



Taste, olfactory, and food reward value processing in the brain



Edmund T. Rolls

Oxford Centre for Computational Neuroscience, Oxford, UK¹

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ABSTRACT

Complementary neuronal recordings in primates, and functional neuroimaging in humans, show that the primary taste cortex in the anterior insula provides separate and combined representations of the taste, temperature, and texture (including fat texture) of food in the mouth independently of hunger and thus of reward value and pleasantness. One synapse on, in a second tier of processing, in the orbitofrontal cortex, these sensory inputs are for some neurons combined by associative learning with olfactory and visual inputs, and these neurons encode food reward value on a continuous scale in that they only respond to food when hungry, and in that activations correlate linearly with subjective pleasantness. Cognitive factors, including word-level descriptions, and selective attention to affective value, modulate the representation of the reward value of taste and olfactory stimuli in the orbitofrontal cortex and a region to which it projects, the anterior cingulate cortex, a tertiary taste cortical area. The food reward representations formed in this way play an important role in the control of appetite, and food intake. Individual differences in these reward representations may contribute to obesity, and there are age-related differences in these value representations that shape the foods that people in different age groups find palatable. In a third tier of processing in medial prefrontal cortex area 10, decisions between stimuli of different reward value are taken, by attractor decision-making networks.

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E-mail address: Edmund.Rolls@oxcns.org.

¹ <http://www.oxcns.org>.

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1. Introduction

1.1. Aims

The aims of this paper are to describe how taste, olfactory, and food texture inputs are processed in the brain, how a representation of reward value is produced and is related to subjective pleasure, how cognition and selective attention influence this value-related processing, and how decisions are taken between stimuli with different reward value. The approach taken here is to consider together, side-by-side, the primate neuronal recording and the human functional magnetic resonance imaging (fMRI) evidence, to build a clear foundation for understanding taste and olfactory cortical processing and the underlying principles in primates including humans. This approach is important, for it appears that some of the underlying principles of taste and olfactory processing are different in rodents, as described below. The focus of this paper is on processing in the brain, with research on peripheral processing described elsewhere (Barretto et al., 2015; Buck and Bargmann, 2013; Chaudhari and Roper, 2010; Mombaerts, 2006; Mori and Sakano, 2011).

1.2. Food reward value and appetite

One reason why it is important to understand the brain systems for processing taste, olfactory, and oral texture inputs is that during cortical processing food reward value becomes, by the secondary taste and olfactory cortex in the orbitofrontal cortex, explicit in the representation, in that the reward value can be decoded simply from the firing rates of the neurons. This is important for understanding the control of food intake, in that the reward value of food (i.e. whether we will work for a food), measures our appetite for a food, and whether we will eat a food. Thus normally we want food (will work for it, and will eat it) when we like it. “We want because we like”: the goal value, the food reward value, makes us want it. For example, neurons in the orbitofrontal cortex and lateral hypothalamus described below respond to the reward value of a food when it is, for example, shown, and these neuronal responses predict whether that food will be eaten (Rolls, 1981, 2005b, 2014; Rolls et al., 1986, 1989). Similarly, in studies on sensory-specific satiety in humans based on these neurophysiological discoveries, the reported pleasantness in humans of a food is closely correlated with whether it will then be eaten, and even with how much is eaten (Rolls et al., 1981b, 1983b, 1984). (The situation when it has been suggested that wanting is not a result of liking (Berridge et al., 2009), is when behavior becomes a habit. A

habit is a stimulus-response type of behavior that is no longer under control of the goal, but is under the control of an overlearned conditioned stimulus involved in stimulus-response, habit, behavioral responses (Rolls, 2005b, 2014).) The concept here is that food reward is a goal that normally drives appetite and eating, and it is therefore important to understand the brain mechanisms involved in food reward, in order to understand the control of appetite and food intake. When the behavior is goal-directed, brain regions such as the cingulate cortex are likely to be engaged (see Fig. 1). However, it is a useful distinction to bear in mind that sometimes feeding can become an overlearned habit, and that then the brain systems likely to be engaged are likely to include the striatum and rest of the basal ganglia (see Fig. 1). The distinction between these two types of processing is that when humans operate from habit, they may less consciously evaluate the costs and benefits of a choice than when goal-directed behavior is engaged. Further discussion of these issues is provided elsewhere (Rolls, 2014).

1.3. Investigations in primates including humans

The focus of the approach taken here is on complementary neurophysiological investigations in macaques and functional neuroimaging in humans. There are a number of reasons for this focus.

First, there are major anatomical differences in the neural processing of taste in rodents and primates (Rolls and Scott, 2003; Rolls, 2014; Scott and Small, 2009; Small and Scott, 2009). In rodents (and also in primates) taste information is conveyed by cranial nerves 7, 9 and 10 to the rostral part of the nucleus of the solitary tract (NTS) (Norgren and Leonard, 1971, 1973; Norgren, 1990) (see Fig. 1). However, although in primates the NTS projects to the taste thalamus and thus to the cortex (Fig. 1), in rodents the majority of NTS taste neurons responding to stimulation of the taste receptors of the anterior tongue project to the ipsilateral medial aspect of the pontine parabrachial nucleus (PbN), the rodent ‘pontine taste area’ (Cho et al., 2002; Small and Scott, 2009). The remainder project to adjacent regions of the medulla. From the PbN the rodent gustatory pathway bifurcates into two pathways: (1) a ventral ‘affective’ projection to the hypothalamus, central gray, ventral striatum, bed nucleus of the stria terminalis and amygdala; and (2) a dorsal ‘sensory’ pathway, which first synapses in the thalamus and then the agranular and dysgranular insular gustatory cortex (Norgren and Leonard, 1971; Norgren, 1974, 1976, 1990). These regions, in turn, project back to the PbN in rodents to sculpt the gustatory code and guide complex feeding

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