

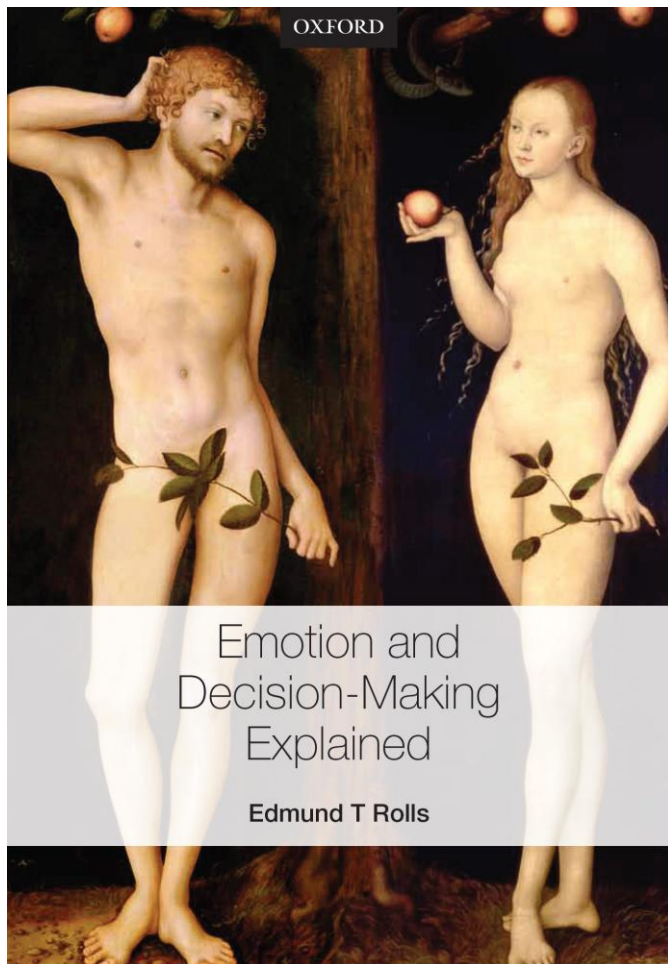
How taste, olfactory, texture and visual inputs as well as cognitive factors produce the reward value of food and rich delicious flavour

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Emotion and
Decision-Making
Explained

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University Press
2014**

Neuroimaging:

F. Grabenhorst

C. McCabe

I. Araujo

B. Parris

Neuropsychology:

J. Hornak

H. Berlin

Orbitofrontal Neurophysiology:

J.V. Verhagen

M. Kadohisa

H. Critchley

Computational Neuroscience

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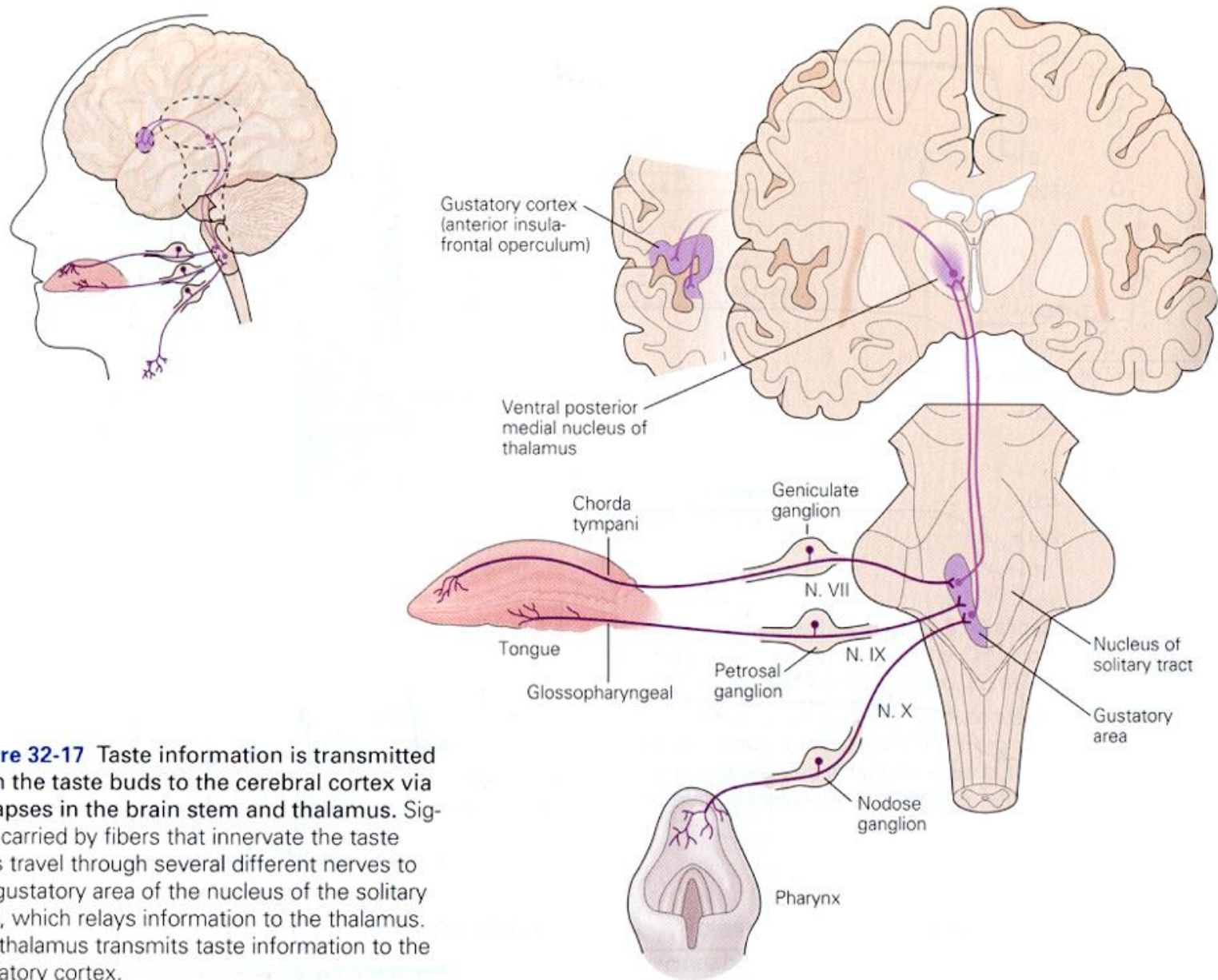
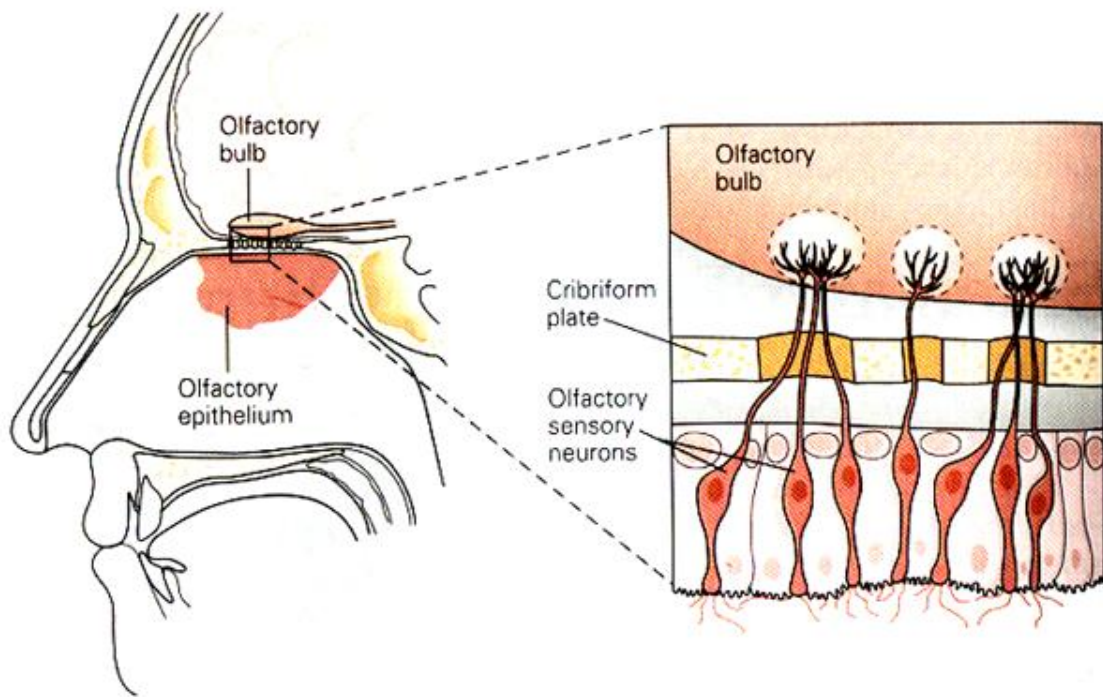
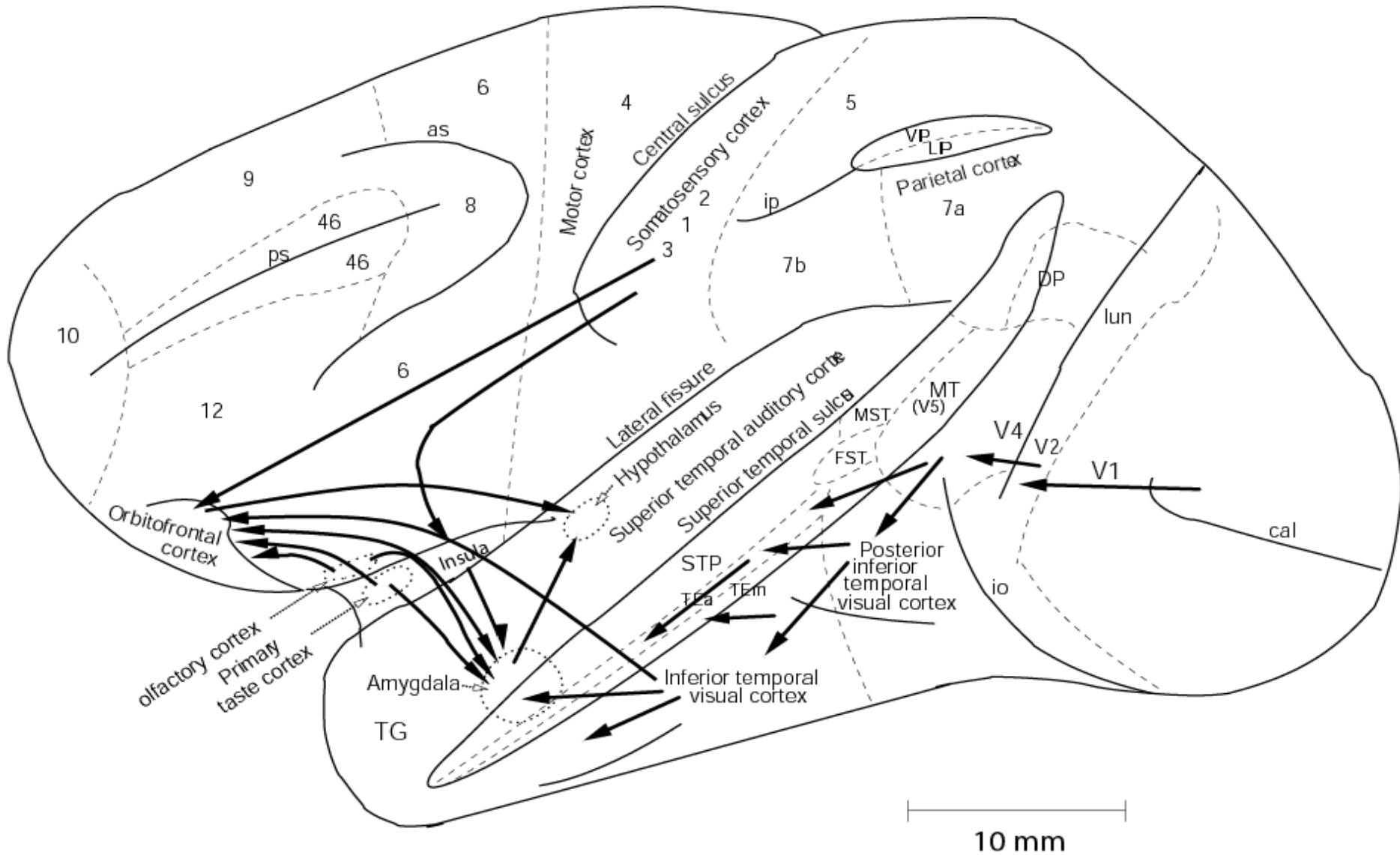


Figure 32-17 Taste information is transmitted from the taste buds to the cerebral cortex via synapses in the brain stem and thalamus. Signals carried by fibers that innervate the taste buds travel through several different nerves to the gustatory area of the nucleus of the solitary tract, which relays information to the thalamus. The thalamus transmits taste information to the gustatory cortex.

