MVST & NST IB

Easter term

Olfaction and taste

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One lecture

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Objectives

This lecture is intended to introduce you to the chemical senses of smell and taste. After this lecture you should understand:

- The transduction processes in the primary chemoreceptive cells.
- The pathways by which this information is conveyed to the CNS.
- The way in which the sensory signal is encoded in these afferent pathways.

Many students find it helpful to contrast these processes in olfaction and taste with the other sensory systems which they have already studied. The textbooks listed below give clear accounts of the chemical senses, and can be used to augment and clarify the material in the lecture. For the especially curious, I have also provided "optional" references to a few more specialist accounts, which provide more depth on specific topics.

Textbooks

Barlow, H.B. & Mollon, J.D. (eds). (1982, revised 1989). *The Senses.* CUP. Sound coverage of taste and smell, especially perception and behaviour.

Carpenter, R.H.S. (1995). *Neurophysiology.* (3rd edition). Edward Arnold. Good for concepts, but a little slim on transduction.

Kandel, E.R., Schwartz, J.H. & Jessell, T.M. (eds). (1991). *Principles of Neural Science.* (3rd edition). Elsevier. Large expensive multi-author text. A clear and sound account of smell and taste. *Essentials of Neural Science* is a shorter version.

Nicolls, J.G., Martin, A.R. & Wallace, B.G. (1992). *From Neuron to Brain: A Cellular approach to the Function of the Nervous System.* (3rd edition). Sinauer. Brief, but clear coverage of olfactory transduction.

Shepherd, G.M. (1994). *Neurobiology.* (3rd edition). OUP. Brief but clear account of principles.

Zigmond, M.J., Bloom, F.E., Landis, S.C., Roberts, J.L. & Squire (1999) ***Fundamental Neuroscience.*** Academic Press. New, large, colourful; provides the most up-to-date coverage of any textbook on olfaction and taste.

For more depth on specific topics

Axel, R. (1995). *The molecular logic of smell.* *Scientific American* **273**, 154-159.

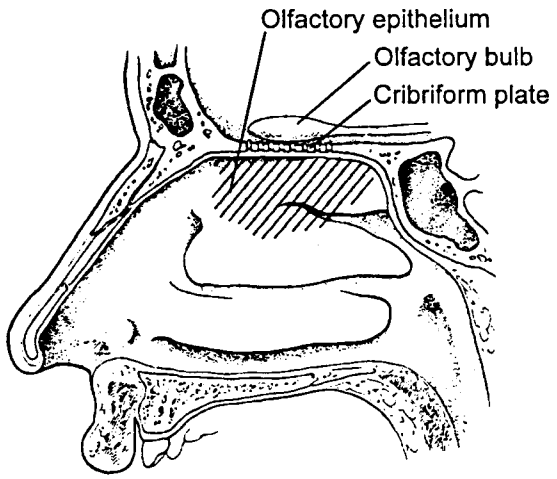
Firestein, S. (1991). *A nosefull of odor receptors.* *Trends in Neurosciences* **14**, 270-272.

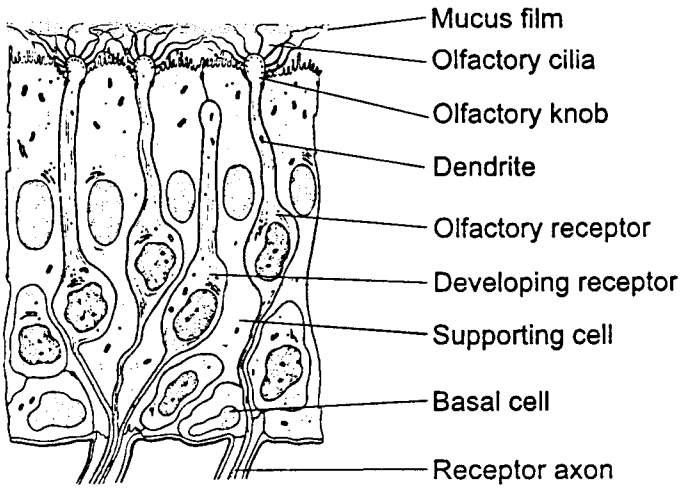
Kinnamon, S.C. (1988). *Taste transduction: a diversity of mechanisms.* *Trends in Neurosciences* **11**, 491-496.

Ronnett, G.V. & Snyder, S.H. (1992). *Molecular messengers of olfaction.* *Trends in Neurosciences* **15**, 508-512.

