyer, 1992). To provide evidence of where the pleasantness of olfactory stimuli is represented in the human brain, O'Doherty et al. (2000) demonstrated that the activation 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 (de Araujo, Rolls, Velazco, Margot, & Cayeux, 2005; Grabenhorst, Rolls, & Margot, 2011; Grabenhorst, Rolls, Margot, da Silva, & Velazco, 2007; Rolls & Grabenhorst, 2008; Rolls, Grabenhorst, & Deco, 2010, 2010; Rolls, Grabenhorst, Margot, da Silva, & Velazco, 2008; Rolls, Grabenhorst, & Parris, 2010; Rolls, Kringelbach, & de Araujo, 2003) is related to sensory-specific satiety, and this is a part of the human brain where the pleasantness of odor is represented (Rolls, Kringelbach, & de Araujo, 2003).

It is important to understand whether the pleasant and reward value of stimuli are processed separately from the identity and intensity of stimuli in the human brain (Rolls, 2014, 2018), and this applies to olfactory stimuli. To elucidate this, we measured the brain activations produced by three pleasant and three unpleasant odors. The pleasant odors were geranyl acetate (floral), linalyl acetate (floral, sweet), and alpha-ionone (woody, slightly food-related). The unpleasant odors were isovaleric acid, octanol, and hexanoic acid. These hedonic categories activated dissociable parts of the human brain (Rolls, Kringelbach, & de Araujo, 2003). Pleasant but not unpleasant odors activated a medial part of the orbitofrontal cortex. Moreover, the subjective pleasantness ratings of the six odors were correlated with the amount of activation of the medial orbitofrontal cortex. The unpleasant odors activated the lateral orbitofrontal cortex (Rolls, Kringelbach, & de Araujo, 2003), a region activated by many other unpleasant stimuli (Grabenhorst & Rolls, 2011; Rolls, 2019b). Activation by the odors was also found in the anterior cingulate cortex (Rolls, Kringelbach, & de Araujo, 2003). These results provide evidence that there is a hedonic map of the sense of smell in brain regions such as the orbitofrontal cortex (Grabenhorst & Rolls, 2011). Such a map could facilitate comparison and scaling of the reward value produced by different stimuli onto a similar value scale by competitive inhibition implemented by local inhibitory interneurons, and this may be important for inputs to a decision mechanism (Grabenhorst, D'Souza, Parris, Rolls, & Passingham, 2010; Grabenhorst & Rolls, 2011; Rolls, 2005; Rolls & Deco, 2010). Very interestingly, activations of the pyriform (primary olfactory) cortex were correlated with the subjective intensity of the odors and not with their pleasantness (Rolls, Kringelbach, & de Araujo, 2003), providing evidence that hedonics is represented especially in the orbitofrontal cortex, and not at earlier stages of cortical processing (Rolls, 2019b).

7.3 | Olfactory-taste convergence to represent flavor, and the influence of satiety

The flavor of food involves combinations of taste, olfactory, and texture stimuli. We studied where in the human brain interactions between taste and odor stimuli may be occur to implement flavor, in and fMRI study with MSG and sucrose taste, and methional (chicken) and strawberry odors, presented unimodally, or in different combinations (de Araujo, Rolls, Kringelbach, McGlone, & Phillips, 2003). We found that a part of the anterior (agranular) insula responded to unimodal taste and to unimodal olfactory stimuli; and that a part of the adjoining anterior frontal operculum is a unimodal taste area (primary taste cortex) not activated by olfactory stimuli. Combinations of olfactory and taste stimuli produced activations 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 (de Araujo, Kringelbach, Rolls, & Hobden, 2003). Similar results were reported by Small et al. (2004), who also found supra-additive interactions between congruent olfactory and taste stimuli in areas including the caudal orbitofrontal cortex, and anterior cingulate cortex (see also Small & Prescott, 2005). These results provide evidence that taste and olfactory stimuli converge anatomically in the orbitofrontal cortex (see Figure 1) to produce flavor in humans, and that this is where I the human brain the pleasantness of flavor is represented.