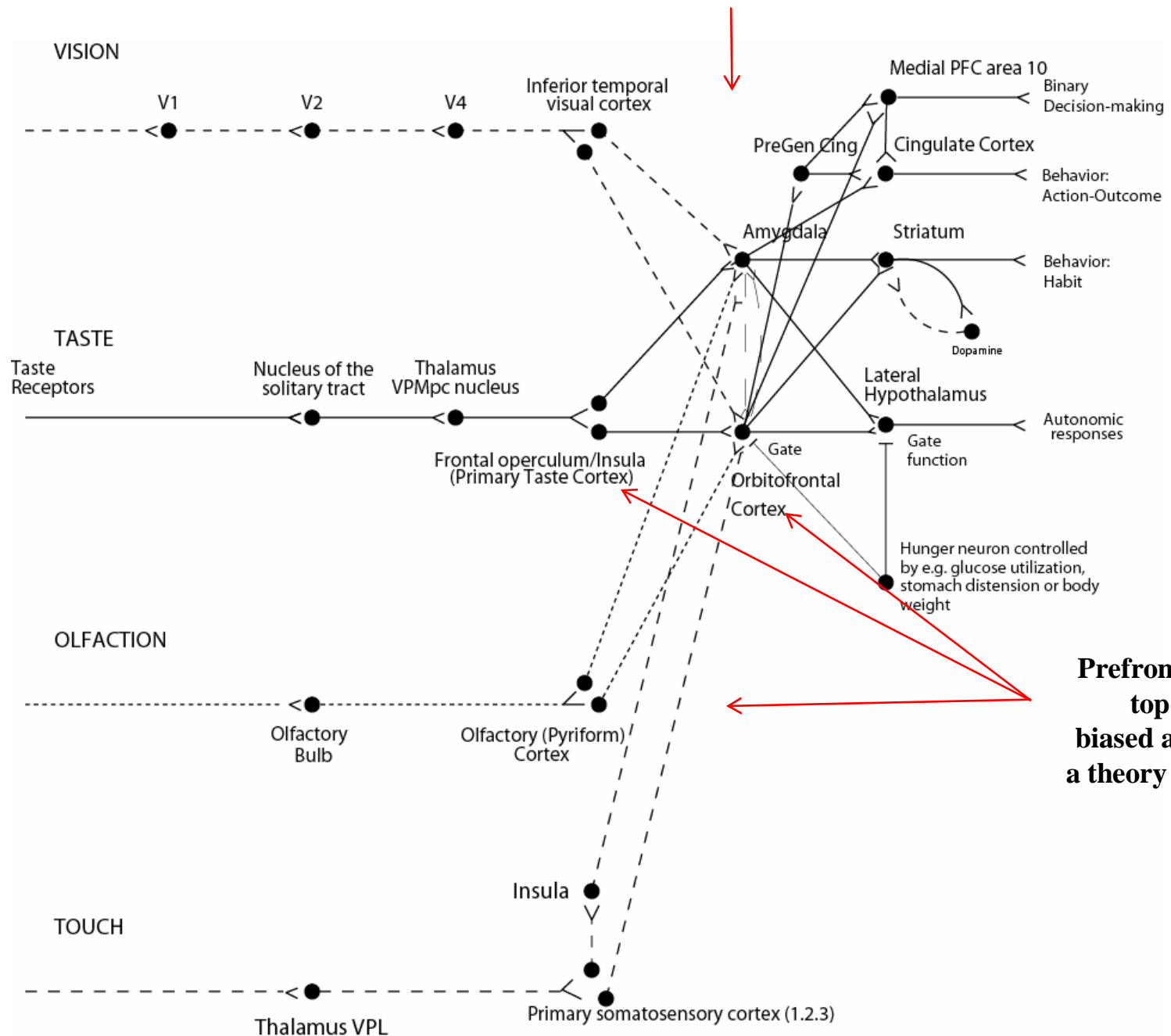
Figure 32-1 Olfactory sensory neurons are embedded in a small area of specialized epithelium in the dorsal posterior recess of the nasal cavity. These neurons project axons to the olfactory bulb of the brain, a small ovoid structure that rests on the cribriform plate of the ethmoid bone.

