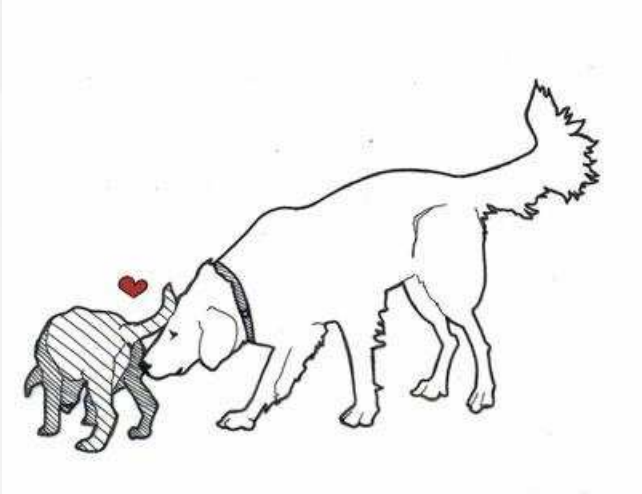
Chapter 15: The Chemical Senses

Detecting Odors

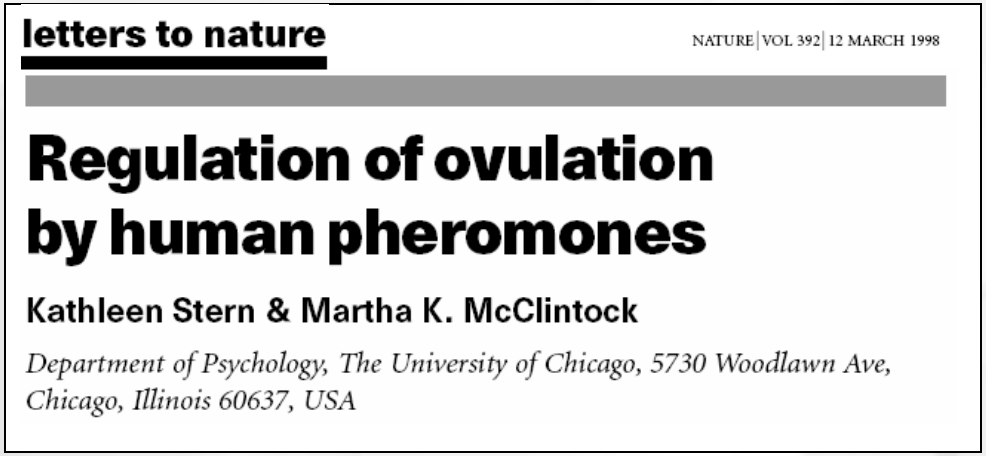
- Rats are 8 to 50 times more sensitive to odors than humans
- Dogs are 300 to 10,000 times more sensitive
- However, individual receptors for all of these animals are equally sensitive
- The difference lies in the *number* of receptors they each have
  - Humans have 10 million and dogs have 1 billion olfactory receptors

Functions of Olfaction

- Many animals are *macrosmatic* - having a keen sense of smell that is necessary for survival
- Humans are *microsmatic* - a less keen sense of smell that is not crucial to survive



Humans are sensitive to pheromones



letters to nature

NATURE | VOL 392 | 12 MARCH 1998

Regulation of ovulation by human pheromones

Kathleen Stern & Martha K. McClintock

Department of Psychology, The University of Chicago, 5730 Woodlawn Ave, Chicago, Illinois 60637, USA

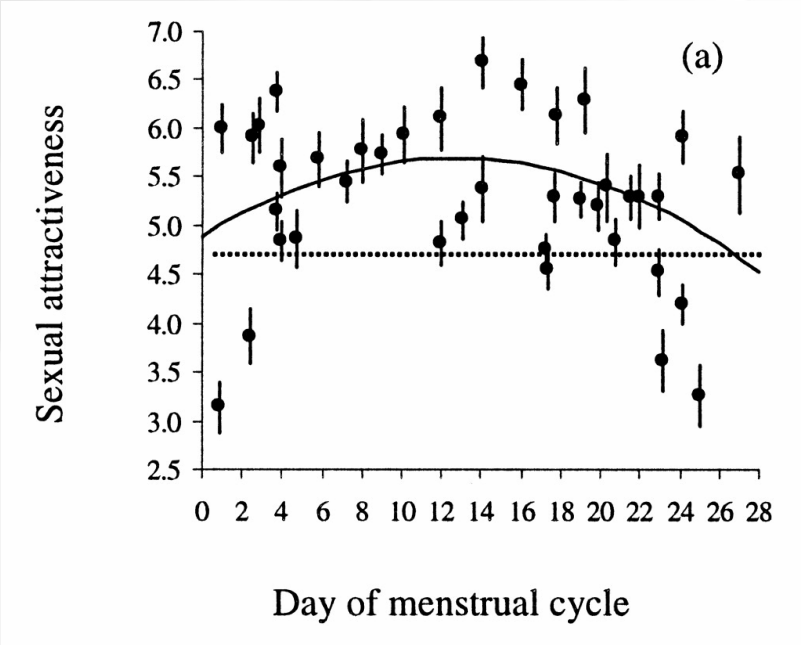
- Underarm secretions were collected from 9 donor women
- These were wiped on the upper lips of recipient women
- Results showed that menstrual synchrony occurred since:
  - Secretions from the donors taken at the beginning of their cycles led to a shortened length of the recipients' cycles
  - Secretions from the ovulatory phase lengthened recipients' cycles
- Pheromones in the secretions, even though the women did not report smelling them, led to the changes

Humans are sensitive to pheromones

Experiment by Kuukasjärvi et al.