The delicious flavor of umami is produced by the convergence of taste and olfactory information in the orbitofrontal and pregenual cingulate cortex (McCabe & Rolls, 2007). The combination of glutamate and a consonant, savory, odor (vegetable), was much more pleasant than either alone, and produced supralinear activation of these brain areas compared to the sum of the taste and olfactory stimuli presented separately. Nonlinear effects were not found for sodium chloride and vegetable odor. McCabe and Rolls thus proposed that glutamate acts by the nonlinear effects it can produce when combined with a consonant odor. It is proposed 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 (Rolls, 2009b). Glutamate is thus a flavor enhancer because of the way that it can combine nonlinearly with consonant odors (Rolls, 2009b).

7.4 | Oral viscosity and fat texture

To investigate how oral including fat texture is represented in the human brain, de Araujo and Rolls (2004) used fMRI with stimuli of 3 viscosities (1 cP, and 50 and 1,000 cP carboxymethyl cellulose), a fatty oil, or 1 M sucrose used to localize taste areas, delivered intraorally in volumes of 0.75 ml. The fat stimulus was vegetable oil with a measured viscosity of 50 cP. This oil was chosen as it was the most odorless and tasteless available. A tasteless solution (containing the main ionic components of saliva, 25 mM KCl + 2.5 mM $NaHCO_3$ in distilled water (de Araujo, Kringelbach, Rolls, & McGlone, 2003)) was used as a control which was subtracted from the activations to the test stimuli.

First, activation of the anterior insular (primary) taste cortex of humans was produced by oral viscosity stimuli (Figure 10, middle), in a region that was taste-related shown by its activations to oral sucrose. Very interestingly, the BOLD (blood oxygenation-level dependent) activation here was proportional to the log of the viscosity of the oral stimuli (de Araujo & Rolls, 2004), as are the subjective thickness ratings of these viscosity stimuli (Kadohisa et al., 2005a). Fat also activated this region (Figure 10, middle), though not in a way that was identified with the fMRI method as being qualitatively different from the activation produced by a viscosity stimulus, carboxymethyl cellulose, of the same viscosity value. We hypothesized therefore that the activation of this region in humans corresponds to the details revealed by single neuron recording in macaques, namely that some neurons in the primary taste cortex are activated by taste unimodally, some by viscosity unimodally, some by both taste and viscosity, and some by