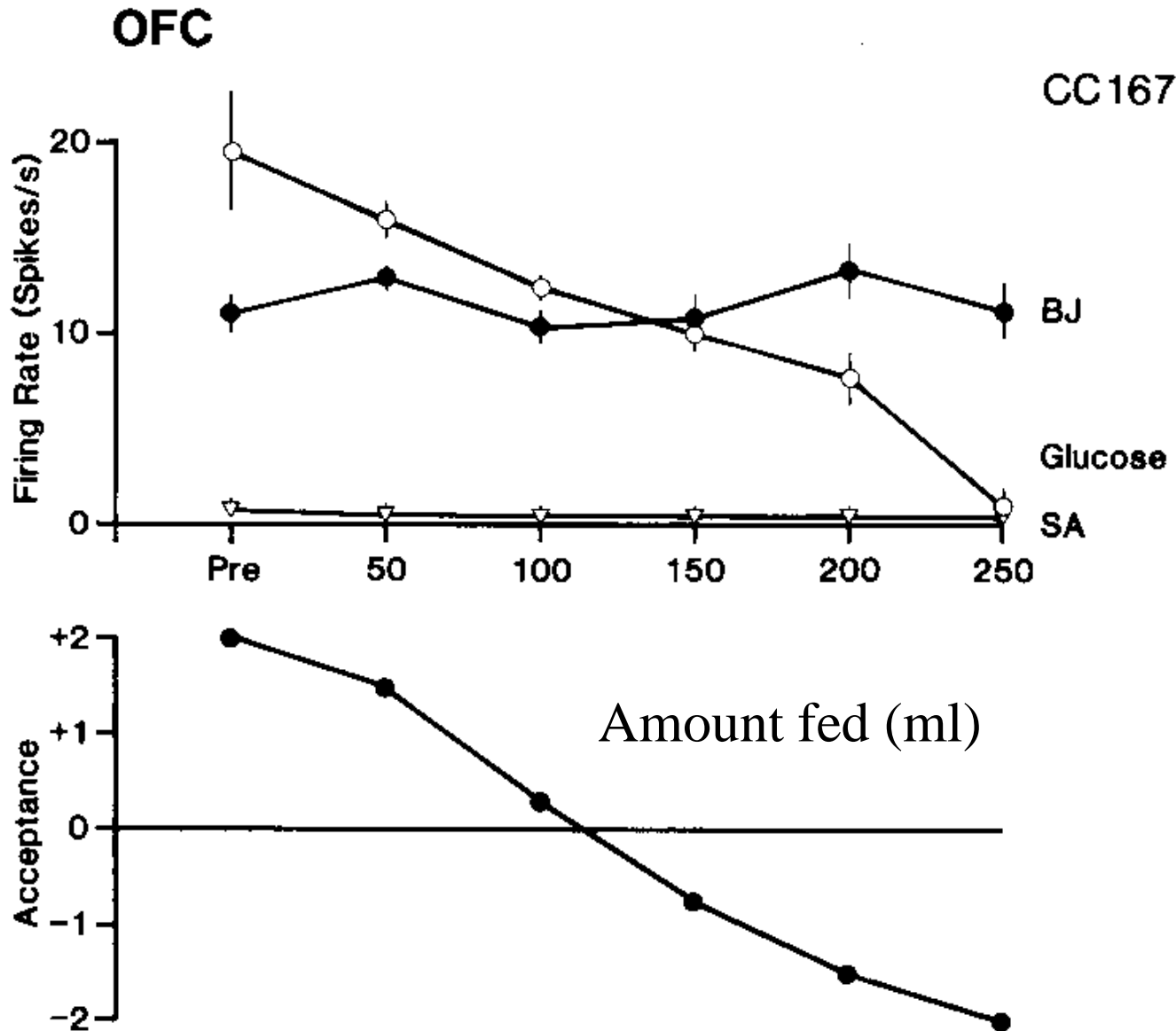


Taste, olfactory, somatosensory and visual inputs to the orbitofrontal cortex



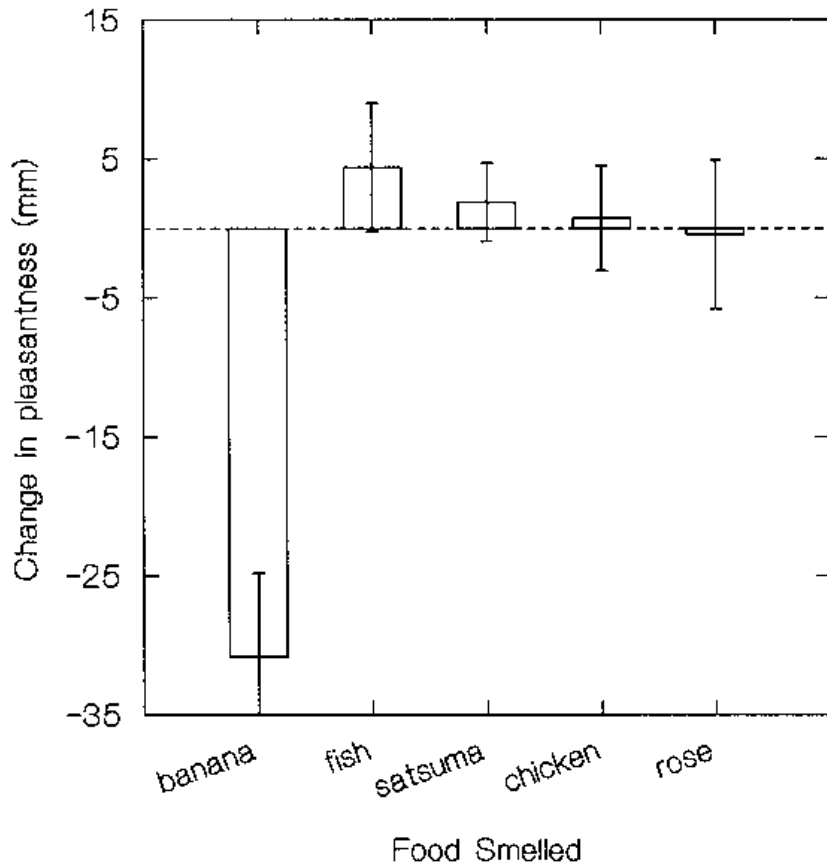
What **Reward** Decision/Action



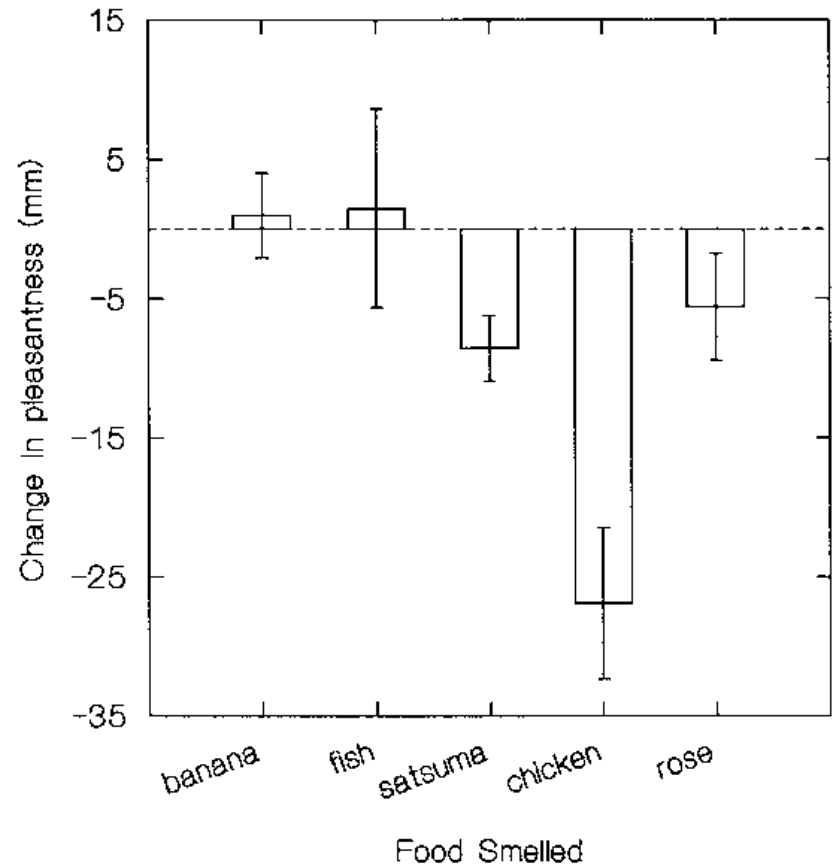


Sensory-specific satiety in the macaque orbitofrontal cortex

Banana Eaten

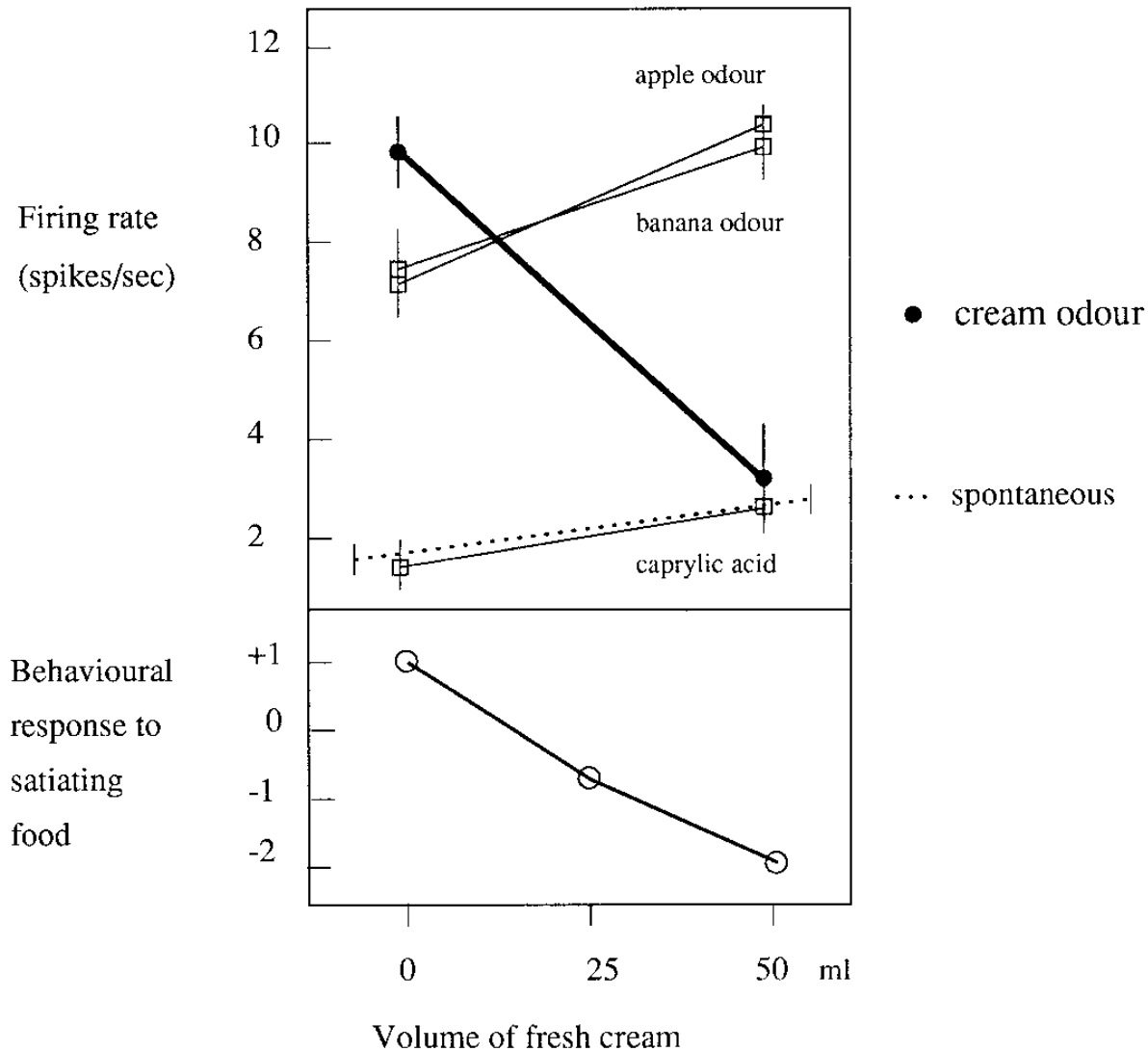


Chicken Eaten



Olfactory sensory-specific satiety in humans
(Rolls, E.T. and Rolls, J.H. 1997, *Physiol. Behav* 61: 461-473)

Orbitofrontal cortex neurons implement olfactory sensory-specific satiety / reward: here for cream



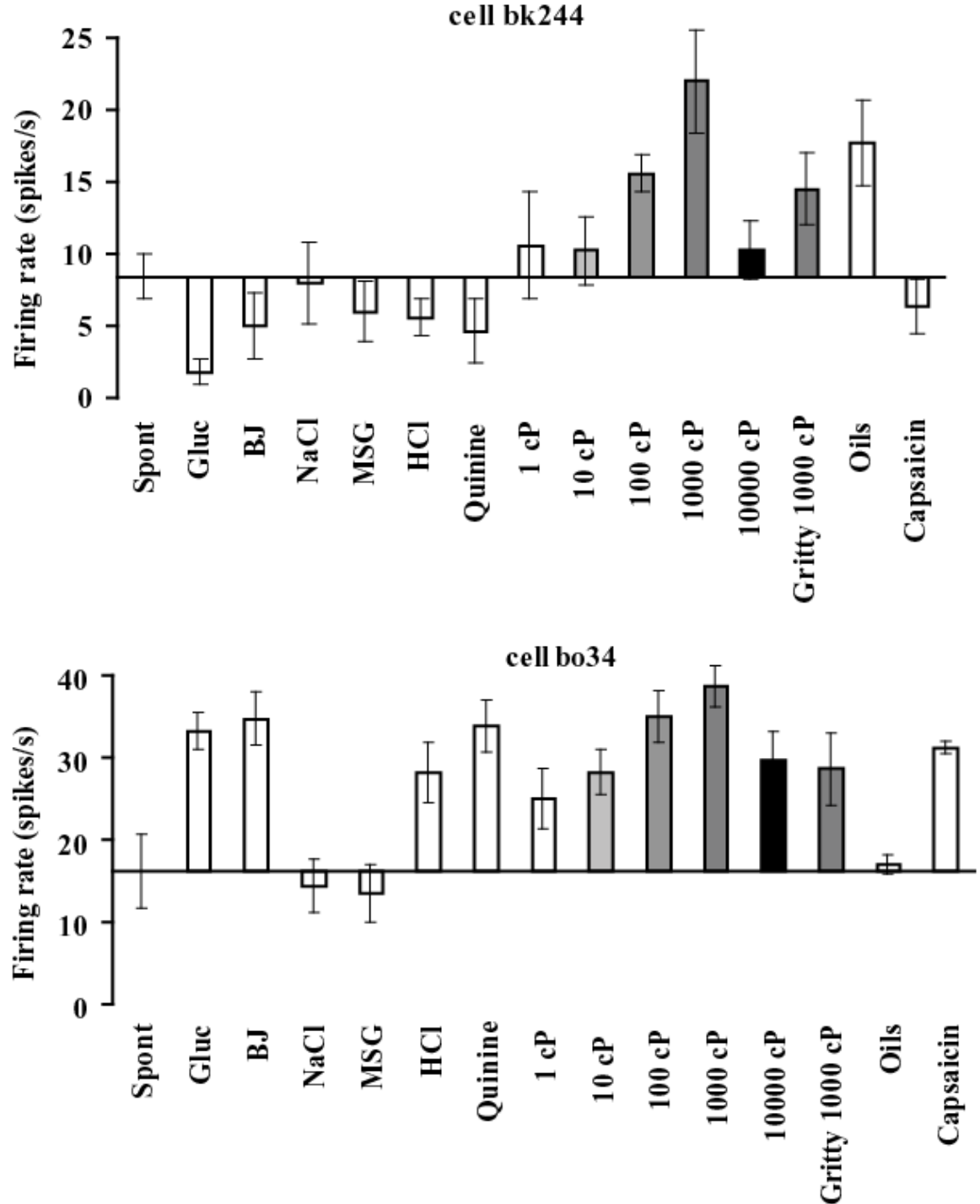
Critchley, H.D. and Rolls, E.T. (1996)

Hunger and satiety modify the responses of olfactory and visual neurons in the primate orbitofrontal cortex. *Journal of Neurophysiology* 75: 1673-1686.

Each orbitofrontal cortex neuron responds to a different combination of taste, odor, texture and temperature stimuli: as a population they provide information about a rich variety of reward stimuli:

and provide for behaviours such as sensory-specific satiety that are specific to combinations.

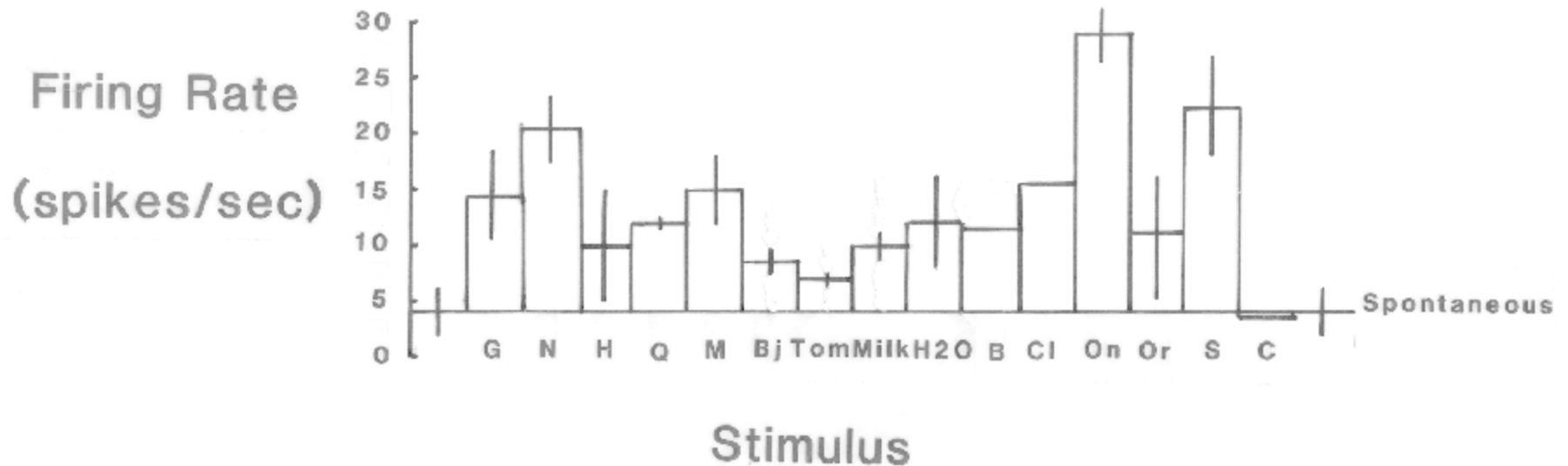
A reward representation as a goal for action must be specific for a particular reward (cf dopamine).



Orbitofrontal cortex: flavour is formed by convergence of taste and smell onto single neurons using associative learning.