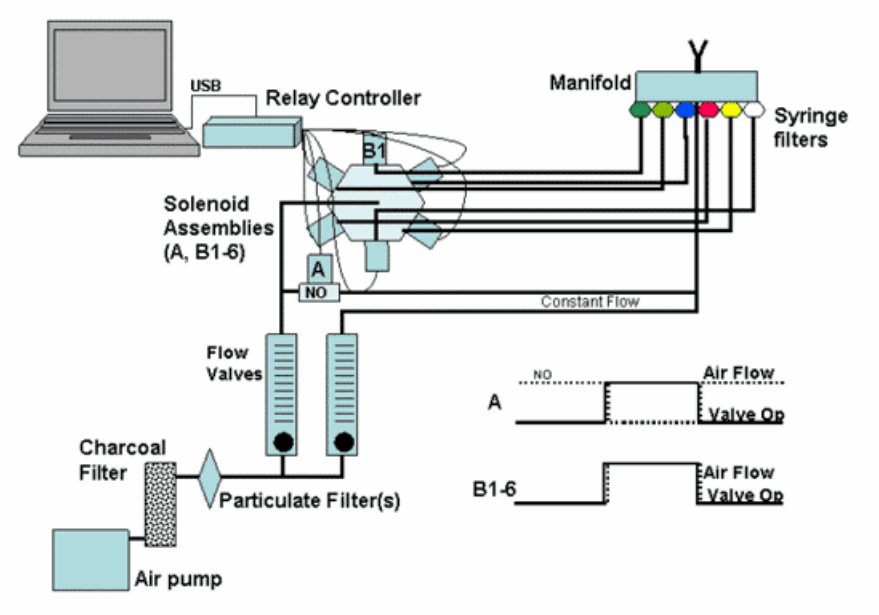
Males rated the sexual attractiveness and intensity of T-shirts' odors worn by 42 women.

Males rated the sexual attractiveness of nonusers highest at midcycle.

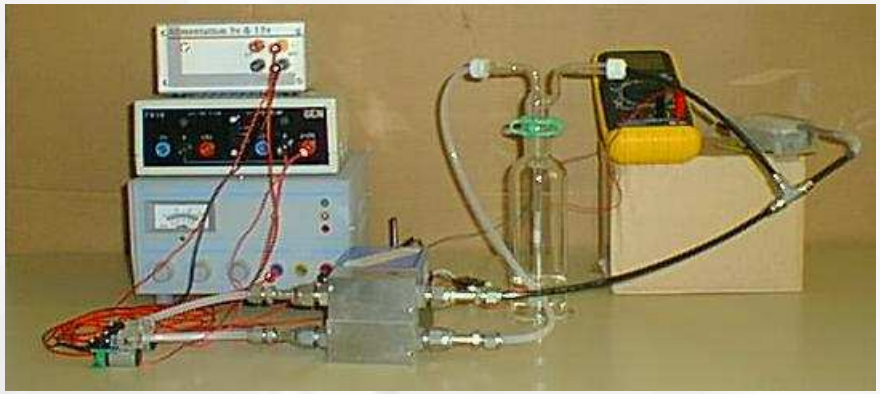


From Kuukasjärvi S, et al. (2004).. Behav Ecol 15:579–584:

Delivering Odors



An ‘olfactometer’



Psychophysics of smell

- Measuring the detection threshold
  - Yes/no procedure - participants are given trials with odors along with “blank” trials
    - They respond by saying yes or no
    - This can result in bias in terms of when the participant decides to respond
  - Forced-choice - two trials are given, one with odorant and one without
    - Participant indicates which smells strongest

Sensitivity to different odors

Table 15.1 *Human odor detection thresholds*

Compound	Odor Threshold in Air (parts per billion)
Methanol	141,000
Acetone	15,000
Formaldehyde	870
Menthol	40
T-butyl mercaptan	0.3

Source: From Devos et al. (1990).

Mercaptan is the harmless, non-toxic chemical that is added to natural gas to make it easier to detect in case of a leak. The most important thing to know about mercaptan is that it stinks. Some people compare it to the smell of rotten eggs.

Measuring the difference threshold (just noticeable difference)

- Smallest difference in concentration that can be detected between two samples
- This research must be done with carefully controlled concentrations using a device called a *olfactometer*
- Olfaction follows Weber's law with a Weber fraction of approximately 11%

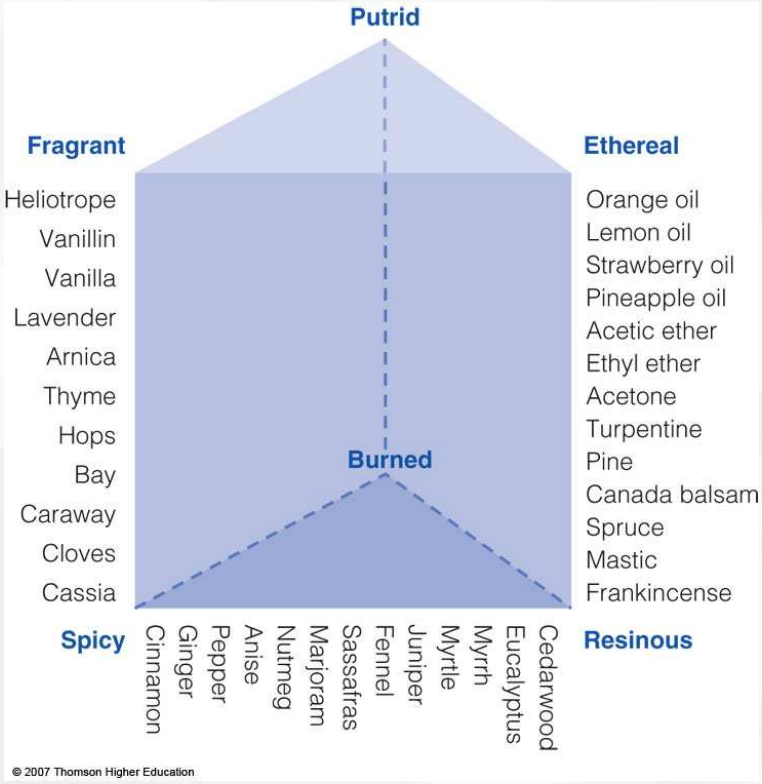
Identifying Odors

- Recognition threshold - concentration needed to determine quality of an odorant
- Humans can discriminate among 100,000 odors but they cannot label them accurately.
- This appears to be caused by an inability to retrieve the name from memory, from a lack of sensitivity.

