Physiology & Behavior 85 (2005) 45 – 56

PHYSIOLOGY & BEHAVIOR

Taste, olfactory, and food texture processing in the brain, and the control of food intake

Edmund T. Rolls*

University of Oxford, Department of Experimental Psychology, South Parks Road, Oxford OX1 3UD, England, UK

Abstract

Complementary neurophysiological recordings in macaques and functional neuroimaging in humans show that the primary taste cortex in the rostral insula and adjoining frontal operculum provides separate and combined representations of the taste, temperature, and texture (including viscosity and fat texture) of food in the mouth independently of hunger and thus of reward value and pleasantness. One synapse on, in the orbitofrontal cortex, these sensory inputs are for some neurons combined by learning with olfactory and visual inputs. 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 is computed in the primate (including human) orbitofrontal cortex. Consistently, activation of parts of the human orbitofrontal cortex correlates with subjective ratings of the pleasantness of the taste and smell of food. Cognitive factors, such as a word label presented with an odour, influence the pleasantness of the odour, and the activation produced by the odour in the orbitofrontal cortex. These findings provide a basis for understanding how what is in the mouth is represented by independent information channels in the brain; how the information from these channels is combined; and how and where the reward and subjective affective value of food is represented and is influenced by satiety signals. Activation of these representations in the orbitofrontal cortex may provide the goal for eating, and understanding them helps to provide a basis for understanding appetite and its disorders.

Keywords: Sensory-specific satiety; Fat; Food texture; Taste; Olfaction; Temperature

1. Introduction

The aims of this paper are to describe the rules of the cortical processing of taste and smell, how the pleasantness or affective value of taste and smell are represented in the brain, and to relate this to the brain mechanisms underlying emotion. To make the results relevant to understanding the control of human food intake, complementary evidence is provided by neurophysiological studies in non-human primates, and by functional neuroimaging studies in humans. A broad perspective on brain processing involved in emotion and in hedonic aspects of the control of food intake is provided by Rolls in *The Brain and Emotion* [1], and *Emotion Explained* [2].

* Tel.: +44 1865 271348; fax: +44 1865 310447.
E-mail address: Edmund.Rolls@psy.ox.ac.uk.
URL: www.cns.ox.ac.uk.

0031-9384/$ - see front matter © 2005 Elsevier Inc. All rights reserved.
doi:10.1016/j.physbeh.2005.04.012

1.1. Taste processing in the primate brain

1.1.1. Pathways

A diagram of the taste and related olfactory, somatosensory, and visual pathways in primates is shown in Fig. 1. Of particular interest is that in primates there is a direct projection from the rostral part of the nucleus of the solitary tract (NTS) to the taste thalamus and thus to the primary taste cortex in the frontal operculum and adjoining insula, with no pontine taste area and associated subcortical projections as in rodents [3,4]. This emphasis on cortical processing of taste in primates may be related to the great development of the cerebral cortex in primates, and the advantage of using extensive and similar cortical analysis of inputs from every sensory modality before the analysed representations from each modality are brought together in multimodal regions, as is documented below. The multimodal convergence that enables single neurons to respond

