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# Taste and Related Systems in Primates Including Humans

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The cortical processing of taste and related sensory inputs is being investigated at the neuronal level in macaques to help understand the operation of these cortical areas in humans. The primary taste cortex of macaques in the rostral insula and adjoining frontal operculum contains neurons tuned to different tastes including umami (Scott *et al.*, 1986; Yaxley *et al.*, 1990; Baylis and Rolls, 1991; Rolls *et al.*, 1996b, 1998). Neurons in the macaque primary taste cortex respond to the identity and intensity of taste, in that their responses are not affected when taste reward is decreased to zero by feeding to satiety (Rolls *et al.*, 1988). Other neurons in the primary taste cortex respond to somatosensory inputs by representing the viscosity of what is in the mouth, oral fat texture, the temperature of what is in the mouth, capsaicin (Verhagen *et al.*, 2004), and tannic acid (astringency) (Critchley and Rolls, 1996a). Not only are these qualities represented independently by different neurons, but other neurons respond to combinations of these inputs (Verhagen *et al.*, 2004). The macaque primary taste cortex does not represent the smell or sight of food (Verhagen *et al.*, 2004).

The macaque orbitofrontal cortex contains the secondary taste and olfactory cortices, in that different parts of it receive from the primary taste cortex (Baylis *et al.*, 1995), and the primary olfactory cortical areas. Neurons in the secondary taste cortex not only represent taste, but other neurons respond to somatosensory inputs by representing the viscosity of what is in the mouth (Rolls *et al.*, 2003b), oral fat texture (Rolls *et al.*, 1999; Verhagen *et al.*, 2003), the temperature of what is in the mouth (Kadohisa *et al.*, 2004), capsaicin (Kadohisa *et al.*, 2004) and tannic acid (astringency) (Critchley and Rolls, 1996a). Other neurons respond to combinations of these inputs. The orbitofrontal cortex also contains neurons that respond to olfactory stimuli and to the sight of food, and for many neurons these olfactory and taste representations are learned by olfactory to taste or visual to taste associative learning (Rolls and Baylis, 1994; Rolls *et al.*, 1996a; Critchley and Rolls, 1996b). Orbitofrontal cortex neurons represent the reward value of what is in the mouth, in that the neuronal responses to the taste, smell, and sight of food decrease to zero as the monkey is fed to satiety (Rolls *et al.*, 1989; Critchley and Rolls, 1996c). Further, orbitofrontal cortex neurons represent sensory-specific reductions in their responses to the particular foods that have been eaten to satiety, and thus implement sensory-specific satiety (Rolls *et al.*, 1999; Critchley and Rolls, 1996c; Rolls, 1999, 2004).

In human functional neuroimaging studies, it has been shown that activation of the orbitofrontal cortex (OFC) and adjoining anterior cingulate cortex (ACC) by odours (O'Doherty *et al.*, 2000) and by liquid food (Kringelbach *et al.*, 2003) is hunger-dependent, and indeed the pleasantness of the food is correlated with the degree of activation found. In both studies, it was shown that the modulation is sensory-specific, so that sensory-specific satiety is implemented in the human OFC. The viscosity of food is represented in the human taste and non-taste insula, and in the orbitofrontal cortex (De Araujo and Rolls, 2004). Fat in the mouth is detected by its texture, and this is represented in the anterior cingulate and orbitofrontal cortex (De Araujo and Rolls, 2004). The pleasantness of odours is represented in the orbitofrontal cortex (Rolls *et al.*, 2003a), and flavour representations are formed by combining taste and olfactory inputs in the orbitofrontal cortex (De Araujo *et al.*, 2003b).