Is there an equivalent of a color space for odors?

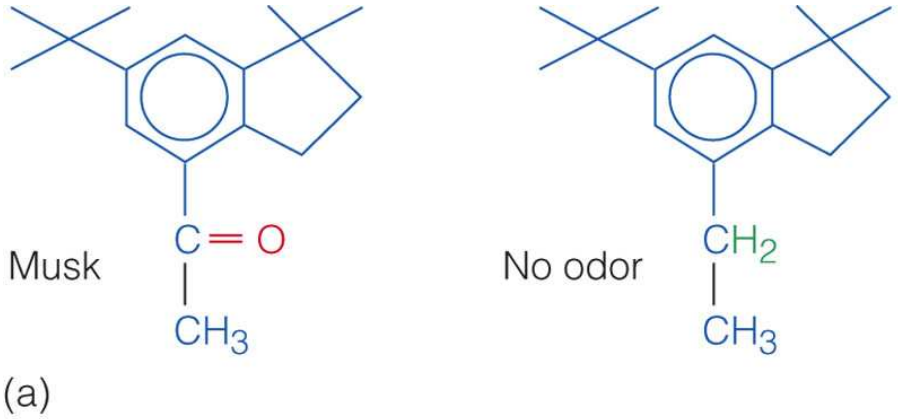
Researchers have found it difficult to map perceptual experience onto physical attributes of odorants.

- Henning's odor prism (1916)
  - 6 corners with the qualities putrid, ethereal, resinous, spicy, fragrant, and burned
  - Other odors located in reference to their perceptual relation to the corner qualities
  - Unfortunately, Henning's prism has proven of little use in olfactory research



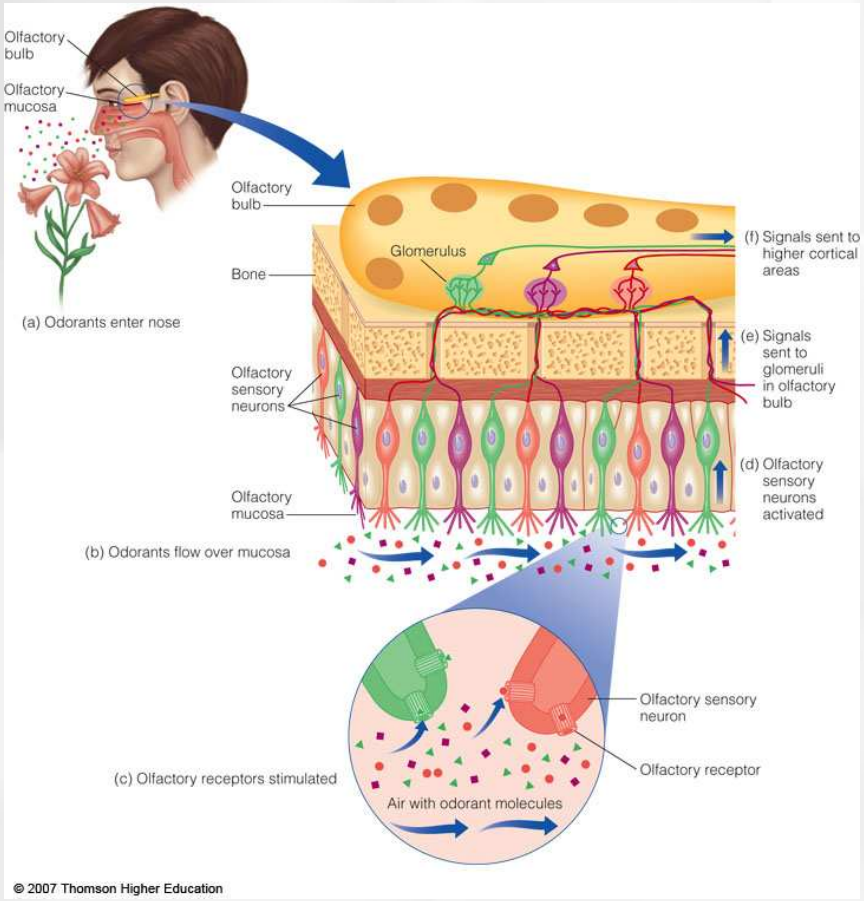
Linking chemical structure to types of smells

- Initial attempts showed difficulties since:
  - Some molecules with similar shapes have very different smells
  - Some similar smells come from molecules with different shapes