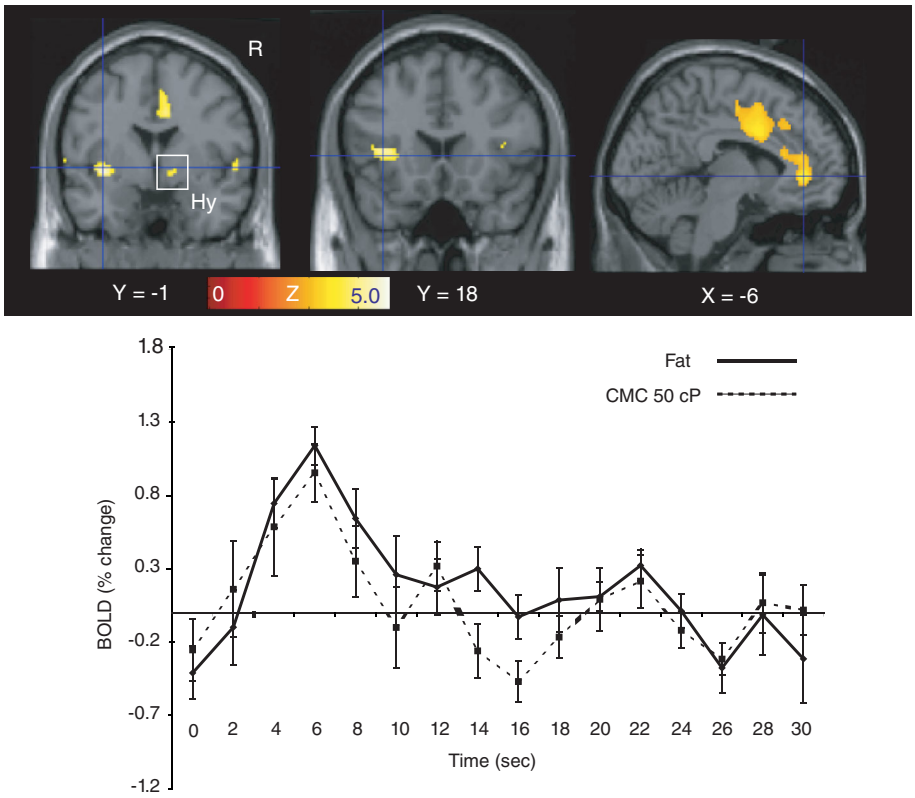

FIGURE 10 fMRI study of the responses to the oral delivery of fat as assessed by the comparison (fat—control). Activations were observed in the mid insula and hypothalamus (Hy) (top row left), anterior insula (top row middle), and anterior cingulate cortex (top row right). The average time-course data (across trials and subjects) from the mid-insular cortex (from the voxels marked by the cross hairs in the top row left) are shown in the bottom row for the conditions Fat and carboxymethyl cellulose (CMC) 50 cP
Source: After de Araujo and Rolls (2004)

fat texture (Verhagen et al., 2004). The fMRI findings are consistent with the hypothesis that the same processing is performed in the human anterior insular cortex (de Araujo & Rolls, 2004).

Second, a mid-insular region posterior to the main primary insular taste cortex was activated by viscosity and fat but not taste (Figure 10, left). This may be a mainly somatosensory part of the insula that is a higher order somatosensory cortical area, this part of which is devoted to intra-oral somatosensory inputs. The somatosensory representation of the oral cavity is located in this part of the insula extending anteriorly to the orbitofrontal cortex (Jain et al., 2001; Manger et al., 1996). This mid-insular cortex may represent a range of somatosensory properties of the oral activity, for in a study of the effects of intraoral water, we found that activation in the same mid-insular region was produced by water when thirsty but not after thirst was quenched by drinking to satiety. We interpreted this as a somatosensory effect related to relief of a dry mouth by water, in that this region was not activated by taste stimuli (de Araujo, Kringelbach, Rolls, & McGlone, 2003).

Third, fat in the mouth activated the orbitofrontal cortex, where some neurons in macaques specifically encode oral fat independently of viscosity (Rolls, Verhagen, & Kadohisa, 2003; Verhagen, Rolls, & Kadohisa, 2003). Oral fat also activated a region to which this projects, the pregenual cingulate cortex (Figure 10, right, at the location shown by the crosshairs), and also more dorsally in the anterior supracallosal cingulate cortex (Figure 10, right). The activation in the human pregenual cingulate cortex by oral fat was especially interesting, in that the activation here to fat was independent of viscosity (produced by carboxymethyl cellulose) (see Figure 11). This pregenual cingulate region was also activated by sucrose taste, and is a strong candidate for a brain region activated by the hedonic properties of fat. This pregenual cingulate region has been shown to contain taste-responsive neurons (Rolls, 2008a). Further evidence linking this pregenual cingulate region to pleasant affective properties (Bush, Luu, & Posner, 2000) of sensory stimuli is that the same region is activated by water when it tastes pleasant during thirst (de Araujo, Kringelbach, Rolls, & McGlone, 2003), by pleasant but not unpleasant odors (Rolls, Kringelbach, & de Araujo, 2003), and by pleasant but not by painful touch (Rolls et al., 2003). Further, this pregenual cingulate region is also implicated in the control of autonomic function (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Rolls, 2019a). The human anterior cingulate cortex can also be activated by many hedonically relevant stimuli, including chemosensory and somatosensory stimuli (Du et al., 2019; Grabenhorst et al., 2008; Grabenhorst & Rolls, 2008; McCabe & Rolls, 2007; McCabe, Rolls, Bilderbeck, & McGlone, 2008; Rolls, 2005, 2009a, 2019a; Rolls & Grabenhorst, 2008; Rolls, Grabenhorst, Margot, et al., 2008; Rolls, Grabenhorst, & Parris, 2008; Rolls & McCabe, 2007; Small et al., 1999; Zald et al., 1998; Zatorre, Jones-Gotman, & Rouby, 2000).