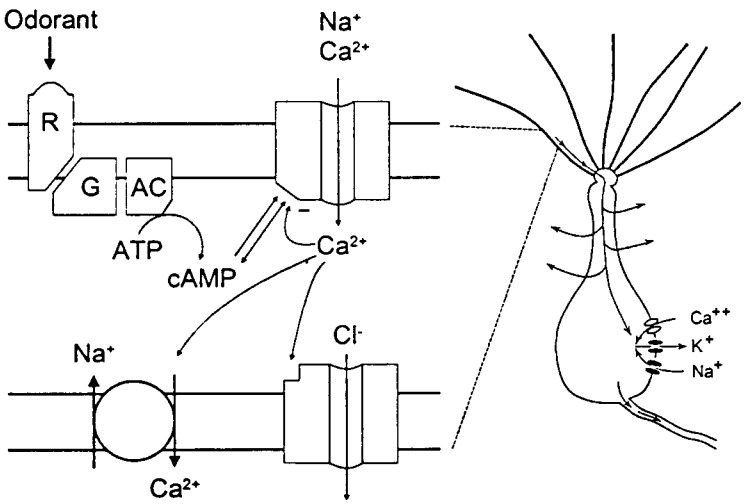
1: OLFACTION

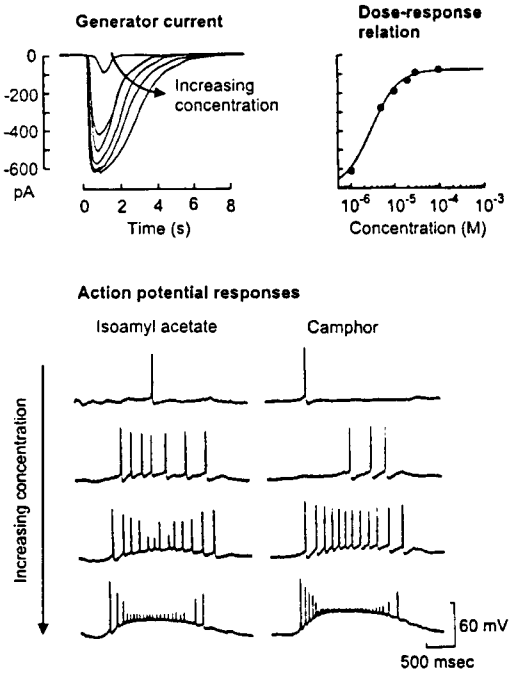
1.1: Olfactory transduction





Odorants dissolve in the **mucus film**, possibly in association with an **odorant binding protein**, and interact with specific receptors on the **olfactory cilia**. Olfactory receptors are renewed approximately every 60 days by division of **basal cells**.