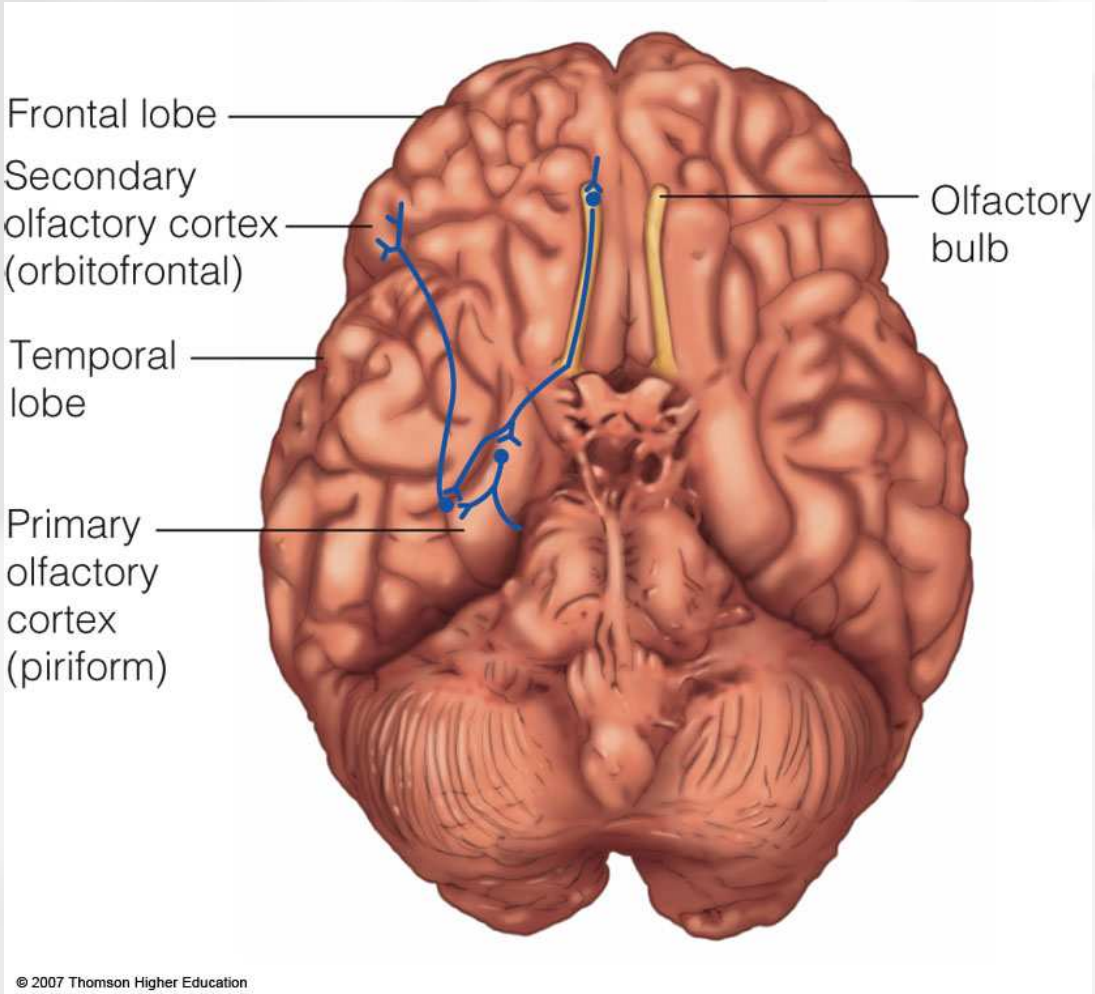


Structure of the Olfactory System

- Olfactory mucosa is located at the top of the nasal cavity
  - Odorants are carried along the mucosa coming in contact with the sensory neurons
  - Cilia of these neurons contain the receptors
  - Humans have about 350 types of receptors



- Signals are carried to the glomeruli in the olfactory bulb
- From there, they are sent to
  - Primary olfactory (piriform) cortex in the temporal lobe
  - Secondary olfactory (orbitofrontal) cortex in the frontal lobe
  - Amygdala deep in the cortex



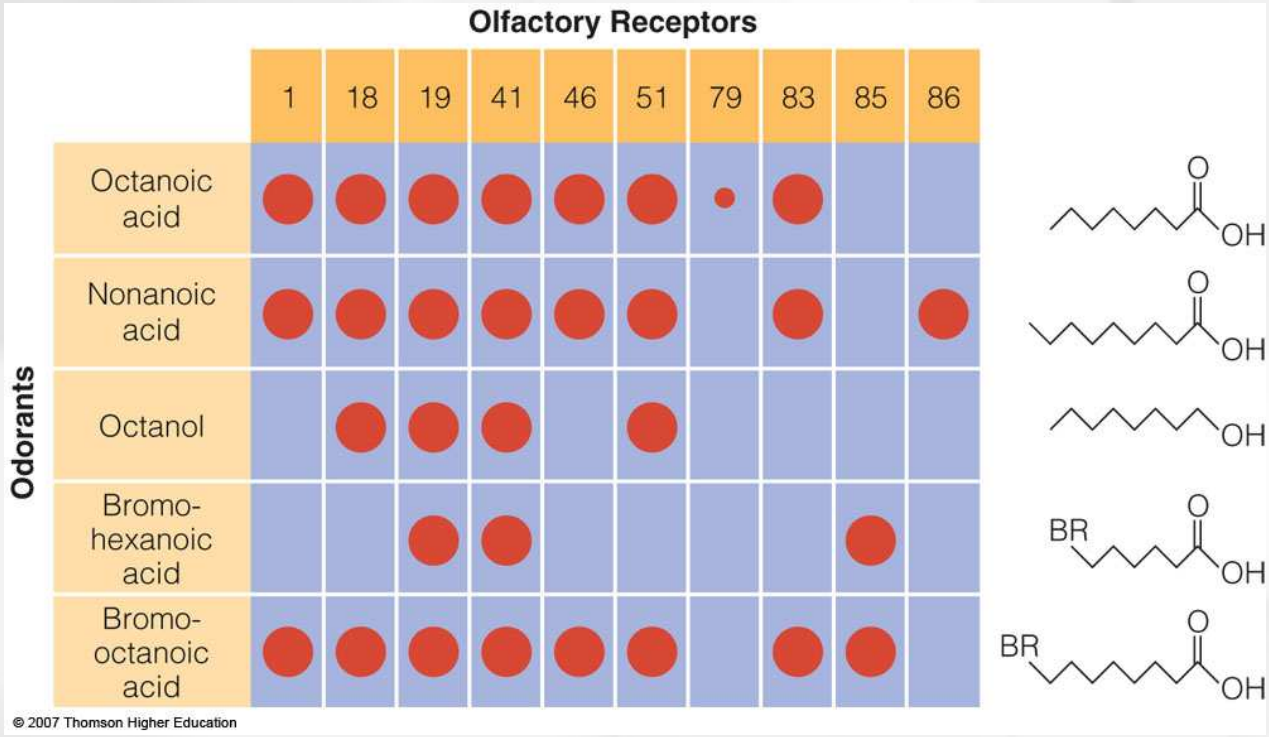
Specificity vs. Distributed coding

Specificity coding: Each receptor produces its own sensation.

Distributed coding: sensations are determined by *combinations* of receptor responses.