This primate neurophysiological and human functional neuroimaging evidence thus shows that the orbitofrontal cortex is involved in decoding some primary reinforcers such as taste, odour, texture, touch and temperature; in learning and reversing associations of visual and other stimuli to these primary reinforcers; and in representing the pleasantness of food in a way that correlates directly with whether food is eaten. The orbitofrontal cortex and connected areas play key roles in representing the sensory qualities and affective value of food, and thus in the control of eating (Rolls *et al.*, 1990; Rolls, 1997, 1999, 2000, 2001a,b, 2005; O'Doherty *et al.*, 2001; Rolls and Scott, 2003; Kringelbach and Rolls, 2004).

## References

**Baylis, L.L.** and **Rolls, E.T.** (1991) *Responses of neurons in the primate taste cortex to glutamate.* Physiol. Behav., 49, 973–979.

**Baylis, L.L., Rolls, E.T.** and **Baylis, G.C.** (1995) *Afferent connections of the caudolateral orbitofrontal cortex taste area of the primate.* Neuroscience, 64, 801–812.

**Critchley, H.D.** and **Rolls, E.T.** (1996a) *Responses of primate taste cortex neurons to the astringent tastant tannic acid.* Chem. Senses, 21, 135–145.

**Critchley, H.D.** and **Rolls, E.T.** (1996b) *Olfactory neuronal responses in the primate orbitofrontal cortex: analysis in an olfactory discrimination task.* J. Neurophysiol., 75, 1659–1672.

**Critchley, H.D.** and **Rolls, E.T.** (1996c) *Hunger and satiety modify the responses of olfactory and visual neurons in the primate orbitofrontal cortex.* J. Neurophysiol., 75, 1673–1686.

**De Araujo, I.E.T.** and **Rolls, E.T.** (2004) *Representation in the human brain of food texture and oral fat*. J. Neurosci., 24, 3086–3093.

**De Araujo, I.E.T., Kringelbach, M.L., Rolls, E.T.** and **Hobden, P.** (2003a) *Representation of umami taste in the human brain*. J. Neurophysiol., 90, 313–319.

**De Araujo, I.E.T., Rolls, E.T., Kringelbach, M.L., McGlone, F.** and **Phillips, N.** (2003b) *Taste-olfactory convergence, and the representation of the pleasantness of flavour, in the human brain.* Eur. J. Neurosci., 18, 2059–2068.

**Kadohisa, M., Rolls, E.T.** and **Verhagen, J.V.** (2004) *Orbitofrontal cortex neuronal representation of temperature and capsaicin in the mouth.* Neuroscience, 127, 207–221.

**Kringelbach, M.L., O'Doherty, J., Rolls, E.T.** and **Andrews, C.** (2003) *Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness.* Cereb. Cortex, 13, 1064–1071.

**Kringelbach, M.L.** and **Rolls, E.T.** (2004) *The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology.* Prog. Neurobiol., 72, 341–372.

**O'Doherty, J., Rolls, E.T., Francis, S., Bowtell, R., McGlone, F., Kobal, G., Renner, B.** and **Ahne, G.** (2000) *Sensory-specific satiety related olfactory activation of the human orbitofrontal cortex.* Neuroreport, 11, 399–402.

**O'Doherty, J., Rolls, E.T., Francis, S., Bowtell, R.** and **McGlone, F.** (2001) *The representation of pleasant and aversive taste in the human brain*. J. Neurophysiol., 85, 1315–1321.

**Rolls, E.T.** (1997) *Taste and olfactory processing in the brain and its relation to the control of eating.* Crit. Rev. Neurobiol., 11, 263–287.

**Rolls, E.T.** (1999) The Brain and Emotion. Oxford University Press, Oxford

**Rolls, E.T.** (2000) *The orbitofrontal cortex and reward*. Cereb. Cortex, 10, 284–294.

**Rolls, E.T.** (2001a) *The rules of formation of the olfactory representations found in the orbitofrontal cortex olfactory areas in primates.* Chem. Senses, 26, 595–604.