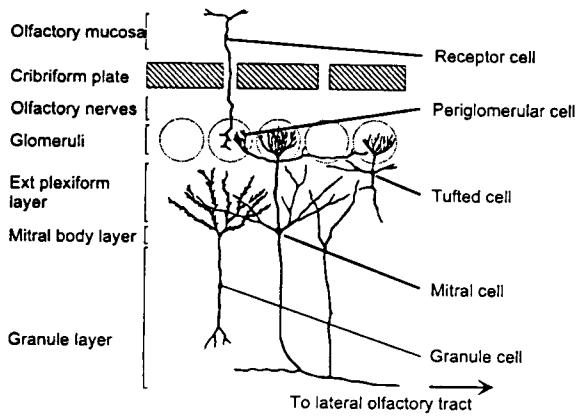


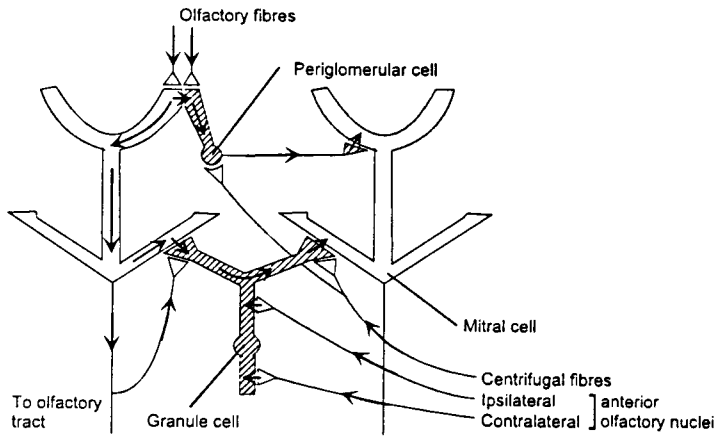


Transduction takes place in the **olfactory cilia**. The odorant interacts with a **receptor molecule**, one of a family of perhaps a thousand. The receptor activates a **G-protein** (G_{olf}), which stimulates **adenylyl cyclase** to produce **cAMP**. Cyclic AMP opens cyclic nucleotide-gated **cation channels** in the ciliary membrane, leading to an inward-flowing **receptor current** carried by Na^+ and Ca^{2+} which depolarizes the cell body, causing it to fire action potentials. Cl^- ions flow outward through a Ca^{2+} gated channel, augmenting this depolarization. The receptor current increases with increasing odorant concentration, leading to a graded increase in firing rate. Ca^{2+} also acts via **calmodulin** to reduce the sensitivity of the cation channels to cAMP, thus contributing to **olfactory adaptation**. Ca^{2+} is believed to be extruded by **sodium-calcium exchange**. Each individual olfactory

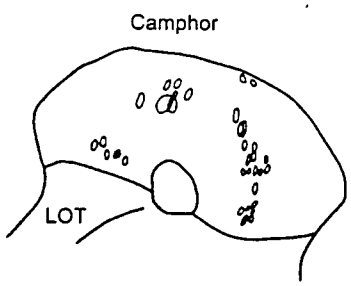
receptor expresses only a single type of receptor molecule, but can respond to a range of different odorants.

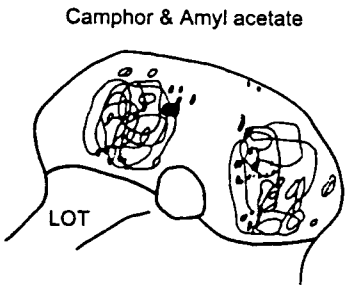
1.2: Processing in the olfactory bulb

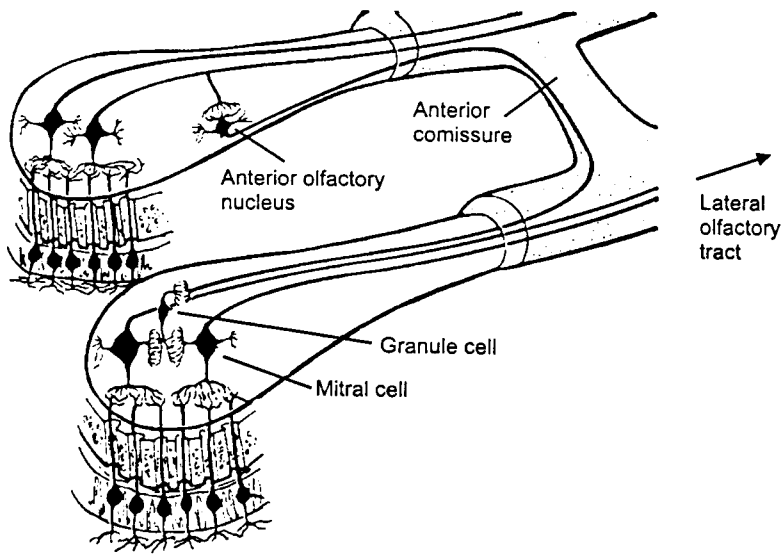




Olfactory receptor axons pass through the **cribriform plate** to the **olfactory bulb**. There they excite **mitral cells** and smaller **tufted cells** in the **olfactory glomeruli**. The afferent fibres from olfactory receptor cells expressing a particular receptor molecule selectively converge on just one or two glomeruli. **Periglomerular cells** and **granule cells** make reciprocal dendro-dendritic synapses with mitral cells, mediating "**lateral inhibition**" within the olfactory bulb.