The findings show that the representation of fat and oral texture the details of which have been uncovered by single neuron analyses in the macaque insula, orbitofrontal cortex, and connected areas, is likely to also apply in humans in the corresponding areas in which activations to similar stimuli have been found (de Araujo & Rolls, 2004). The details of the representation can only be discovered and

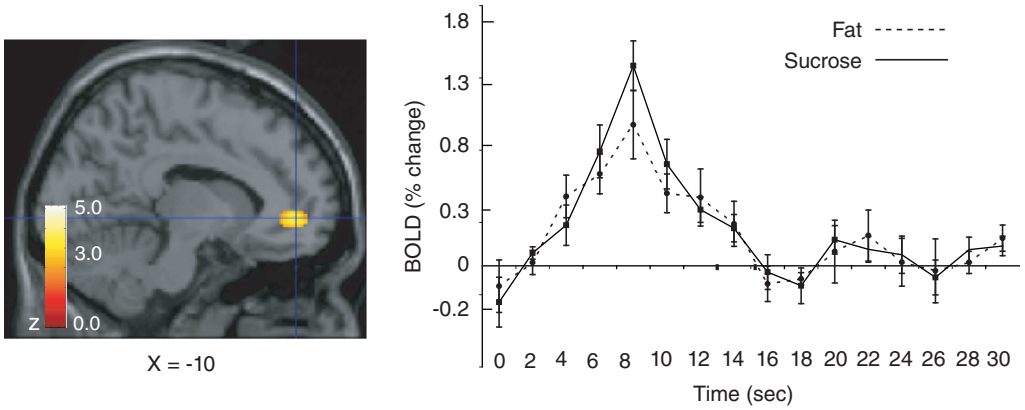

FIGURE 11 Top: Rostral anterior cingulate cortex activation by (fat—control) AND (sucrose—control), as revealed by conjunction analysis. Bottom: The corresponding average time-course data (across trials and subjects) from the voxel marked by the cross hairs are shown. *Source:* After de Araujo and Rolls (2004)

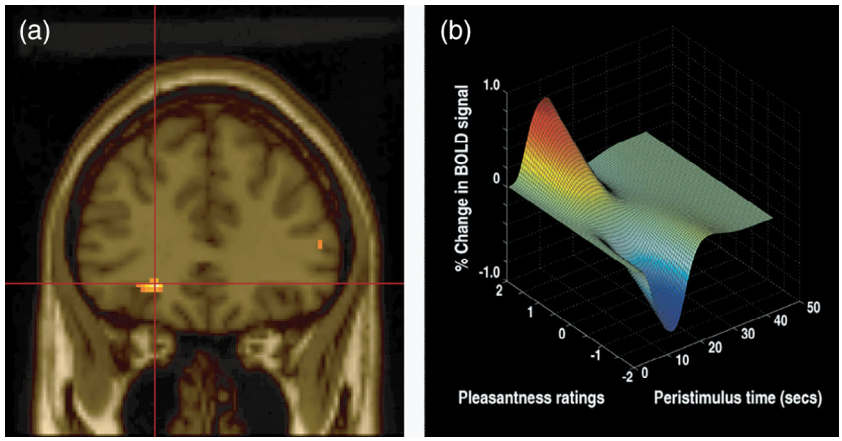

FIGURE 12 Areas of the human orbitofrontal cortex with activations correlating with pleasantness ratings for food in the mouth. (a) Coronal section through the region of the orbitofrontal cortex from the random effects group analysis showing the peak in the left orbitofrontal cortex (Talairach co-ordinates *x*, *y*, *z* = −22, 34, −8, *Z*-score = 4.06), in which the 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. *Source:* After Kringelbach et al. (2003)

established by single neuron recordings, for each neuron conveys relatively independent information, and neuroimaging reflects the activity of tens of thousands of neurons (Rolls, 2016b; Rolls & Treves, 2011).