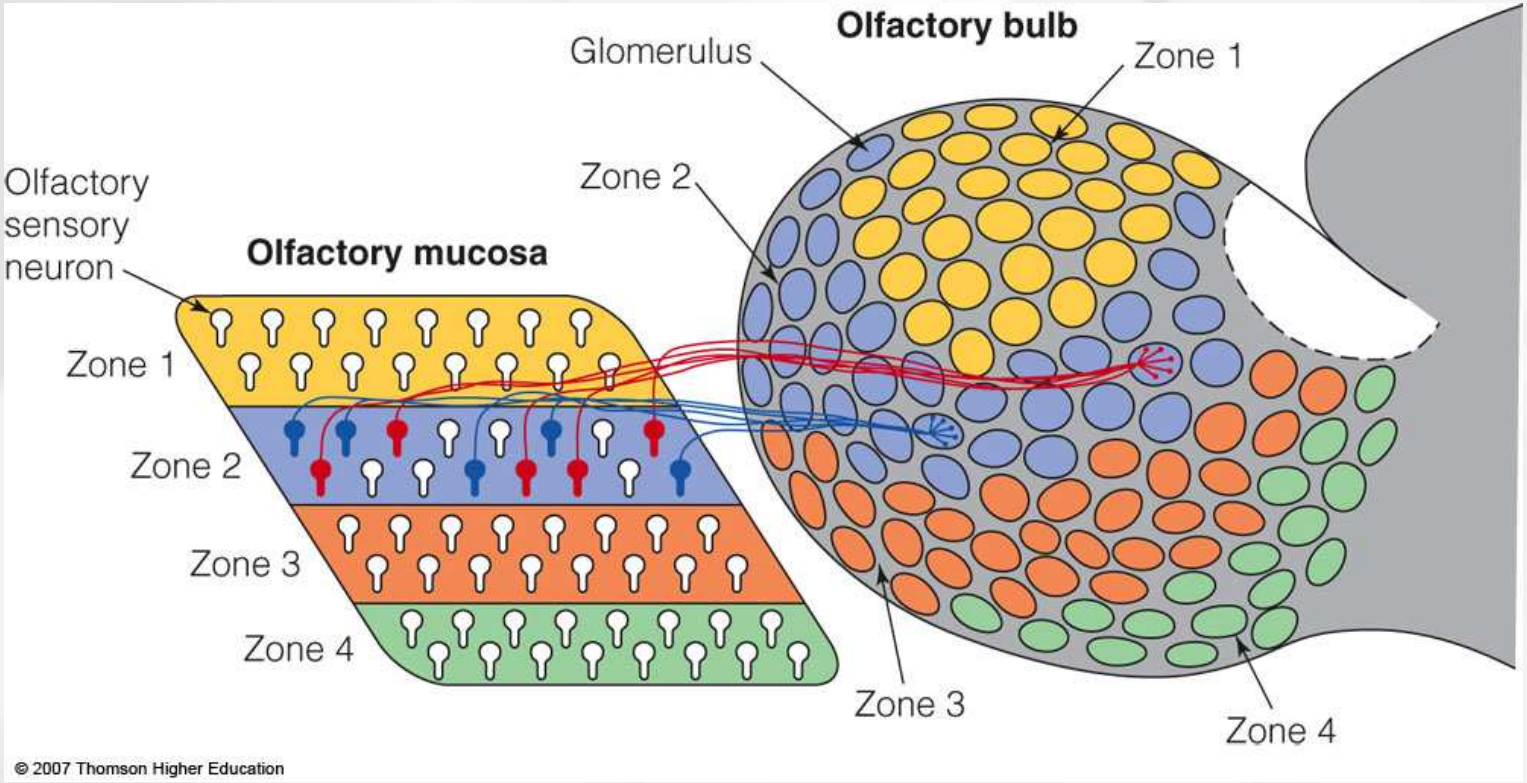
Evidence distributed coding for odor

- Proposed by Malnic et al. from results of calcium imaging experiments
- Odorants are coded by combinations of olfactory receptors called *recognition profiles*
- Specific receptors may be part of the code for multiple odorants



