Mechanisms for Sensing Fat in Food in the Mouth*

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Edmund T. Rolls

Abstract: The brain areas that represent taste including the primary taste cortex and the orbitofrontal cortex also provide a representation of oral texture. 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 and paraffin oil, indicating that the sensing is texture-specific not chemo-specific. This fat sensing is not related to free fatty acids such as linoleic acid, and a few other neurons that respond to free fatty acids typically do not respond to fat in the mouth. Complementary human functional neuroimaging studies show that the pleasantness of food texture is represented in the orbitofrontal cortex. These findings have implications for the design of foods that mimic the pleasant texture of fat in the mouth but have low energy content, and thus for the prevention and treatment of obesity.

Keywords: fat texture, food texture, obesity, olfaction, sensory-specific satiety, taste, viscosity

Introduction

This paper summarizes evidence on how fat in food is sensed in the mouth, how the pleasantness of fat texture is represented in the brain (Rolls 2011b), and some of the implications for the design of foods relevant to the prevention and treatment of obesity (Rolls 2011c). This is an important issue, for it is not yet clear how oral fat is sensed. Evidence from neuroscience is providing indications about this by showing what must have been transduced by receptors in the mouth to produce the neuronal responses found in the brain. Moreover, fat in the diet may be pleasant, yet fat intake must be controlled, so understanding the rules by which the pleasantness of fat is regulated is important. In addition, the brain's representation of oral fat is frequently in terms of particular combinations with other sensory aspects of food, including taste, texture, and olfactory inputs, and these combinations are important for understanding the full impact of the fat in a food in the mouth on the pleasantness of food.

A broad perspective on brain processing involved in hedonic aspects of the control of food intake and in affective responses more generally is provided by Rolls (2005). By oral texture I mean texture, somatosensory, signals produced by stimuli in the mouth. By oral fat texture I mean the oral texture stimulus produced by fat in the mouth. The perceptual qualities of these stimuli have been investigated by Kadohisa and others (2005).

Oral Fat Texture Represented in the Brain

Texture in the mouth is an important indicator of whether fat is present in a food, which is important not only as a high value energy source, but also as a potential source of essential fatty acids. In the orbitofrontal cortex, Rolls and others (1999) discovered a population of neurons (single brain cells) that responds to the texture of fat in the mouth. The cells receive their inputs via sensors in the mouth that are connected to neural pathways to the brain, and the information reaches the orbitofrontal cortex (which is secondary taste cortex) via the primary taste cortex in the insula (Verhagen and others 2004; Rolls 2011b). Figure 1 shows an example of a fat-responsive neuron in the orbitofrontal cortex where the evoked neuronal firing rate activity to the indicated stimuli is plotted as a function of viscosity (Verhagen and others 2003). The cell showed strong and similar responses to all the oils tested including mineral oil and silicone oil, but did not respond to any of the carboxy-methyl-cellulose (CMC) viscosity series.

The results of these studies on orbitofrontal cortex neurons (Rolls and others 1999; Verhagen and others 2003) 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 which 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 also provide evidence that the responses of fat-sensitive neurons are not based on a texture information channel that is tuned to viscosity. In particular, although some other neurons in the orbitofrontal cortex are tuned to viscosity, many (10/14) of the fat-sensitive neurons did not respond to the viscosity series of stimuli (see example in Figure 1).

Important conclusions then about the representation of oral texture in the brain are: (1) There is an information channel that represents fat independently of viscosity. (2) There is an information channel that represents viscosity and also responds to fat based on the viscosity of the fat. This channel thus responds to viscosity independently of whether the eliciting stimulus is a nonfat or a fat. (3) There is an information channel that encodes viscosity provided that it is not associated with an oily substance such as a fat (Rolls 2011b).

MS 20111000 Submitted 8/19/2011, Accepted 12/1/2011. Author Rolls is with Oxford Centre for Computational Neuroscience, Oxford, UK. Direct enquiries to Rolls (E-mail: Edmund.Rolls@oxcns.org; URL: http://www.oxcns.org).