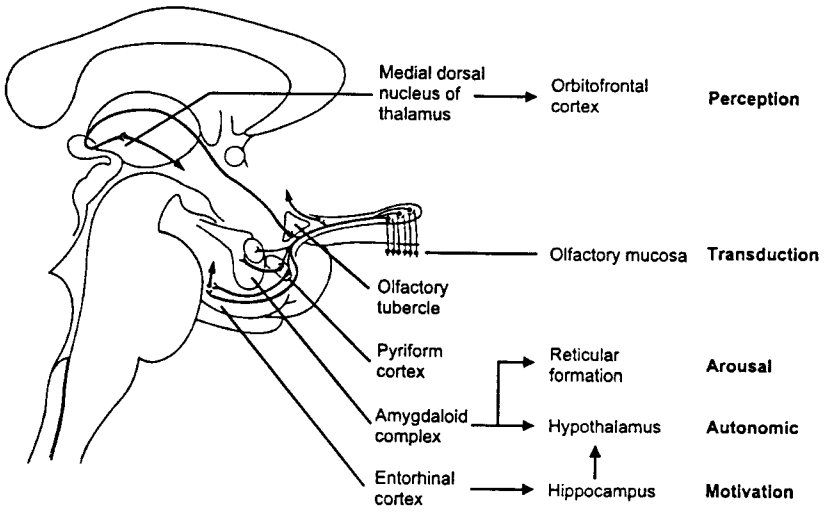


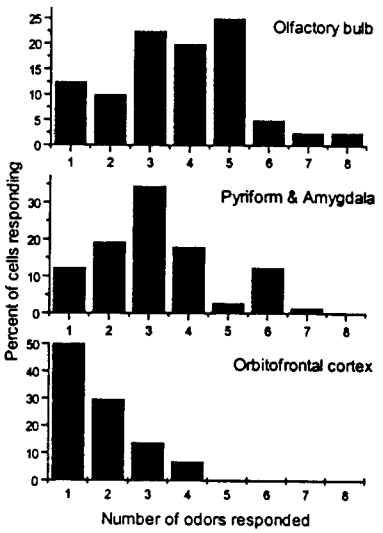




Different odorants evoke distinct, but overlapping patterns of activity within the olfactory bulb. The mitral cell axons leave the olfactory bulb in the **lateral olfactory tract**. The **anterior olfactory nucleus** mediates inhibitory interactions between the two olfactory bulbs via the **anterior commissure**.

1.3: Higher olfactory pathways

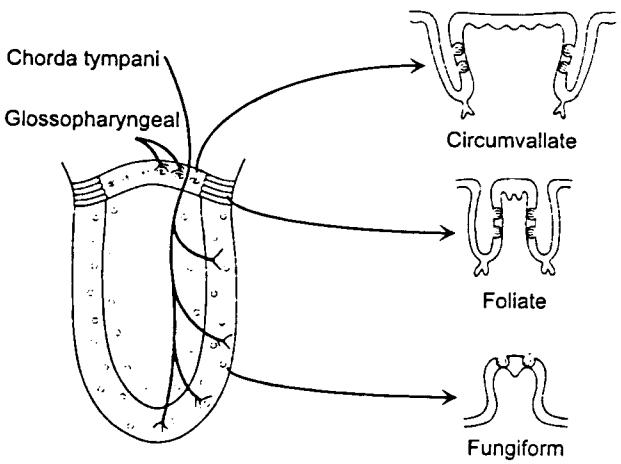


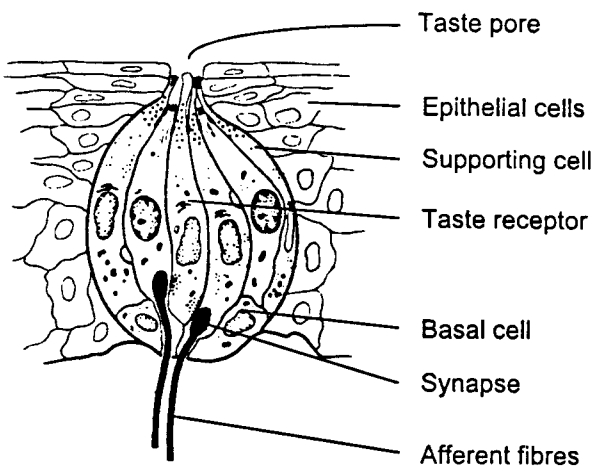


The **lateral olfactory tract** synapses on neurons in five regions of the olfactory cortex. The **anterior olfactory nucleus** has been described above. The **olfactory tubercle** projects to the **medial dorsal nucleus of the thalamus**, which in turn projects to **orbitofrontal cortex**, mediating conscious perception of odour. The **pyriform cortex** projects to other olfactory cortical regions. The **amygdala** and the **entorhinal cortex** form part of the **limbic system**, which is involved in the **affective component** of odour perception, mediating emotional and autonomic responses. At higher levels in the pathway cells become progressively more **odour-specific**: the majority of cells in the olfactory bulb respond to a wide range of odorants, while those in orbitofrontal cortex mostly respond to just one or two.