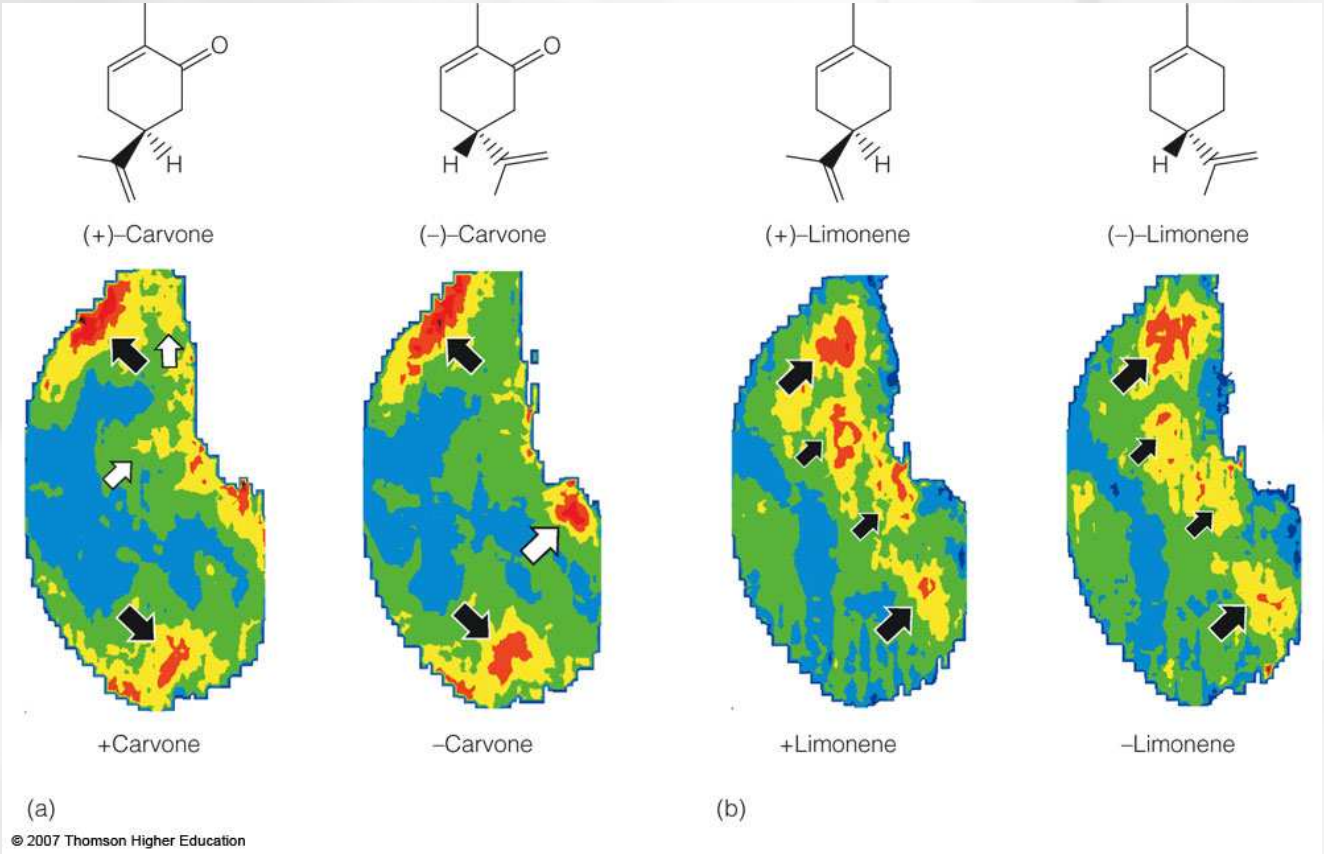
Activating the Olfactory Bulb

- Olfactory mucosa is divided into 4 zones
  - Each zone contains a variety of different receptors
  - Specific types of receptors are found in only one zone
  - Odorants tend to activate neurons within a particular zone
- Specific types of neurons synapse with only one or two glomeruli



Activating the Olfactory Bulb

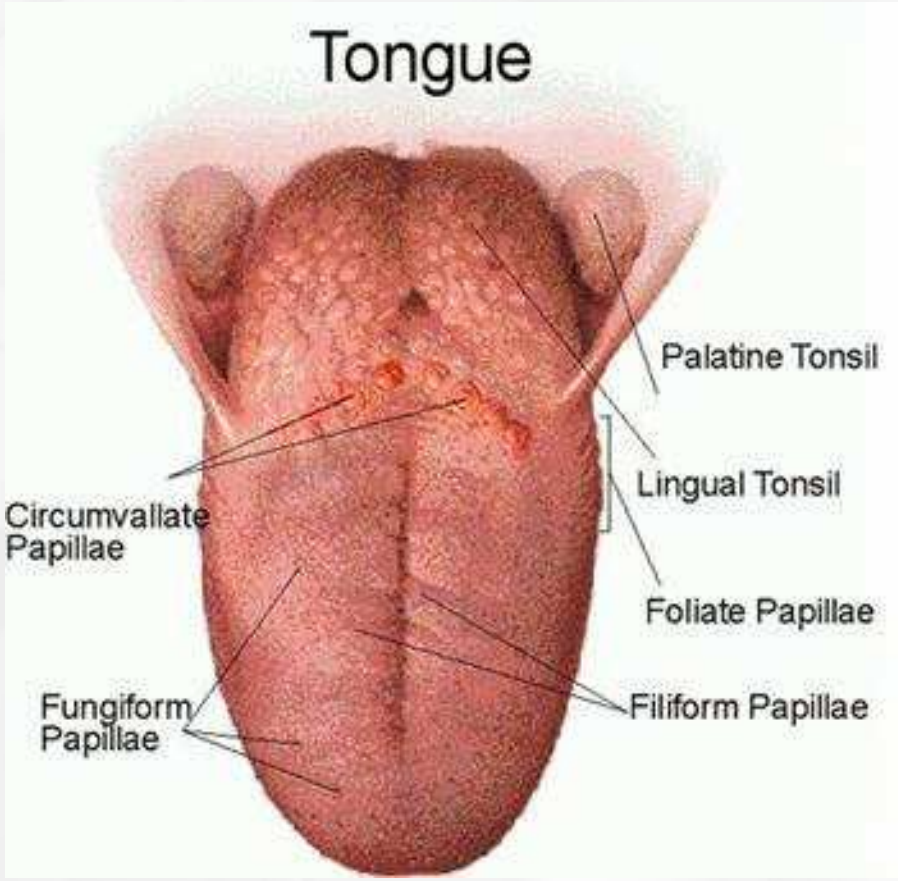
- 2-deoxyglucose (2DG) technique
  - 2DG, which contains glucose, is ingested into an animal
  - Animal (mouse) is exposed to different chemicals
  - Neural activation is measured by amount of radioactivity present
- This technique used with behavioral testing shows the pattern of neural activation is related to both chemical structure and to perception.



Taste

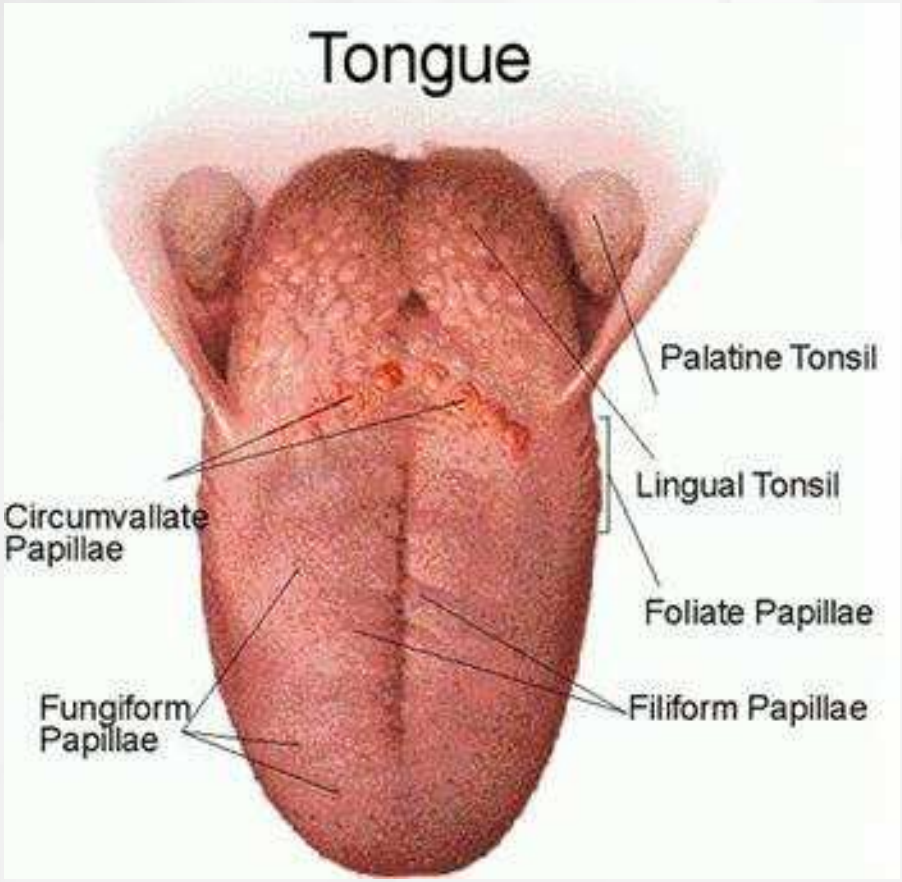
Table 15.2 *Structures in the taste system*