Neurons respond to complementary combinations of the taste, smell, texture and sight of food

Cell 084.1 Bimodal Taste/olfaction



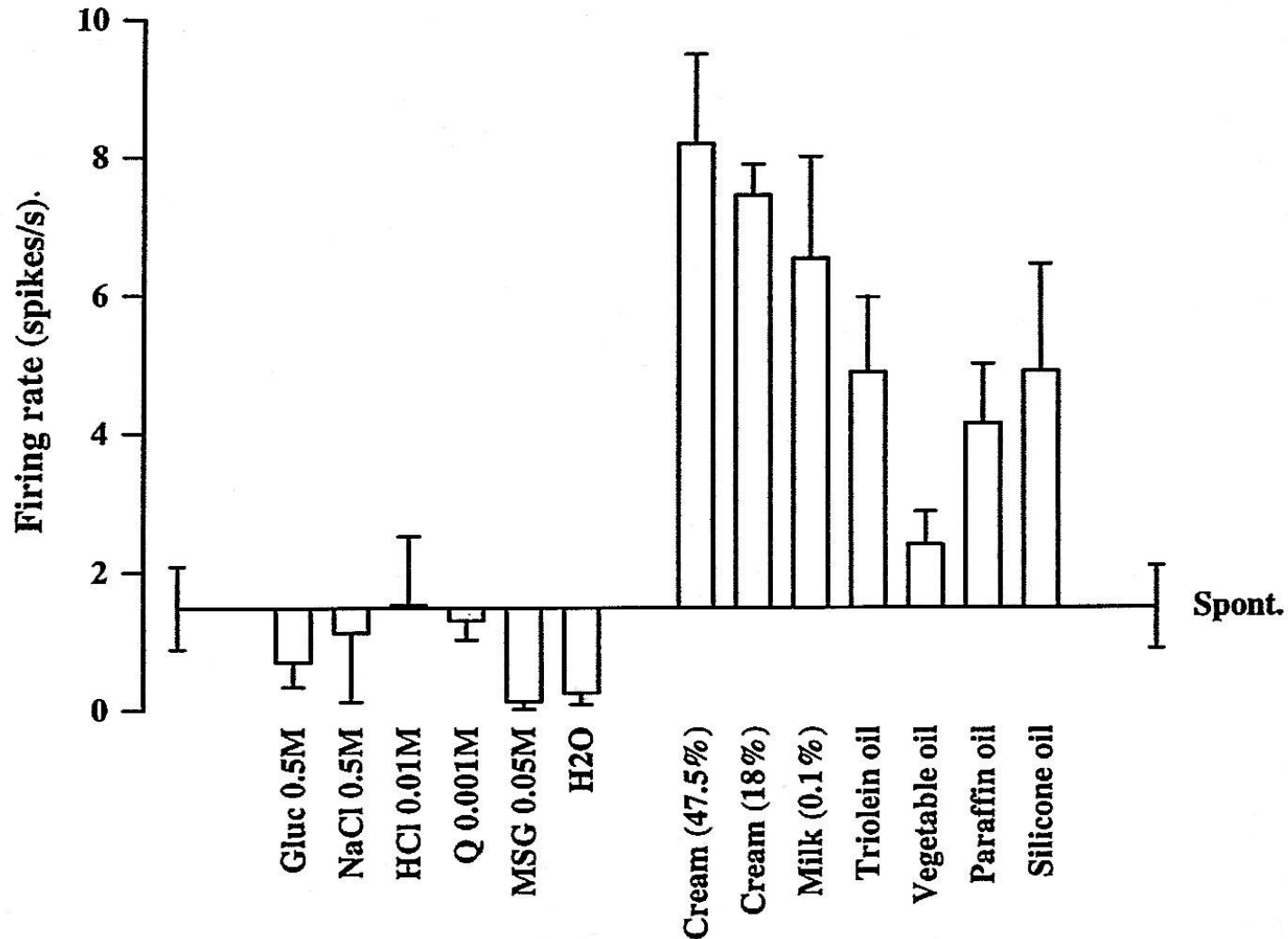
Rolls, E.T. and Baylis, L.L. (1994)

Gustatory, olfactory and visual convergence within the primate orbitofrontal cortex.

Journal of Neuroscience 14: 5437-5452.

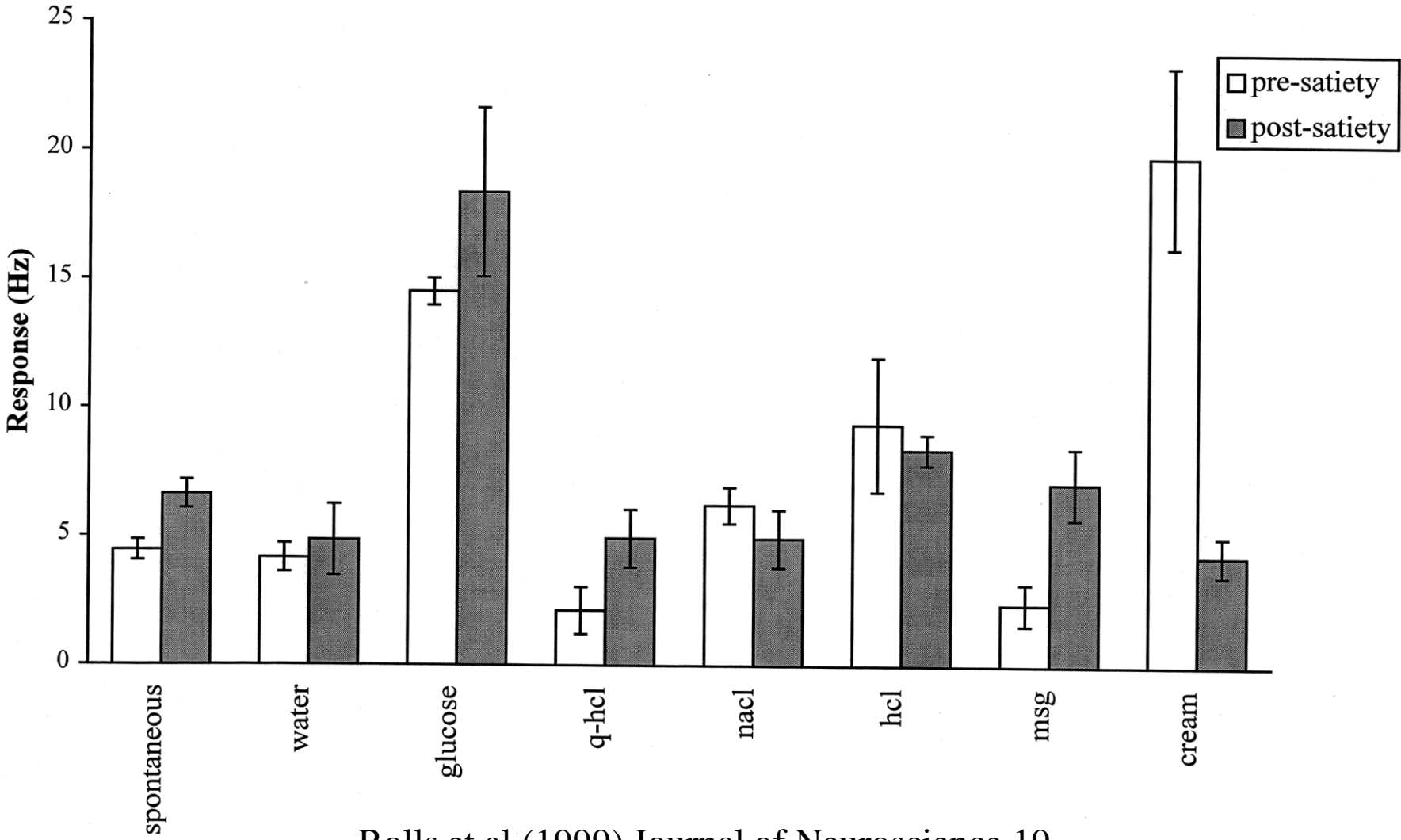
Orbitofrontal cortex fat texture-responsive neurons:

These neurons respond not only to cream and fat, but also to non-fat oils, showing that the brain senses fat by oral texture



Sensory-specific satiety for the texture of fat

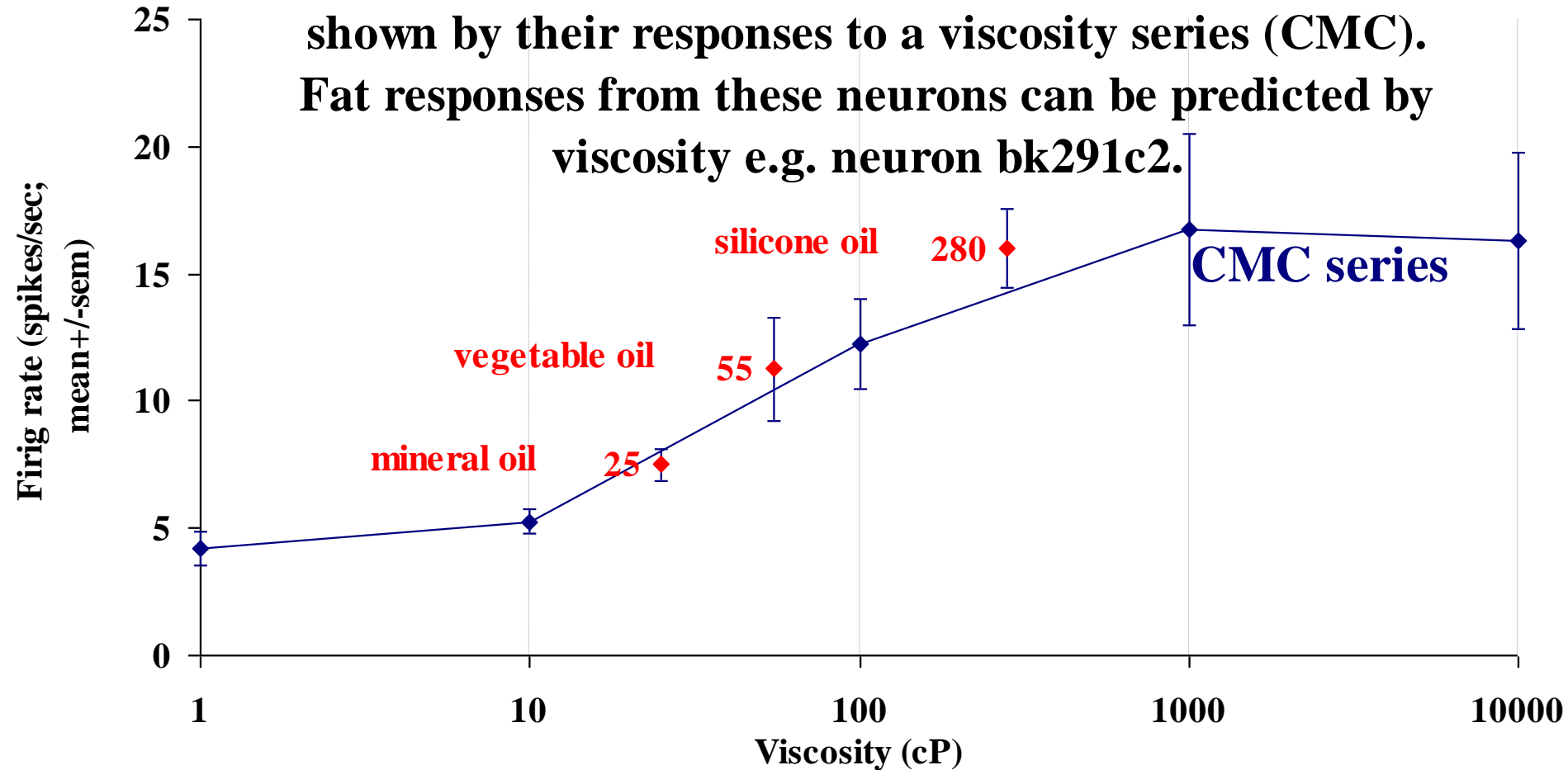
au143(b):
response to stimuli pre- and post- satiety to 45mls cream



Rolls et al (1999) Journal of Neuroscience 19

Responses to the sensory properties of fat of neurons in the primate orbitofrontal cortex.