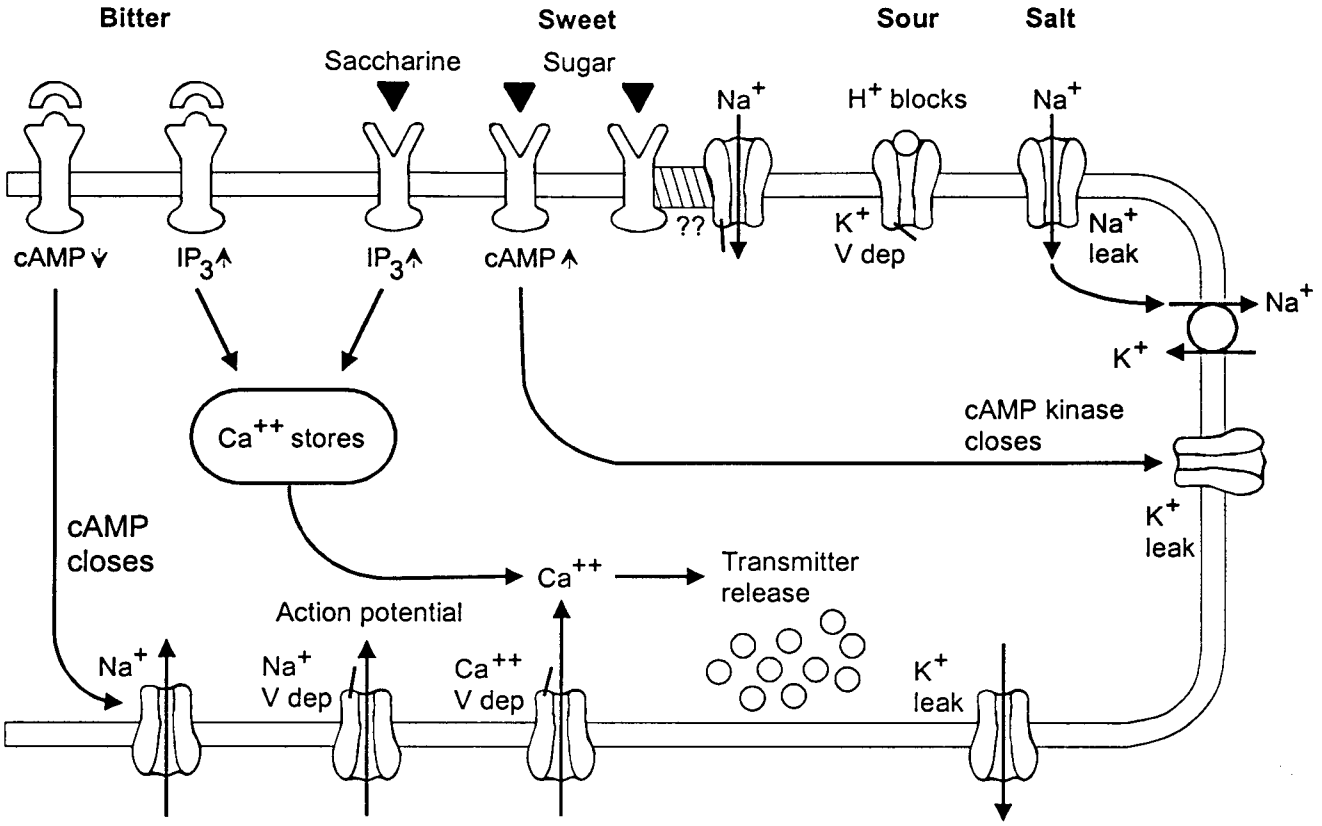
2: TASTE

2.1: Taste transduction





Taste receptor cells are clustered together in **taste buds**, which are located in **papillae** embedded in the epithelia of the tongue. These can be classified into **circumvallate, foliate** and **fungiform**, as shown above. Taste receptors within the taste buds synapse with afferent fibres projecting in the **chorda tympani** and **glossopharyngeal** nerves.



Human taste transduction involves four basic taste qualities. **Bitter** and **sweet** responses involve specific receptor proteins, acting via second messenger mechanisms. **Sour** and **salt** responses are mediated directly by modulation of ion channels in the apical membrane.

Bitter receptors operate via one of two mechanisms. First, they activate **phosphodiesterase** via a G-protein to destroy **cAMP**, which normally **closes** cation channels, thus allowing these channels to open. Second, they activate **phospholipase C** via a G-protein to produce **IP_3**, which releases calcium ions from intracellular stores.