7.5 | The pleasantness of the flavor of food and of oral texture

To measure how satiety modulates the brain activations to a whole food that produces texture, taste, and olfactory stimulation, we measured brain activation by whole foods before and after the food was eaten to satiety (Kringelbach, O'Doherty, Rolls, & Andrews, 2003). The aim was to show, using a food that has texture, taste, and olfactory components, the brain areas that decrease their activation when the food becomes less pleasant, to identify where in the brain the pleasantness of the odor, taste and texture of food are represented. The foods eaten to satiety were either chocolate milk (which had a fat texture component), or tomato juice (which did not have a fat texture component). A decrease in activation by the food eaten to satiety relative to the other food was found in the orbitofrontal cortex (Kringelbach et al., 2003) but not in the primary taste cortex (see Figure 12). This study provided evidence that the pleasantness of the flavor of food, and sensory-specific satiety, are represented in the human orbitofrontal cortex.

We have further shown that the subjective pleasantness and reward value of fat texture is represented in the mid-orbitofrontal and

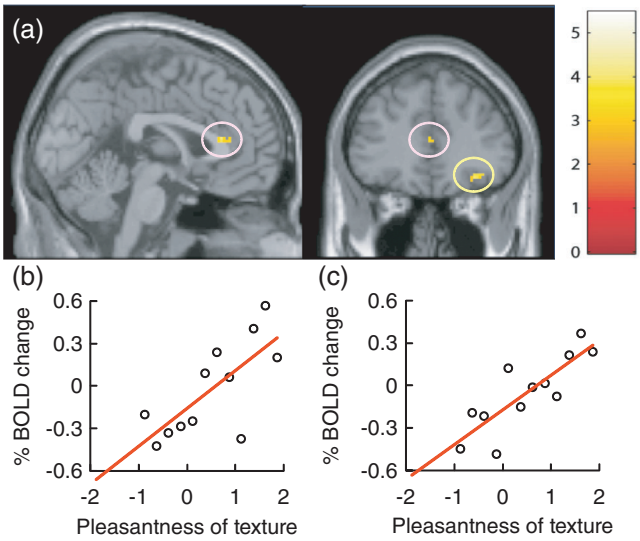

FIGURE 13 Brain regions in which the activations were correlated with the subjective pleasantness of fat texture. The relation between the % change in the BOLD signal and the rating of the pleasantness of the texture for the mid-orbitofrontal cortex ([32 34 −14] $z = 3.38$ $p = .013$) (a, yellow circle, and c); and for the anterior cingulate cortex ([2 30 14] $z = 3.22$ $p = .016$) (a, pink circles, and b). *Source:* After Grabenhorst, Rolls, et al. (2010)

anterior cingulate cortex, where activations are correlated with the subjective pleasantness of oral fat texture (Grabenhorst, Rolls, et al., 2010; Rolls, 2010). In this investigation we correlated humans' subjective reports of the pleasantness of the texture and flavor of a high and low fat food with a strawberry or vanilla flavor, with neural activations measured with fMRI. Activity in the mid-orbitofrontal and anterior cingulate cortex was correlated with the pleasantness of oral fat texture (see Figure 13), and in nearby locations with the pleasantness of flavor. The pregenual anterior cingulate cortex showed a supralinear response to the combination of high fat and pleasant, sweet flavor, implicating it in the convergence of fat texture and flavor to produce a representation of highly pleasant stimuli. This discovery of which brain regions track the subjective hedonic experience of fat texture (Grabenhorst, D'Souza, et al., 2010) will help to unravel possible differences in the neural responses in obese versus lean people to oral fat, a driver of food intake (Rolls, 2011b, 2014, 2016d).

Can individual differences between people in the palatability of food be related to the operation of the orbitofrontal and pregenual cingulate cortex involved in the affective (hedonic) representations of food?