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Gustatory mechanisms have been revealed in rat oral taste cells that may mediate a possible fat taste via the slow modulation of K-channels by polyunsaturated free fatty acids such as linoleic acid (Gilbertson and others 1997; Gilbertson 1998). However, salivary lipase which could release fatty acid from fat in rats to activate such a mechanism, is hardly present in humans (Gilbertson and others 1997; Gilbertson 1998), so that this mechanism may not be important in humans. To the extent that free fatty acids are present in foods, they may impart an unpleasant aroma, with an example being butyric acid, and food manufacturers strive to limit the FFA content of foods. However, to test this possibility, 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 fat-sensitive neurons responses were not found. That is for most neurons the activity evoked by these stimuli was indistinguishable to that evoked by water (Verhagen and others 2003). Thus, the responses to fats by this population of neurons cannot be accounted for by sensitivity to lauric acid and linoleic acid. Together, these points of evidence (Verhagen and others 2003) suggest that fat in the mouth can be sensed in primates independently of any oral gustatory mechanism for free fatty acids (a mechanism suggested by Gilbertson 1998 in rodents). These data suggest that different sensing mechanisms and percepts are evoked by FFA as compared to fatty oils. 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).

These findings are from nonhuman primates and are relevant to humans because the taste and related pathways are similar in both species (and different from those in rodents) (Norgren 1984; Rolls and Scott 2003; Rolls 2005; Rolls and Grabenhorst 2008; Small and Scott 2009; Rolls 2011a). These findings are complemented by the following functional neuroimaging studies in humans.

The Representation of the Pleasantness of Oral Fat in the Brain

It has been shown in human studies using functional magnetic resonance imaging (fMRI) 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 probably the secondary taste cortex (Francis and others 1999; Small and others 1999; O'Doherty and others 2001; de Araujo and others 2003). The odor of food is represented in the orbitofrontal cortex (Rolls and others 2003; de Araujo and others 2005; Grabenhorst and others 2007; Rolls and others 2008; Rolls and Grabenhorst 2008; Rolls and others 2010a, 2010b, 2010c; Grabenhorst and others 2011). The pleasantness of the taste, smell, and flavor of food is also represented in the orbitofrontal cortex, as shown by studies in which the brain responses decrease to zero in this region after the food has been fed to satiety and is no longer pleasant (O'Doherty and others 2000; Kringelbach and others 2003; Rolls 2011b, 2011c).

To investigate the representation of oral including fat texture in the human brain, we used event-related functional magnetic resonance imaging. Stimuli of three viscosities (a 1 cP control and carboxymethyl cellulose 50, and 1000 cP), a fatty oil, or 1M sucrose (used to localize taste areas) were delivered intra-orally in volumes of 0.75 mL (de Araujo and Rolls 2004). The fat stimulus was vegetable oil with a measured viscosity of 50 cP. Fat texture activated insular cortex regions, the orbitofrontal cortex, and a tertiary taste cortical area to which it projects, the anterior cingulate cortex.

We have recently shown that the pleasantness and reward value of fat texture is represented in the mid-orbitofrontal and anterior cingulate cortex (Grabenhorst and others 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 vanilla or strawberry 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, and in nearby locations with the pleasantness of flavor. The pregenual 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 and others 2010) will help to unravel possible differences in the neural responses in obese compared with lean people to oral fat, a driver of food intake (Rolls 2011c).