Structures	Description
Tongue	The receptor sheet for taste. Contains papillae and all of the other structures described below.
Papillae	The structures that give the tongue its rough appearance. There are four kinds, each with a different shape.
Taste buds	Contained on the papillae. There are about 10,000 taste buds.
Taste cells	Cells that make up a taste bud. There are a number of cells for each bud, and the tip of each one sticks out into a taste pore. One or more nerve fibers are associated with each cell.
Receptor sites	Sites located on the tips of the taste cells. There are different types of sites for different chemicals. Chemicals contacting the sites cause transduction by affecting ion flow across the membrane of the taste cell.



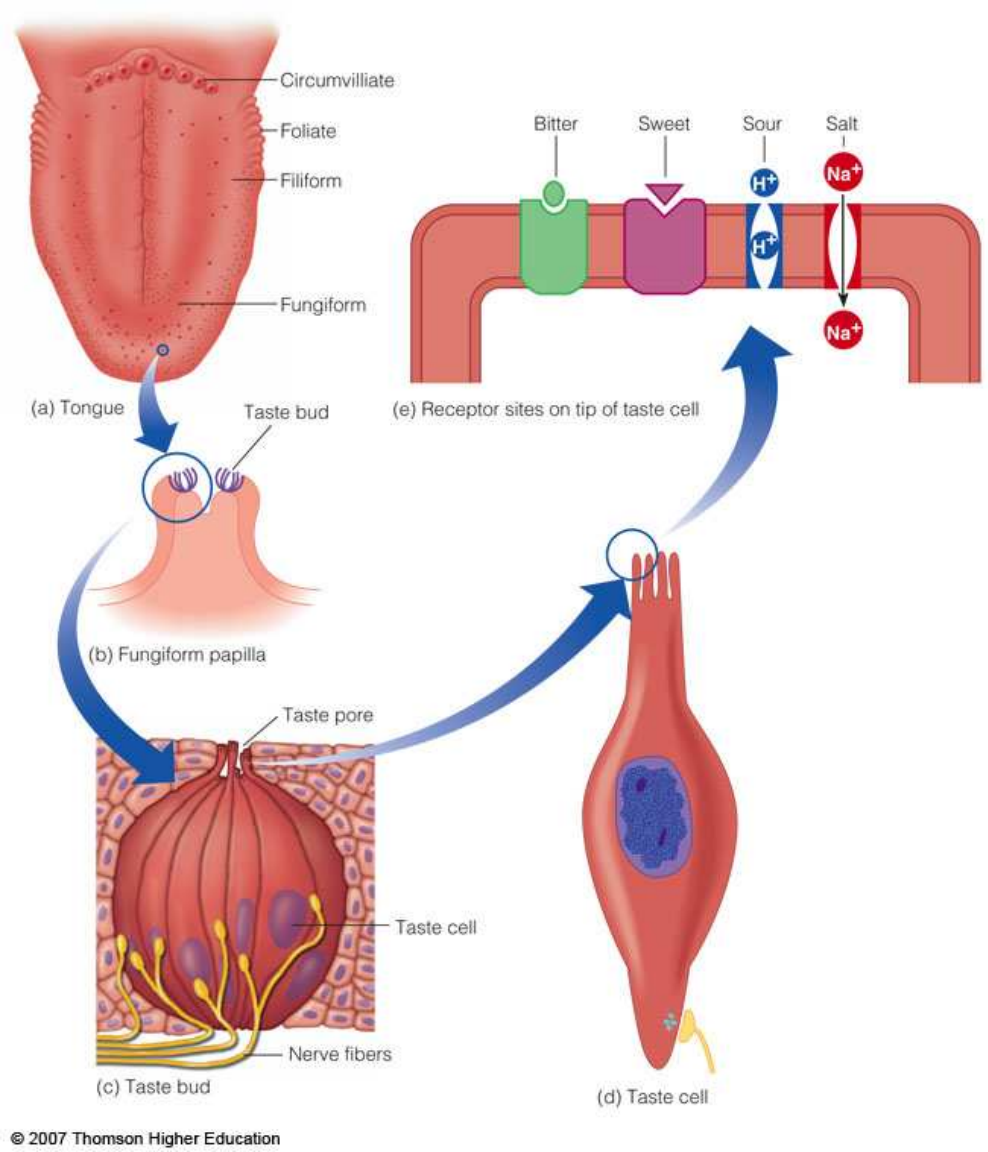
Structure of the Taste System

- Four kinds of papillae (bumps):
  - Filiform - shaped like cones and located over entire surface
  - Fungiform - shaped like mushrooms and found on sides and tip
  - Foliate - series of folds on back and sides
  - Circumvallate - shaped like flat mounds in a trench located at back



Structure of the Taste System

- Taste buds are located in papallae except for filiform
  - Tongue contains approximately 10,000 taste buds
  - Each taste bud has taste cells with tips that extend into the taste pore
  - Transduction occurs when chemicals contact the receptor sites on the tips