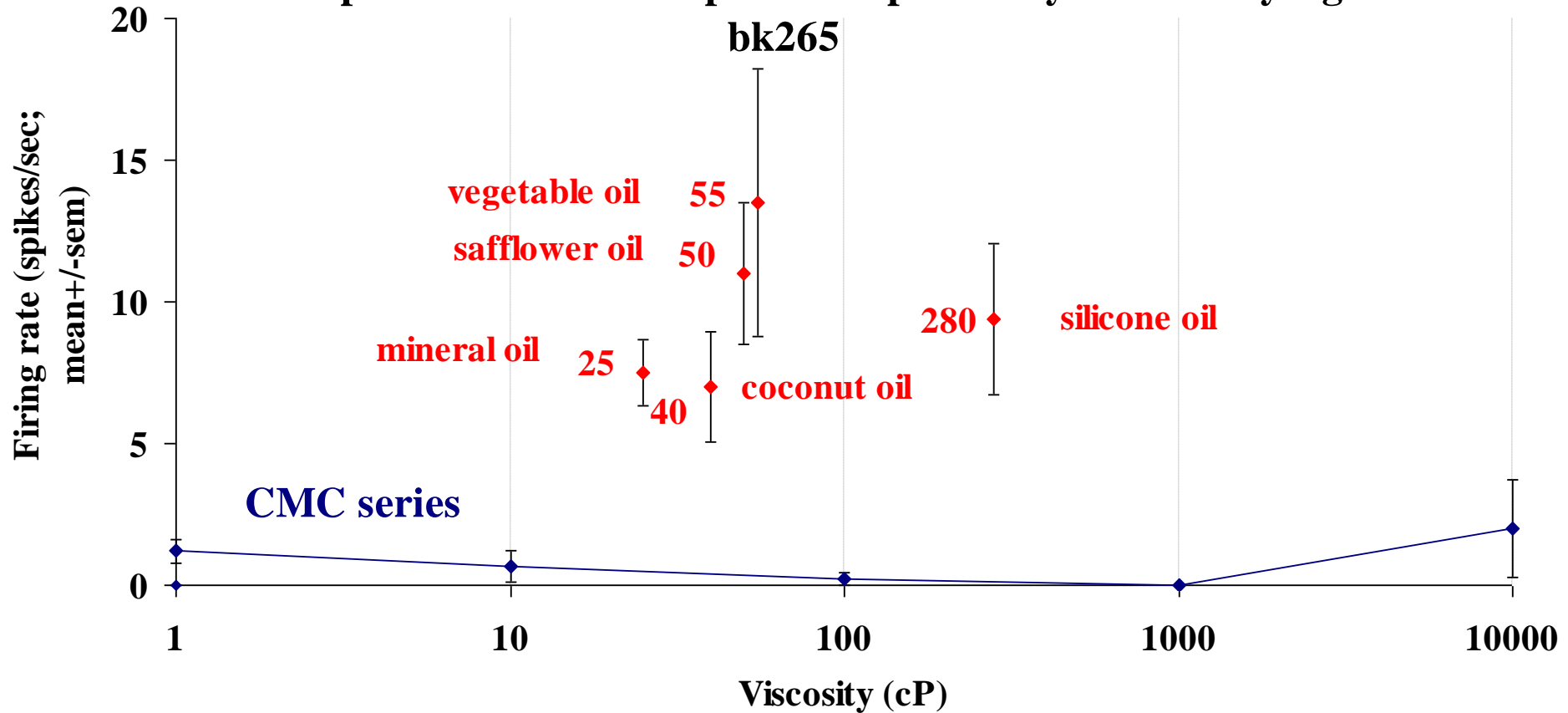
Some neurons encode the viscosity of oral stimuli, as shown by their responses to a viscosity series (CMC). Fat responses from these neurons can be predicted by viscosity e.g. neuron bk291c2.



Rolls, E.T., Verhagen, J.V. and Kadohisa, M. (2003) Journal of Neurophysiology 90
Representations of the texture of food in the primate orbitofrontal cortex:
neurons responding to viscosity, grittiness, and capsaicin.

Orbitofrontal cortex fat texture-responsive neurons show that fat is sensed independently of viscosity

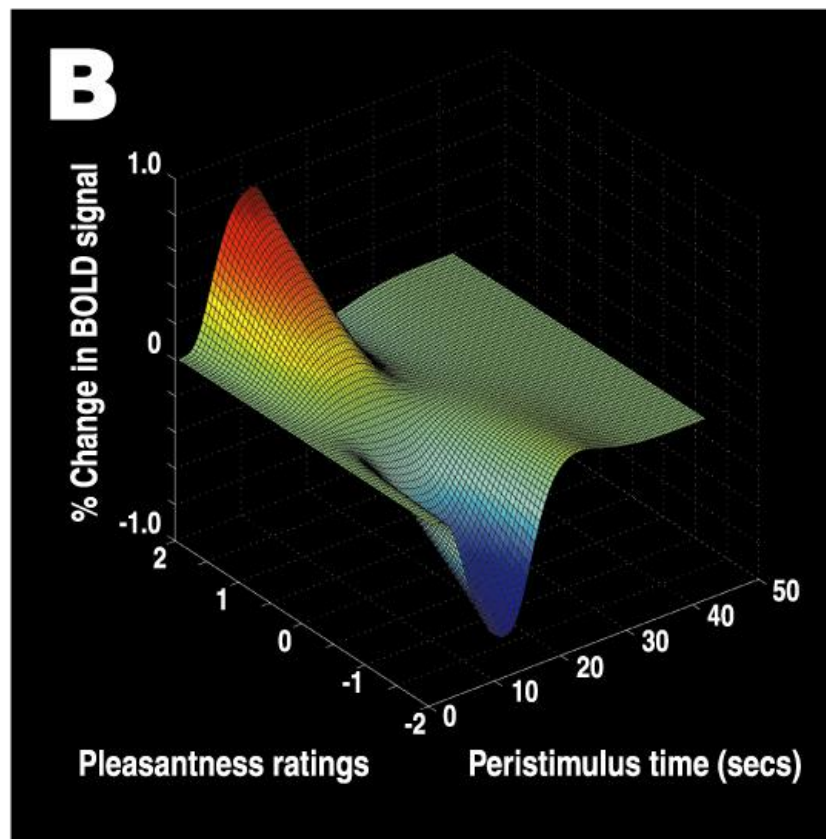
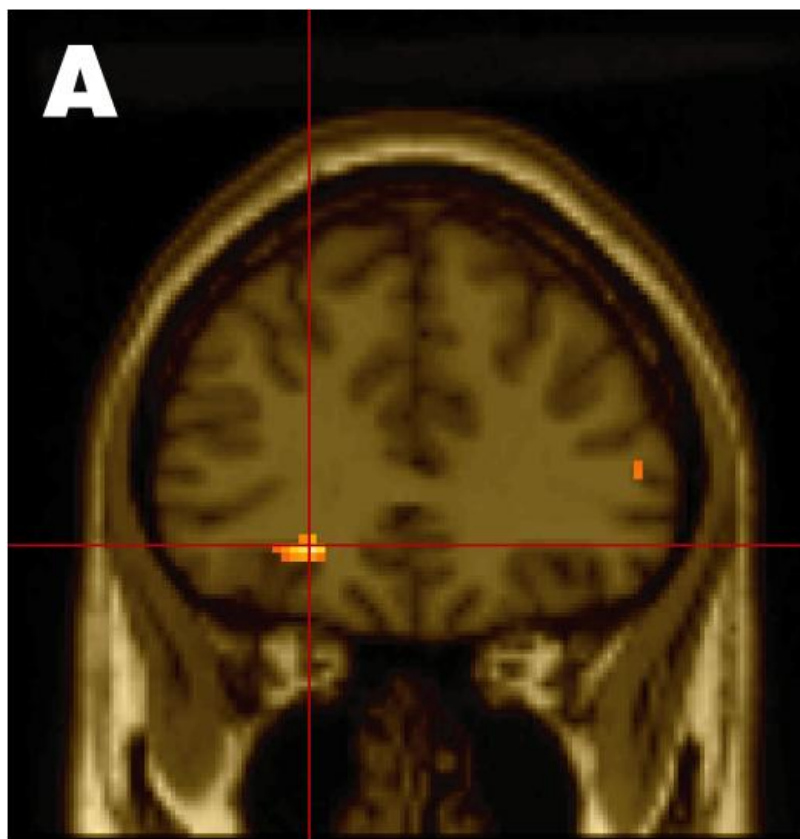
Fat responsive neurons respond independently of viscosity e.g.



Verhagen, J.V., Rolls, E.T. and Kadohisa, M. (2003)

Neurons in the primate orbitofrontal cortex respond to fat texture independently of viscosity. *Journal of Neurophysiology* 90: 1514-1525.

Whole Food Sensory-specific Satiety: Correlation between the BOLD signal in the OFC and subjective, conscious, pleasantness ratings



Correlation with pleasantness ratings

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. *Cerebral Cortex* 13: 1064-1071.

Whole Food Sensory-specific Satiety

Conclusions

- A direct correlation between the subjective state of pleasure produced by food and the activation of the orbitofrontal cortex has been demonstrated.
- The human orbitofrontal cortex, as in non-human primates, plays an important role in representing the reward value of food stimuli, including chocolate, and a food rich in umami, tomato
- This is consistent with the hypothesis that the pleasantness of the flavour of food (with taste, olfactory and texture components) is represented in the human OFC.
- It is suggested that sensory-specific satiety is a general property of reward systems (Rolls, 2005, Emotion Explained. Oxford).

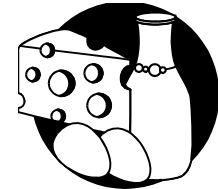
Kringelbach, M.L., O'Doherty, J., Rolls, E.T. and Andrews, C. (2003)

Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness. *Cerebral Cortex* 13: 1064-1071.

Free glutamate in cheese and milk

Cheese	(mg/100g)
Emmenthal	308
Parmesan Reggiano	1680
Cheddar cheese	182

Milk	
Cow	1
Goat	4
Human breast milk	19



(K. Ninomiya 1998)

What makes umami pleasant?

**Monosodium glutamate (MSG) alone is not very pleasant.
Monosodium glutamate does not interact with other tastes.**

Umami as a flavour:

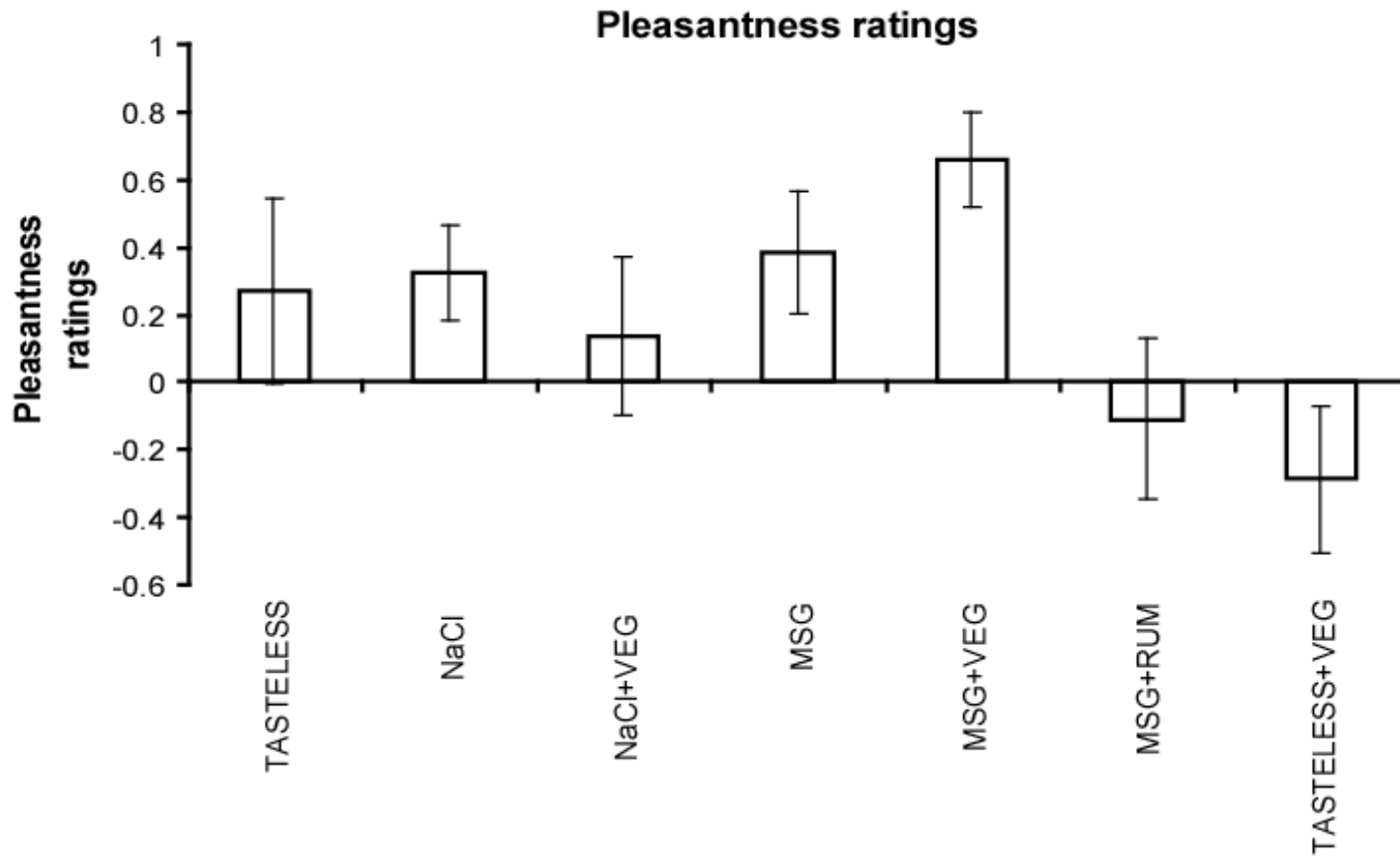
olfactory-taste nonlinear cross-modal effects.