**Rolls, E.T.** (2001b) *The representation of umami taste in the human and macaque cortex.* Sensory Neuron, 3, 227–242.

**Rolls, E.T.** (2004) *The functions of the orbitofrontal cortex*. Brain Cogn., 55, 11–29.

**Rolls, E.T.** (2005) Emotion Explained. Oxford University Press: Oxford.

**Rolls, E.T.** and **Baylis, L.L.** (1994) *Gustatory, olfactory and visual convergence within the primate orbitofrontal cortex.* J. Neurosci., 14, 5437–5452.

**Rolls, E.T.** and **Scott, T.R.** (2003) *Central taste anatomy and neurophysiology*. In Doty, R.L. (ed.), Handbook of Olfaction and Gustation, 2nd edn. Dekker, New York, pp. 679–705.

**Rolls, E.T., Scott, T.R., Sienkiewicz, Z.J.** and **Yaxley, S.** (1988) *The responsiveness of neurones in the frontal opercular gustatory cortex of the macaque monkey is independent of hunger.* J. Physiol., 397, 1–12.

**Rolls, E.T., Sienkiewicz, Z.J.,** and **Yaxley, S.** (1989) *Hunger modulates the responses to gustatory stimuli of single neurons in the caudolateral orbitofrontal cortex of the macaque monkey.* Eur. J. Neurosci., 1, 53–60.

**Rolls, E.T., Yaxley, S.** and **Sienkiewicz, Z.J.** (1990) *Gustatory responses of single neurons in the caudolateral orbitofrontal cortex of the macaque monkey.* J. Neurophysiol., 64, 1055–1066.

**Rolls, E.T., Critchley, H., Mason, R.** and **Wakeman, E.A.** (1996a) *Orbitofrontal cortex neurons: role in olfactory and visual association learning.* J. Neurophysiol., 75, 1970–1981.

**Rolls, E.T., Critchley, H., Wakeman, E.A.** and **Mason, R.** (1996b) *Responses of neurons in the primate taste cortex to the glutamate ion and to inosine 5'-monophosphate.* Physiol. Behav., 59, 991–1000.

**Rolls, E.T., Critchley, H.D., Browning, A.** and **Hernadi, I.** (1998) *The neurophysiology of taste and olfaction in primates, and umami flavor*. Ann. N. Y. Acad. Sci., 855, 426–437.

**Rolls, E.T., Critchley, H.D., Browning, A.S., Hernadi, A.** and **Lenard, L.** (1999) *Responses to the sensory properties of fat of neurons in the primate orbitofrontal cortex*. J. Neurosci., 19, 1532–1540.

**Rolls, E.T., Kringelbach, M.L.** and **De Araujo, I.E.T.** (2003a) *Different representations of pleasant and unpleasant odors in the human brain*. Eur. J. Neurosci., 18, 695–703.

**Rolls, E.T., Verhagen, J.V.** and **Kadohisa, M.** (2003b) *Representations of the texture of food in the primate orbitofrontal cortex: neurons responding to viscosity, grittiness, and capsaicin.* J. Neurophysiol., 90, 3711–3724.

**Scott, T.R., Yaxley, S., Sienkiewicz, Z.J.** and **Rolls, E.T.** (1986) *Gustatory responses in the frontal opercular cortex of the alert cynomolgus monkey*. J. Neurophysiol., 56, 876–890.

**Verhagen, J.V., Rolls, E.T.** and **Kadohisa, M.** (2003) Neuron*s in the primate orbitofrontal cortex respond to fat texture independently of viscosity.* J. Neurophysiol., 90, 1514–1525.

**Verhagen, J.V., Kadohisa, M.,** and **Rolls, E.T.** (2004) *The primate insular/opercular taste cortex: neuronal representations of the viscosity, fat texture, grittiness, temperature, and taste of foods.* J. Neurophysiol., 92, 1685–1699.

**Yaxley, S., Rolls, E.T.** and **Sienkiewicz, Z.J.** (1990) *Gustatory responses of single neurons in the insula of the macaque monkey*. J. Neurophysiol., 63, 689–700.