Given that there are individual differences in the palatability of food, can these individual differences be related to the functioning of brain systems such as the orbitofrontal and pregenual

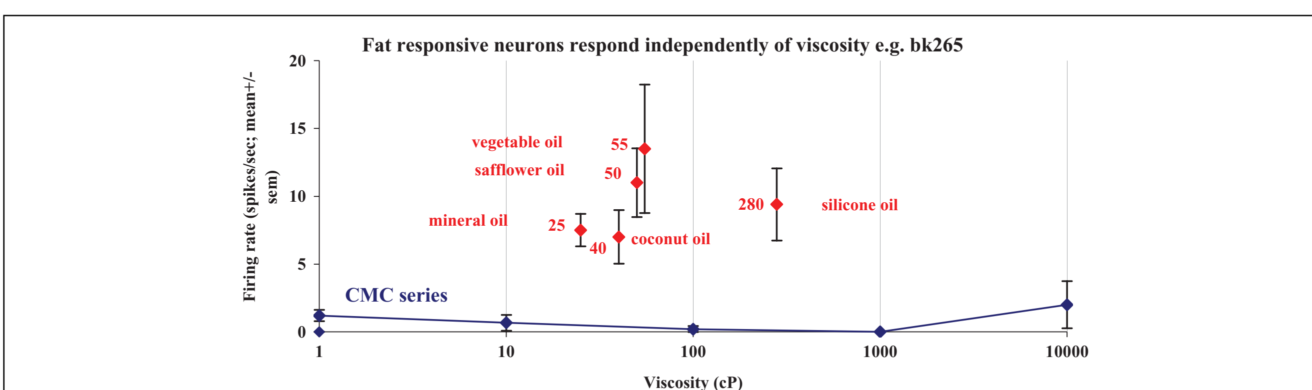

Figure 1–A neuron in the orbitofrontal cortex responding to the texture of fat in the mouth independently of viscosity. The cell (bk265) increased its firing rate to a range of fats and oils (the viscosity of which is shown in centipoise). The information that reaches this type of neuron is independent of a viscosity sensing channel, in that the neuron did not respond to the methyl cellulose (CMC) viscosity series. The neuron responded to the texture rather than the chemical structure of the fat in that it also responded to silicone oil ($(Si(CH_3)_2O)_n$) and paraffin (mineral) oil (hydrocarbon) (after Verhagen and others 2003).

cingulate cortex involved in the affective (hedonic) representations of food? In a test of whether these individual differences are reflected in the affective systems in the orbitofrontal cortex and pregenual cingulate cortex, Rolls and McCabe (2007) used fMRI to measure responses to the flavor of chocolate, the sight of chocolate, and their combination, in chocolate cravers compared with noncravers. It was shown that the sight of chocolate and also the flavor of chocolate produced more activation in chocolate cravers than noncravers in brain areas implicated in hedonic aspects of food stimuli, including the medial orbitofrontal cortex and anterior cingulate cortex.

These individual differences in brain responses to very pleasant foods help us to understand the mechanisms that drive the liking for specific foods. They indicate 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 and McCabe 2007; Rolls 2011c). 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.

Discussion

To what extent therefore could different fats in the mouth be differentiated? One mechanism suggested by this research is by their viscosity. Some neurons respond to fats in terms of their viscosity, and to the extent that different fats have different viscosities, this is one way that fats may be perceptually different. Another factor that could allow discrimination between different fats in the mouth is of course their odor, with butyrate content associated with some fatty foods (such as butter) being one example. A third factor might be taste-transduced fatty acids such as linoleic and lauric acids. However, none of the neurons we have recorded that responded to fat in the mouth responded to linoleic or lauric acid. Thus, the few neurons that do respond to linoleic or lauric acid (but do not respond to fat texture in the mouth) could indicate whether a fat is going off, and is decomposing to release these fatty acids, which would then impart a bad taste (Mattes 2009).

In future work, it will be important to follow up on our neuronal recording studies on fat texture (Rolls and others 1999; Verhagen and others 2003; Kadohisa and others 2005) to identify the physical properties that lead to oral texture being transduced as fat. Discoveries here may have important applications, including in the prevention and treatment of obesity (Rolls 2011c), and in producing highly palatable yet nutritious food.

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