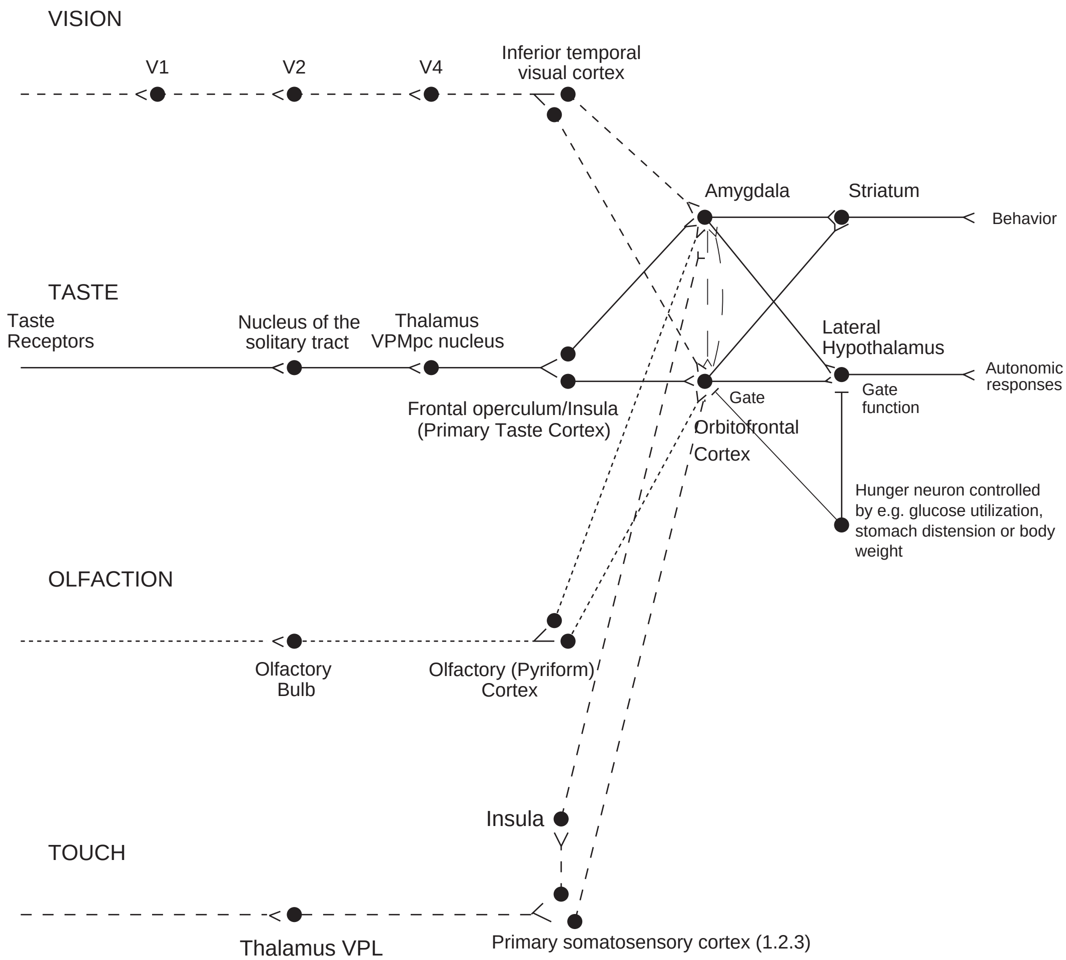

Fig. 1. Schematic diagram of the taste and olfactory pathways in primates showing how they converge with each other and with visual pathways. The gate functions shown refer to the finding that the responses of taste neurons in the orbitofrontal cortex and the lateral hypothalamus are modulated by hunger.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

to different combinations of taste, olfactory, texture, temperature, and visual inputs to represent different flavours produced often by new combinations of sensory input is a theme of recent research that will be described.

1.1.2. The secondary taste cortex

A secondary cortical taste area in primates was discovered by Rolls et al.[5] in the caudolateral orbitofrontal cortex, extending several mm in front of the primary taste cortex. One principle of taste processing is that by the secondary taste cortex, the tuning of neurons can become quite specific, with some neurons responding for example only to sweet taste. This specific tuning (especially when combined with olfactory inputs) helps to provide a basis for changes in appetite for some but not other foods eaten during a meal.

1.1.3. Five prototypical tastes, including umami

In the primary and secondary taste cortex, there are many neurons that respond best to each of the four classical prototypical tastes sweet, salt, bitter and sour [6,7], but also there are many neurons that respond best to umami tastants such as glutamate (which is present in many natural foods such as tomatoes, mushrooms and milk) [8] and inosine monophosphate (which is present in meat and some fish such as tuna) [9]. This evidence, taken together with the identification of a glutamate taste receptor [10], leads to the view that there are five prototypical types of taste information channels, with umami contributing, often in combination with corresponding olfactory inputs [11], to the flavour of protein. In addition, other neurons respond to water, and others to the somatosensory stimuli astringency as exemplified by tannic acid [12], and to capsaicin [13,14].

1.1.4. The pleasantness of the taste of food

The modulation of the reward value of a sensory stimulus such as the taste of food by motivational state, for example hunger, is one important way in which motivational behaviour is controlled [1]. The subjective correlate of this modulation is that food tastes pleasant when hungry, and tastes hedonically neutral when it has been eaten to satiety. We have found that the modulation of taste-evoked signals by motivation is not a property found in early stages of the primate gustatory system. The responsiveness of taste neurons in the nucleus of the solitary tract [15] and in the