How does MSG work to make food pleasant?

- **1) Tasteless control**
- **2) MSG (0.1M with 0.005 M IMP)**
- **3) MSG (0.1M with 0.005 M IMP) + Vegetable odour (a consonant combination)**
- **4) NaCl (0.1M)**
- **5) NaCl (0.1M) + Vegetable odour**
- **6) Tasteless + Vegetable odour**
- **7) MSG (0.1M with 0.005 M IMP) + rum odour (a non-consonant combination)**

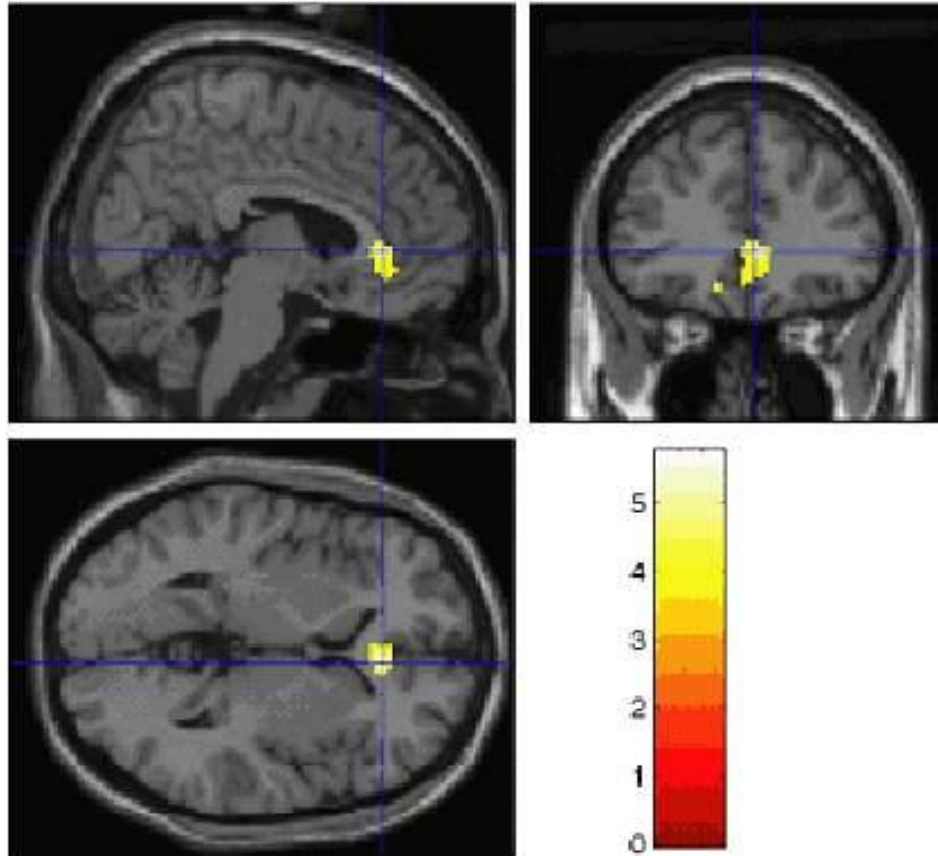
McCabe and Rolls (2007) European Journal of Neuroscience 25: 1855-1864.

Umami taste - savory odor interactions
0.1M MSG + 0.005M IMP + Vegetable odour



MSG taste and Vegetable odor produce supralinear responses

Supralinearity: $\text{MSGV} > (\text{MSG} + \text{V})$ $p=0.001$



Pregenual cingulate and medial orbitofrontal cortex

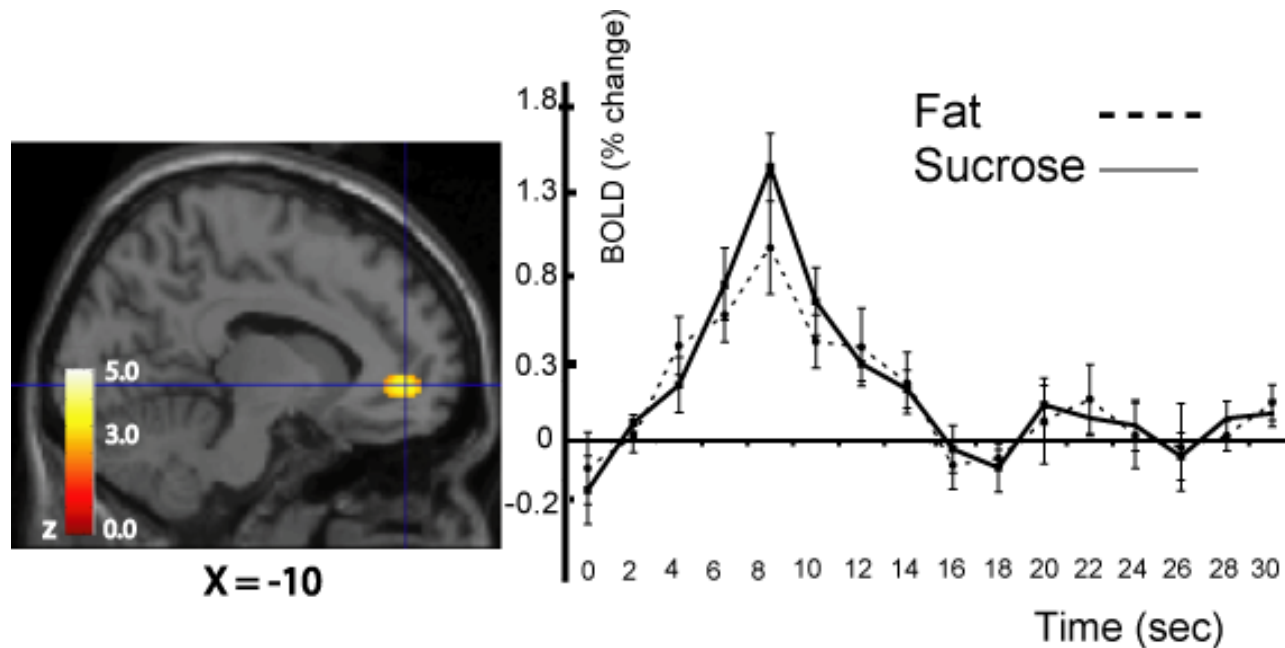
This was found for MSGV and NOT for NaClV

Umami as a flavour: conclusions

1. **MSG taste alone is not very pleasant – approximately neutral.**
2. **MSG taste and a consonant odour can be pleasant.**
3. **The psychophysical effect of combining MSG with a consonant odour is much greater on pleasantness, consonance, and fullness of flavour than when the combination is with NaCl taste.**
4. **MSG taste and vegetable odour produce supralinear activations in only a few brain regions: the pregenual cingulate cortex (which receives from the orbitofrontal cortex and is implicated in affect); the orbitofrontal cortex; and the ventral striatum: (not in the primary taste cortex, or pyriform cortex).**
5. **The supralinear additivity of MSG and vegetable in these regions is much greater than of NaCl and vegetable (which shows almost no supralinearity).**
6. **The activations in the pregenual cingulate cortex and the medial orbitofrontal cortex are correlated with the consonance, pleasantness, and fullness of the flavour.**
7. **We suggest that MSG taste works as a flavour enhancer not by interacting with other tastes (sweet, salt, bitter, sour), but instead by interacting with savoury odours, which can only be performed after the (unimodal) primary taste and primary olfactory areas, in olfactory-taste convergence areas such as the orbitofrontal cortex and the pregenual cingulate cortex.**
8. **The crossmodal combination can not be performed before the taste and olfactory pathways are brought together in the orbitofrontal cortex.**
9. **We propose the concept of umami as a flavour: a combination of MSG taste and a consonant odour, formed in the cortex far beyond the receptors.**

McCabe and Rolls (2007) European Journal of Neuroscience 25: 1855-1864

Representation of fat texture and sweet taste overlap in the pregenual cingulate cortex

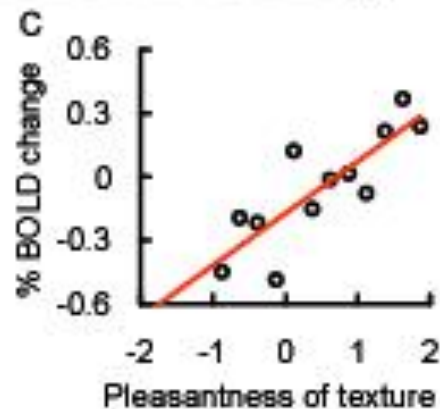
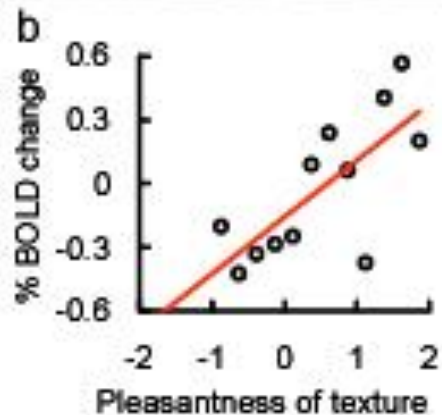
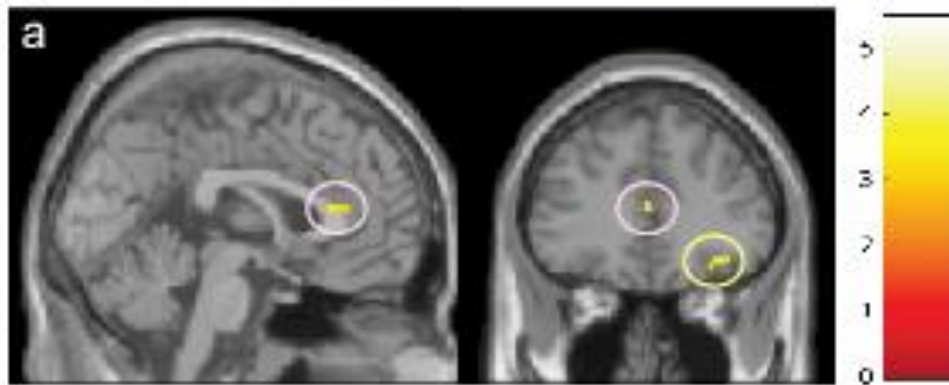


Responses to oral fat and sucrose converge in the most anterior part of the cingulate cortex

De Araujo and Rolls (2004)
Representation in the human brain of
food texture and oral fat.
J Neuroscience 24: 3086-3093.