Some individuals, chocolate cravers, report that they crave chocolate more than noncravers, and this is associated with increased liking of chocolate, increased wanting of chocolate, and eating chocolate more frequently than noncravers (Rodriguez et al., 2007). To whether these individual differences are reflected in the responses of affective systems in the orbitofrontal cortex and pregenual cingulate cortex, Rolls and McCabe (2007) used fMRI to measure the response to the flavor of chocolate, to the sight of chocolate, and to their combination, in chocolate cravers compared to noncravers. The sight of chocolate produced greater activation in chocolate cravers than noncravers in the medial orbitofrontal cortex and ventral striatum. For cravers versus noncravers, a combination of a picture of chocolate with chocolate in the mouth produced a greater effect than the sum of the components (i.e., supralinearity) in the medial orbitofrontal cortex and pregenual cingulate cortex. In addition, the pleasantness ratings of the chocolate and chocolate-related stimuli had higher positive correlations with the fMRI BOLD signals in the pregenual cingulate cortex and medial orbitofrontal cortex in the cravers than in the noncravers. Thus cravers versus noncravers had greater responses to a chocolate in the orbitofrontal cortex, pregenual cingulate cortex, and ventral striatum, and in some of these brain regions the differences are related to the subjective pleasantness of the craved foods. Differences in the insular (primary) taste cortex were not found. An implication is that individual differences in brain responses to very pleasant foods help to understand the mechanisms that drive the liking for specific foods by indicating that some (but not other brain systems such as the insular taste cortex) respond more to the rewarding aspects of some foods, and thus influence and indeed even predict the intake of those foods (which was much higher in chocolate cravers than noncravers) (Rolls & McCabe, 2007). Although fat texture is of course not the only contributor to the effects of chocolate, it is one important aspect of the sensory properties of chocolate.

There are also important age differences in the neural representation and sensory perception of foods that may relate in part to oral texture as well as taste (Rolls, Kellerhals, & Nichols, 2015). For example, a vegetable flavor was much more acceptable to older (40 and 60 years of age) than to a younger (22 years of age group, and these differences were related to activations in brain areas that represent oral texture as well as taste (Rolls et al., 2015).

8 | DISCUSSION

fMRI of the human orbitofrontal cortex is difficult because signal loss can occur in this region. However, we have developed procedures to overcome these difficulties as described in the original papers and elsewhere (Wilson et al., 2002). Confidence in the conclusions reached on these oral texture and taste systems is that they are complemented by single neuron studies in macaques (Kadohisa et al., 2004; Kadohisa et al., 2005a; Rolls, 2008a; Rolls et al., 2010; Rolls & Grabenhorst, 2008; Rolls, Verhagen, & Kadohisa, 2003; Verhagen et al., 2004; Verhagen, Rolls, & Kadohisa, 2003). Moreover complementary results are being obtained now by a number of groups using fMRI in humans (Bender, Veldhuizen, Meltzer, Gitelman, & Small, 2009; de Araujo, Lin, Veldhuizen, & Small, 2013; Small, 2010), with others cited above. I note that fMRI has limitations in analyzing neural encoding because it averages together the activity of thousands of neurons, whereas information about stimuli is the brain is encoded by the fact that different neurons respond to different stimuli, and that the information encoded by different neurons even in the same brain

regions is almost independent (Rolls, 2008b, 2016b; Rolls et al., 2009; Rolls & Treves, 2011).

One of the key points made here is that the coefficient of sliding friction of a food in the mouth is closely related to how fat is represented in the brain. Consistent with this, research in the field of sensory science provides evidence that the coefficient of sliding friction is related to oral fat perception (Kupirovic, Elmadfa, Juillerat, & Raspor, 2017). Another key point made here is that although for the types of oral stimuli considered here there is a correlation between the tribology measurements (coefficient of sliding friction) and rheological measurements (viscosity), the neuronal representations in the brain of these different types of stimuli (fat vs. thickness) are much less correlated. This is due to nonlinear processing in the brain, which is an essential property of neural systems to enable them to analyze sensory stimuli effectively (Rolls, 2016b). A number of processes contribute to this nonlinearity, including the threshold nonlinearity of the current to firing rate activation function of neurons, and competitive learning forcing different populations of neurons to reduce the correlation between their responses (Rolls, 2016b). An important conceptual contribution of the research described here is therefore that what may appear to be somewhat small differences between the physical properties of stimuli when assessed with for example tribology and rheology may become amplified into large differences in the neuronal representations in the brain. This may be a useful conceptual implication of the research described here for the sensory testing of foods. Another implication of the research described here is that it does point a way forward for the design of new foods with the pleasant mouth feel of fat and with specified nutritional content. The research described here also shows that there are separate representations of fatty acids by neurons in cortical areas, which do not appear to be related strongly to the sensory perception of fat, but instead to tastes that may be associated with foods, including important warning "off" tastes.