Sweet receptors stimulate **adenylyl cyclase** via a G-protein to produce **cAMP**, which reduces the potassium leak conductance. There is also evidence for a second mechanism which opens an apical sodium channel, but the mechanism is not yet understood. It has recently been suggested that **artificial sweeteners** may operate via **IP_3**.

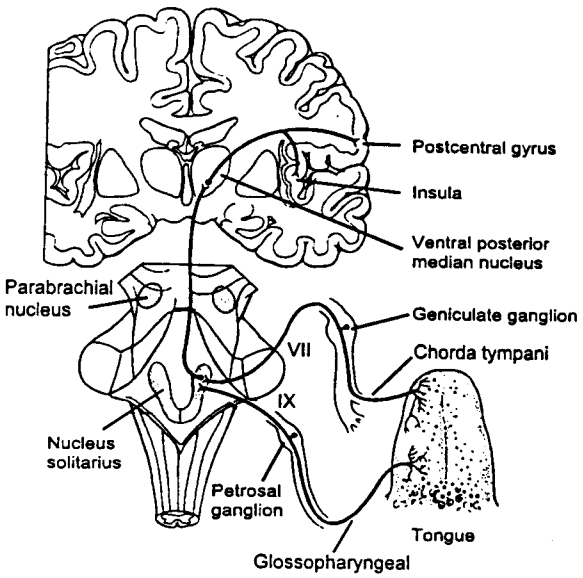
Sour transduction involves block by protons of a voltage gated potassium channel in the apical membrane, leading to depolarization.

Salt transduction involves the entry of sodium ions through a sodium leak conductance, thereby depolarizing the cell.

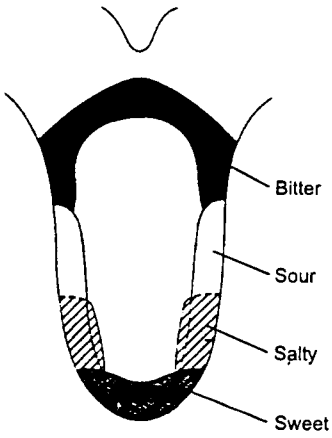
Each taste receptor probably possesses several of these transduction mechanisms. Either by reaching threshold and evoking an **action potential** or through smaller **sub-threshold potential changes**, these mechanisms lead to an increase in synaptic transmitter release onto the afferent terminals. Each afferent fibre innervates many receptor cells.

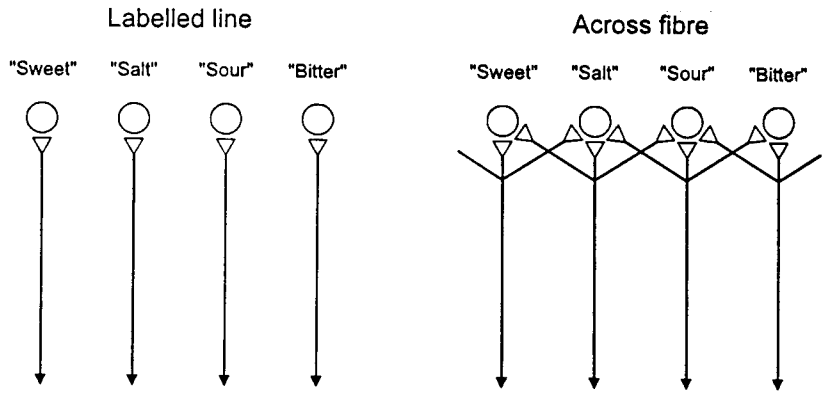
2.2: Higher taste pathways

Taste afferents in the **chorda tympani** and **glossopharyngeal** nerves proceed via cranial nerves **VII** and **IX** to synapse in the solitary nuclear complex of the medulla within the **gustatory nucleus**. An uncrossed pathway projects to the **ventral posterior medial nucleus** of the thalamus, and thence to **taste area I** in the **postcentral gyrus**, and **taste area II** in the **insula**. A projection from the gustatory nucleus to the **parabrachial nucleus** is believed to mediate autonomic reflexes and the affective responses to taste stimuli.



2.3: Sensory coding of taste signals





Different regions of the tongue respond preferentially to different taste stimuli. This suggests that afferent information might be carried by taste-specific **labelled lines**. However, recordings from afferents in the chorda typani show that individual fibres respond to a range of stimuli, but tend to prefer just one of these. This indicates instead an **across-fibre** code, in which taste is identified by the pattern of afferent activity evoked in different fibres.