Pleasantness of fat texture

- High fat vs low fat dairy drink
- Vanilla vs strawberry flavor
- 2x2 factorial design
- Activations in the pregenual cingulate cortex and orbitofrontal cortex were correlated with the pleasantness of fat texture

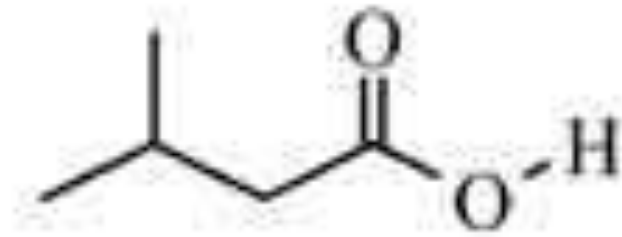


Grabenhorst, Rolls et al 2010 Cerebral Cortex

Conclusions: A visually presented word label modulates representations of odors in olfactory areas in the orbitofrontal cortex, amygdala, and olfactory tubercle. Cognition can influence subjective, conscious, affective representations in the orbitofrontal and pregenual cingulate cortices.

Isovaleric Acid

Cheddar Cheese

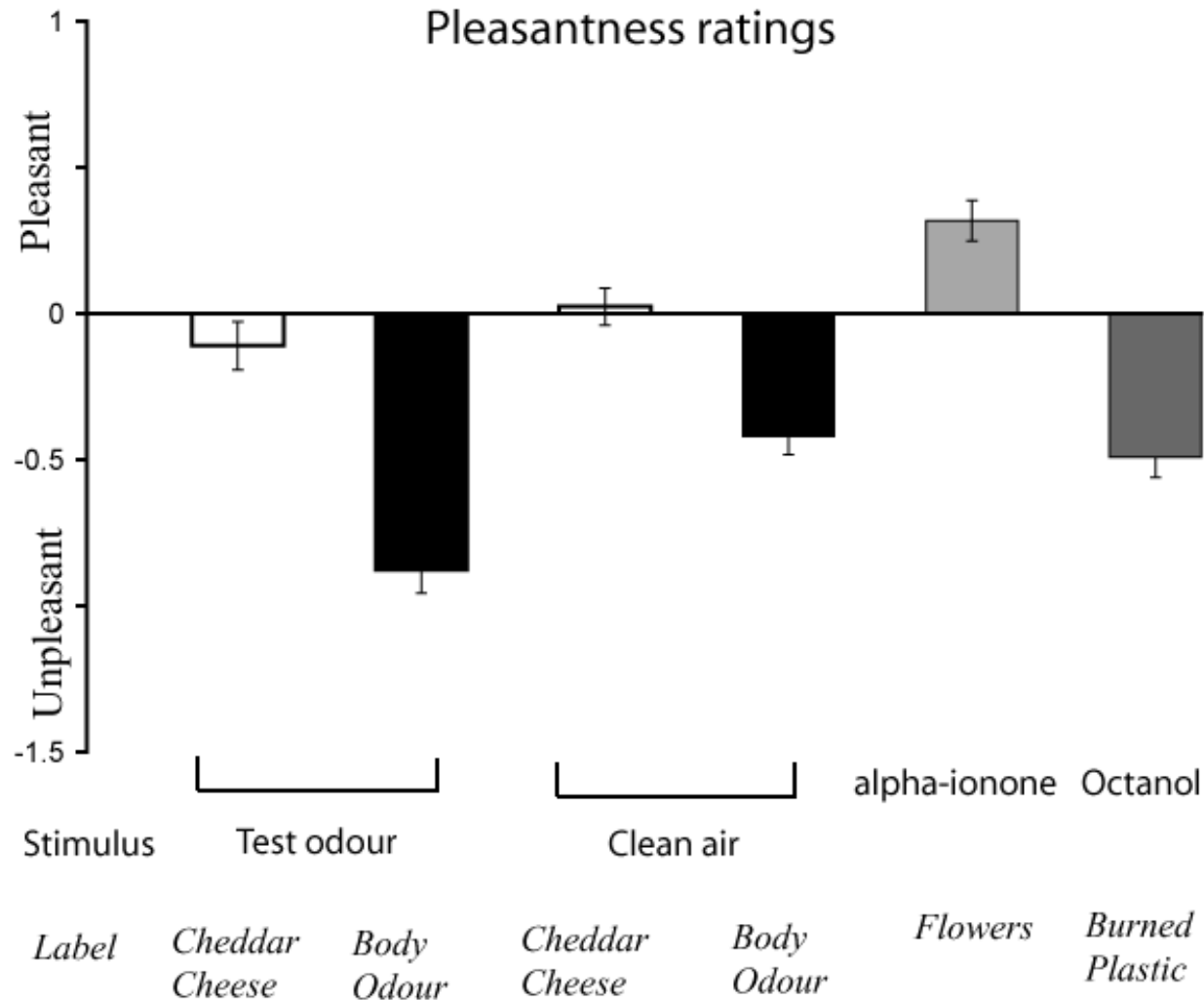


Body odour



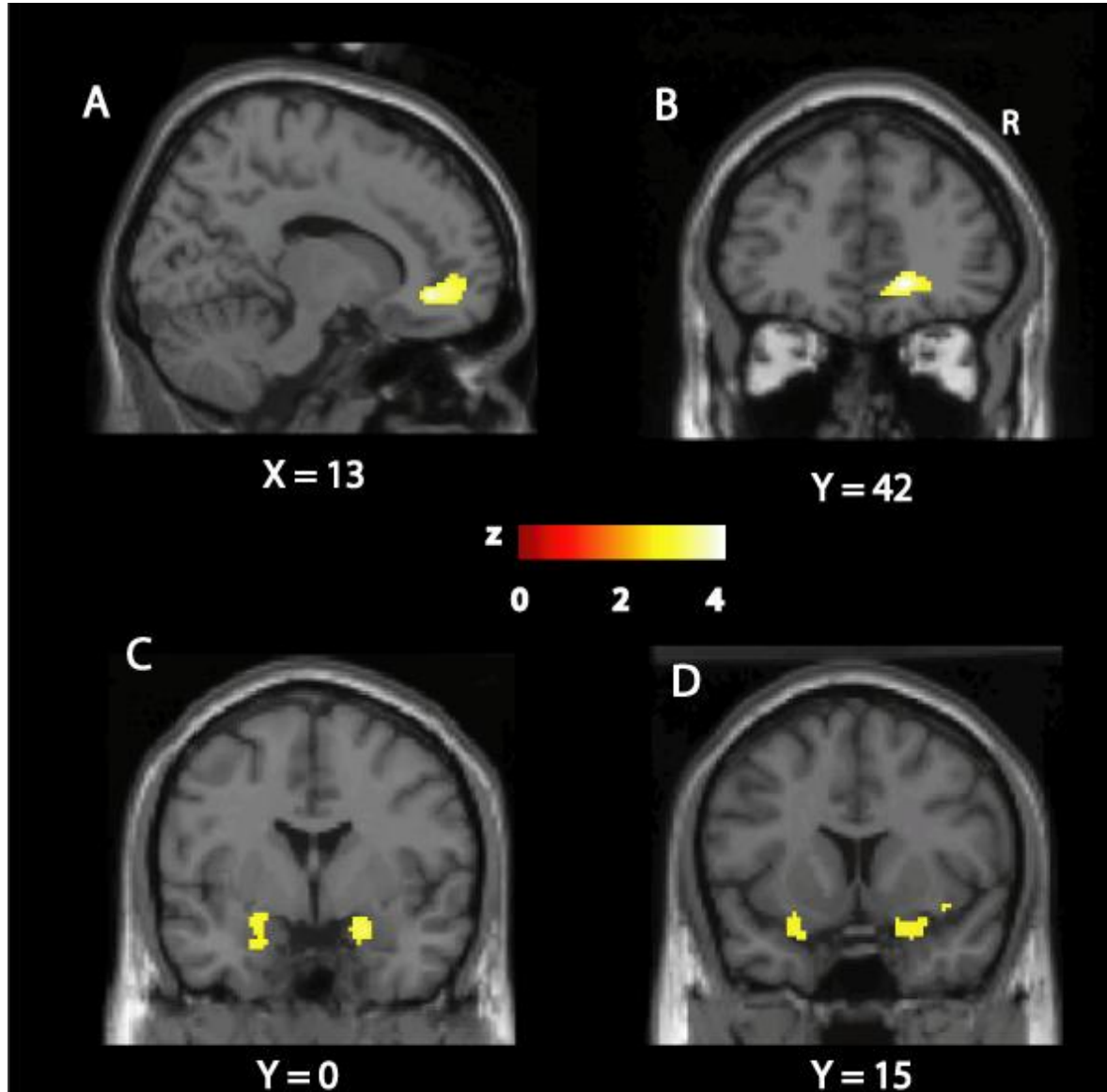
De Araujo, I.E.T., Rolls, E.T., Velazco, M.I., Margot, C. and Cayeux, I. (2005)
Cognitive modulation of olfactory processing. *Neuron* 46: 671-679.

Effect of visually presented words ('cheddar cheese' vs 'body odor') on responses to a single Test odor, isovaleric acid



Cognitive modulation revealed by a correlation between the BOLD signal and the pleasantness ratings given to the Test odour.

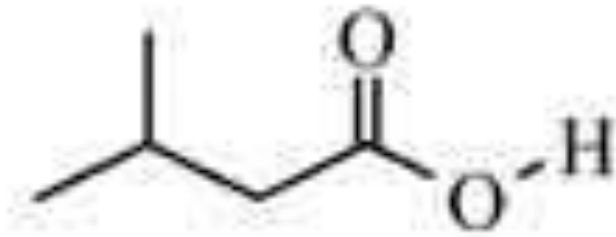
A, B: anterior cingulate; C: amygdala; D: olfactory tubercle



Conclusions: A visually presented word label modulates representations of odors in olfactory areas in the orbitofrontal cortex, amygdala, and olfactory tubercle. Cognition can influence subjective, conscious, affective representations in the orbitofrontal and pregenual cingulate cortices.

Isovaleric Acid

Cheddar Cheese



Body odour



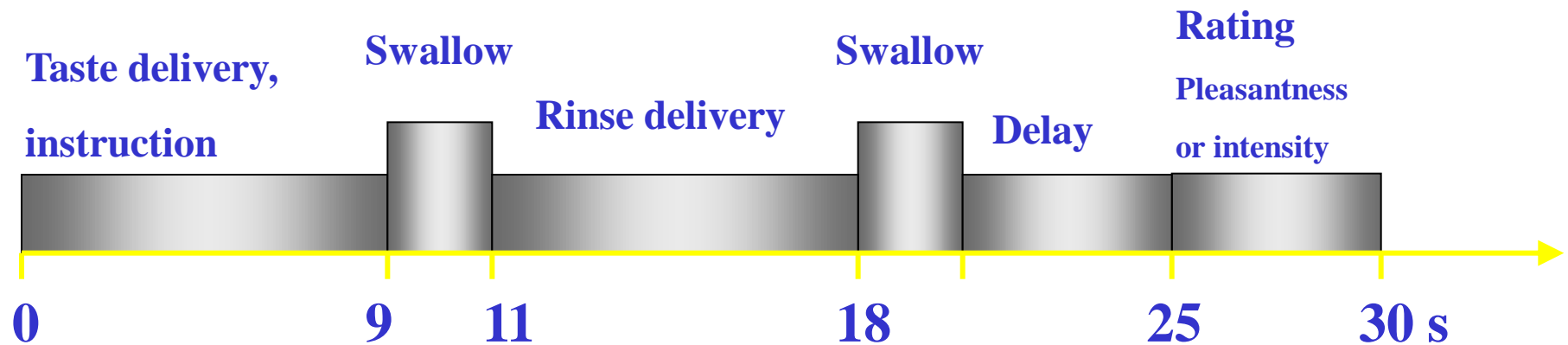
De Araujo, I.E.T., Rolls, E.T., Velazco, M.I., Margot, C. and Cayeux, I. (2005)
Cognitive modulation of olfactory processing. *Neuron* 46: 671-679.