Obesity is an increasing problem in the developed world with reports suggesting that more than 40% of adults are already obese or overweight (Alwan, 2011). As a consequence, the food industry is attempting to reduce the calorific load of foods (Norton, Fryer, & Moore, 2006) that are consumed on a daily basis (e.g., for sauces, dressing, spreads, biscuits, cakes, chocolate, etc.). As fat is a major contributor to calories in foods, reduction has been investigated with some degree of success. However, this has relied on linking the tribology or viscosity to sensory data with no understanding of the way the mouth encodes the presence of fat. With the recent work described here, we have been able to link fat texture sensitive neuron firing with the coefficient of sliding friction (Rolls, Mills, et al., 2018). In addition, we have shown how the use of simple thickeners (such as carboxymethyl cellulose) can produce some change in the firing rates of the neurons as a result of some change in sliding friction (Rolls, Mills, et al., 2018). It is therefore not surprising that simple approaches to fat reduction with hydrocolloids have not delivered products that have the required level of consumer acceptability to make it into main stream usage. Our recent study (Rolls, Mills, et al., 2018) suggests a low sliding friction as a target for foods that can mimic the effects of fat in the mouth, yet may contain little fat and can be designed for optimal nutrition. The use of fluid gels offers potential as these systems have similar rheological and tribological properties to fat-containing structures (Farrés, Douaire, & Norton, 2013; Gabriele, Spyropoulos, & Norton, 2010; Garrec & Norton, 2012; Mills et al., 2013).

9 | CONCLUSIONS

Fat in the mouth is represented by its texture in the primary taste cortex in the insula, in the orbitofrontal cortex, in the anterior cingulate cortex, and in the amygdala. Fat texture is represented by neurons independently of viscosity: some neurons respond to fat independently of viscosity, and other neurons encode viscosity. The neurons that respond to fat also respond to silicone oil and paraffin oil, indicating that the sensing is not chemospecific, but is instead based on texture. The parameter that is being encoded by fat-sensitive neurons is the coefficient of sliding friction (Rolls, Mills, et al., 2018). The fat sensing is not related to free fatty acids, in that these neurons typically do not respond to free fatty acids such as linoleic acid. Moreover, a few neurons with responses to free fatty acids typically do not respond to fat in the mouth. The fat texture representations by neurons may be combined with taste and/or oral temperature responses, and in the orbitofrontal cortex with olfactory responses. Different neurons respond to different combinations, providing a rich representation of the sensory properties of food. In the orbitofrontal cortex, feeding to satiety with one food decreases the responses of these neurons to that food, but not to other foods, showing that sensory-specific satiety and appetite modulation are represented in the orbitofrontal cortex. In humans, individual differences in activations in areas such as the orbitofrontal cortex and pregenual cingulate cortex to a complex food such as chocolate are related to the affective value of the foods, and how much is eaten. In summary, one way in which fat in the mouth is represented in the brain is by its texture, and an indication of what must be transduced has been provided by these neuroscience studies. Other oral texture representations found in the insular taste cortex, the orbitofrontal cortex, and the amygdala include representations of viscosity, astringency, and grittiness, and a representation of oral temperature is also found (Rolls, 2015; Rolls, 2016a; Rolls, 2016c, 2016d, 2018, 2019b).

These investigations have implications for understanding how fat is sensed in the mouth; how the pleasantness of food is computed in the brain, and how this differs between individuals; how sensory-specific satiety is computed; how to develop new foods with sensory properties that produce good taste and mouth feel yet are independent of energy content; and for developing new approaches to appetite control and obesity.

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research on fat sensing in the mouth and the coefficient of sliding friction and other recent research, but in still covering the neuroscience of food oral texture sensing, some overlap of parts of the text with my earlier papers is acknowledged.

AUTHOR CONTRIBUTION

The author wrote the paper. The research described involved many excellent collaborations, as shown in the acknowledgements and in the publications cited.

ETHICAL STATEMENTS

Conflict of Interest: The author declares that he does not have any conflict of interest.

Ethical Review: This is a review paper and does not involve any human or animal testing.

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