How cognition modulates affective responses to taste and flavor: Cognition helps to make umami pleasant

- **Top-down language-level cognitive effects reach far down into the earliest cortical areas that represent the appetitive value of taste and flavor.**
- **The labels that modulate pleasantness influence activations in the orbitofrontal cortex, pregenual cingulate cortex, and ventral striatum where the pleasantness of taste and flavor are represented.**
- **The labels that modulate pleasantness do not influence activations in the insular (primary) taste cortex.**
- **Cognition has a strong influence on the representations of taste and flavor in the brain.**
- **Cognitive influences on the appetite for particular foods, and appetite control.**

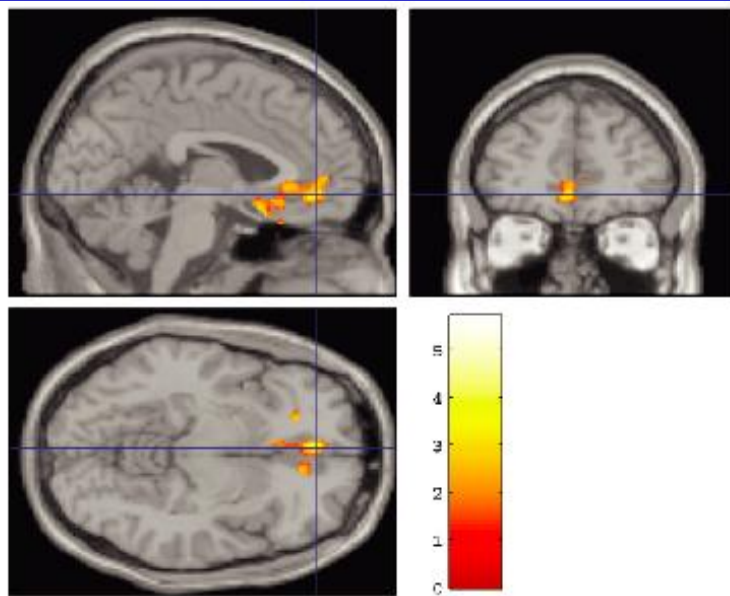
Selective attention to affective value alters how the brain processes taste stimuli

- We delivered the identical taste (MSG) on every trial.
- Instructions were on different trials to ‘remember and rate pleasantness’ or to ‘remember and rate intensity’

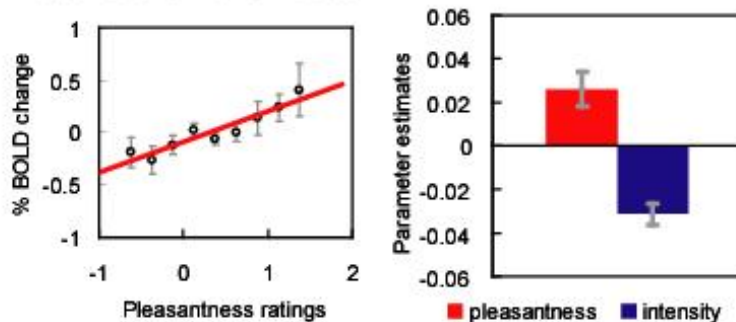


Orbitofrontal and pregenual cingulate cortex

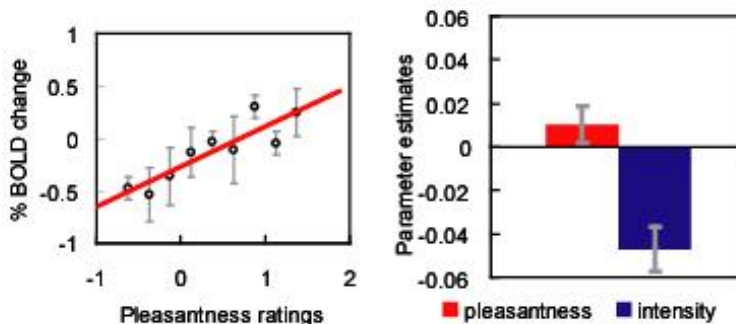
Paying attention to pleasantness vs intensity produces greater activation to taste in the orbitofrontal and pregenual cingulate cortices.



Medial orbitofrontal cortex



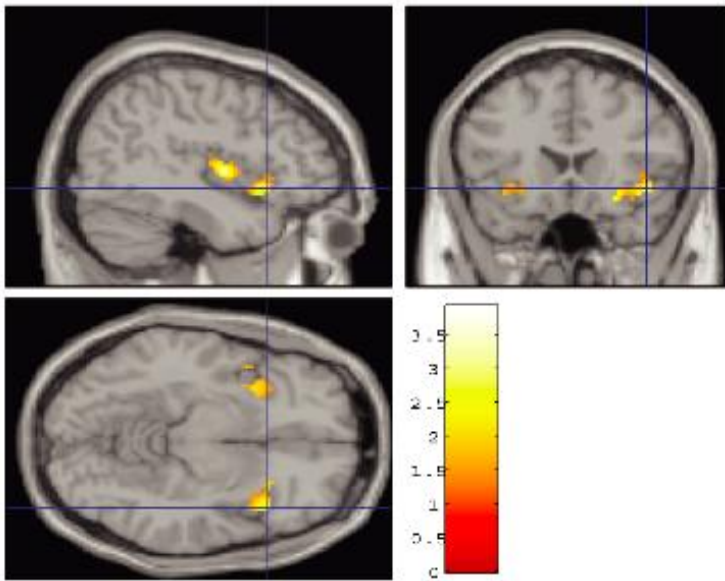
Pregenual cingulate cortex



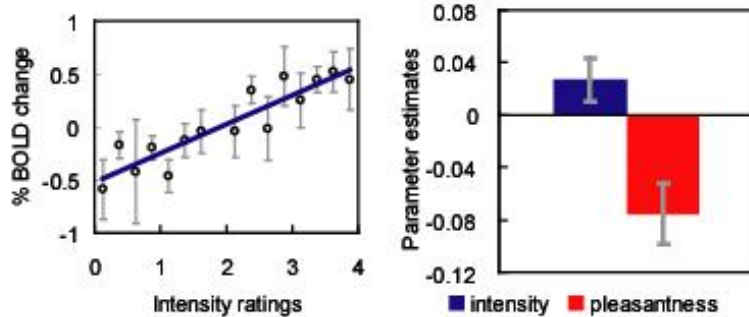
Activations were correlated with subjective pleasantness ratings.

Anterior and mid insular cortex

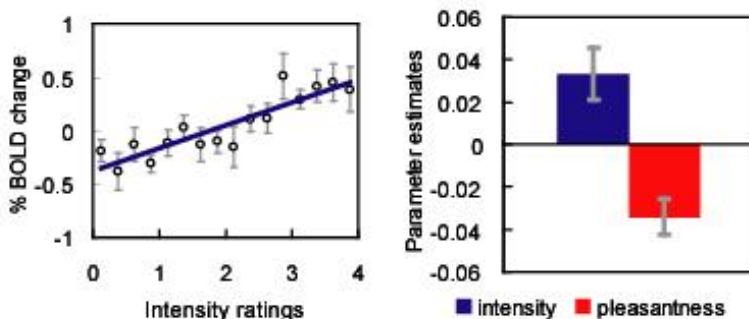
Paying attention to intensity vs pleasantness produced larger activations in the anterior and mid insula.



Taste insula



Mid-insula



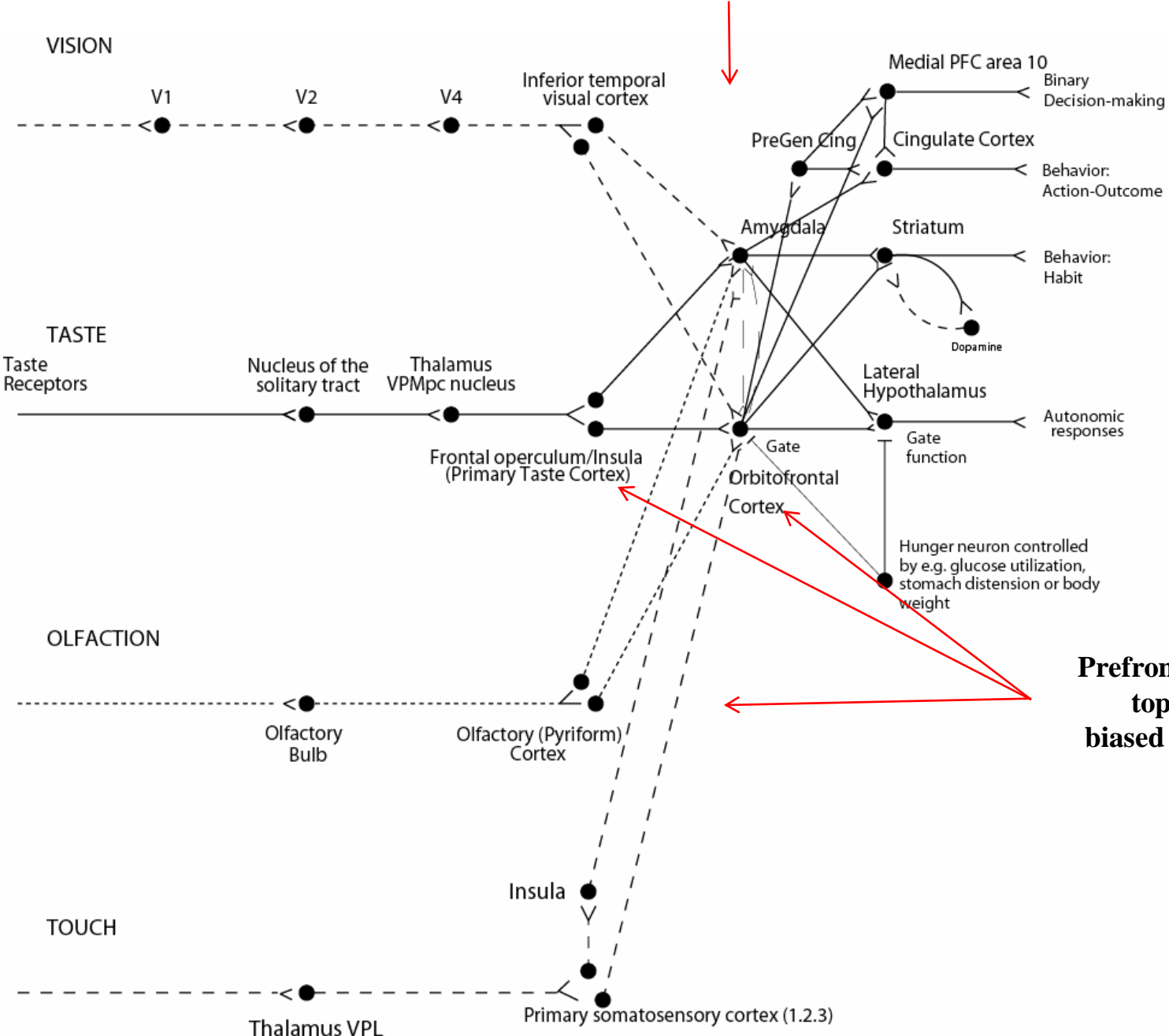
Activations were correlated with subjective intensity ratings.

Selective attention to affective value alters how the brain processes taste stimuli

- **Top-down selective attention allows processing in different brain areas to be emphasized for different types of decision-making**
- **Decisions about affective value recruit the orbitofrontal cortex and pregenual cingulate cortex.**
- **Decisions about the intensity of a stimulus recruit the primary sensory (insular taste) cortical area.**
- **In sensory testing, psychophysics and marketing, it is important to ensure that attention is being paid to pleasantness or to the physical properties: different brain systems are engaged by these two types of attention**

Grabenhorst and Rolls (2008) European Journal of Neuroscience

What **Reward** Decision/Action



**Prefrontal cortex:
top-down
biased activation**

Taste and nutrition: Professor E T Rolls

- **Flavour e.g. umami pleasantness is produced by a combination of a taste and a complementary odour**
- **Fat is sensed by oral texture, and is separate from viscosity**
- **Cognition reaches down into the flavour system to modulate pleasantness**
- **Pleasantness (hedonics) is separate from what the taste is and its intensity (perception)**
- **Selective attention to pleasantness vs intensity engages different brain systems. This may be very important for product development, and for marketing.**
- **Discoveries in neuroscience about taste and flavour processing in the brain have many implications for and applications to product development.**
- **Rolls ET 2014 Emotion and Decision-Making Explained. Oxford University Press**
- **Rolls ET 2016 Annual Reviews of Nutrition 36:**