Basic Taste Qualities

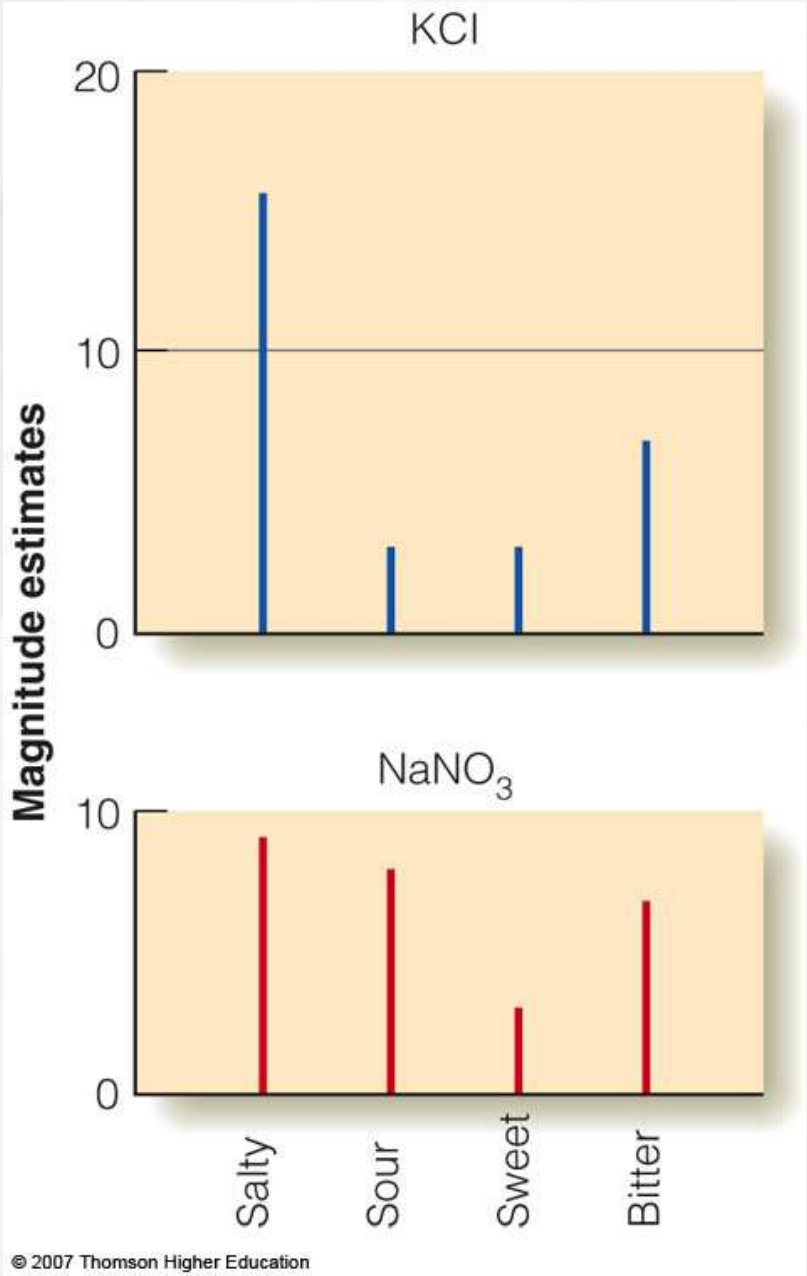
- Five basic taste qualities:
  - Salty
  - Sour
  - Sweet
  - Bitter
  - Umami - described as meaty, brothy or savory and associated with MSG

Contrary to popular belief, sensations of different qualities are not localized to specific parts of the tongue.

Tastes can (usually) be described as a combination of the basic taste qualities.

Potassium Chloride

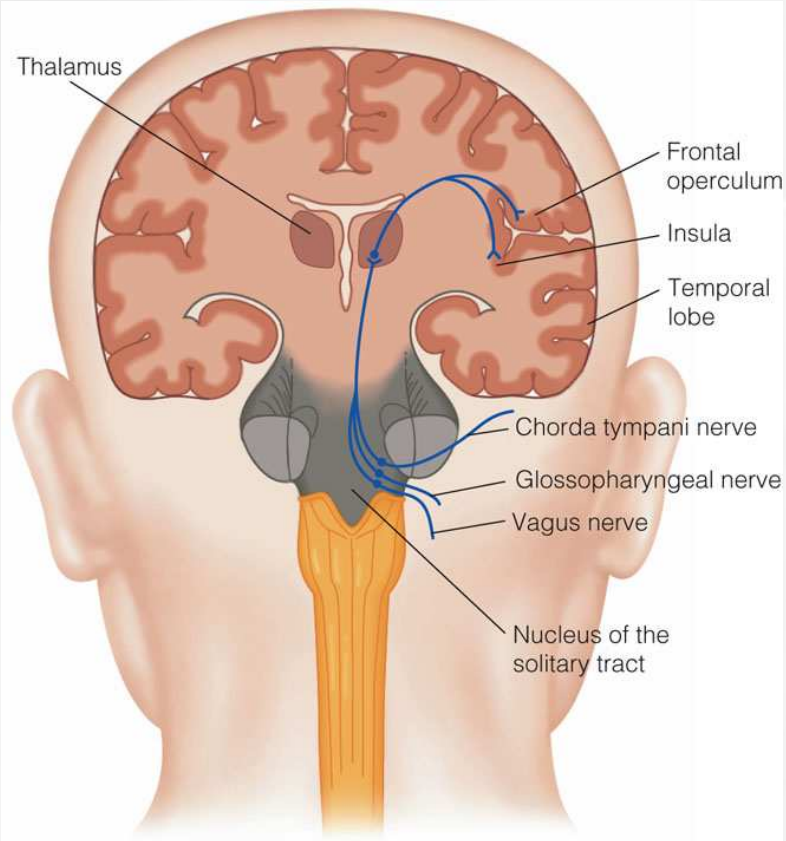
Sodium nitrate



McBurney (1969)

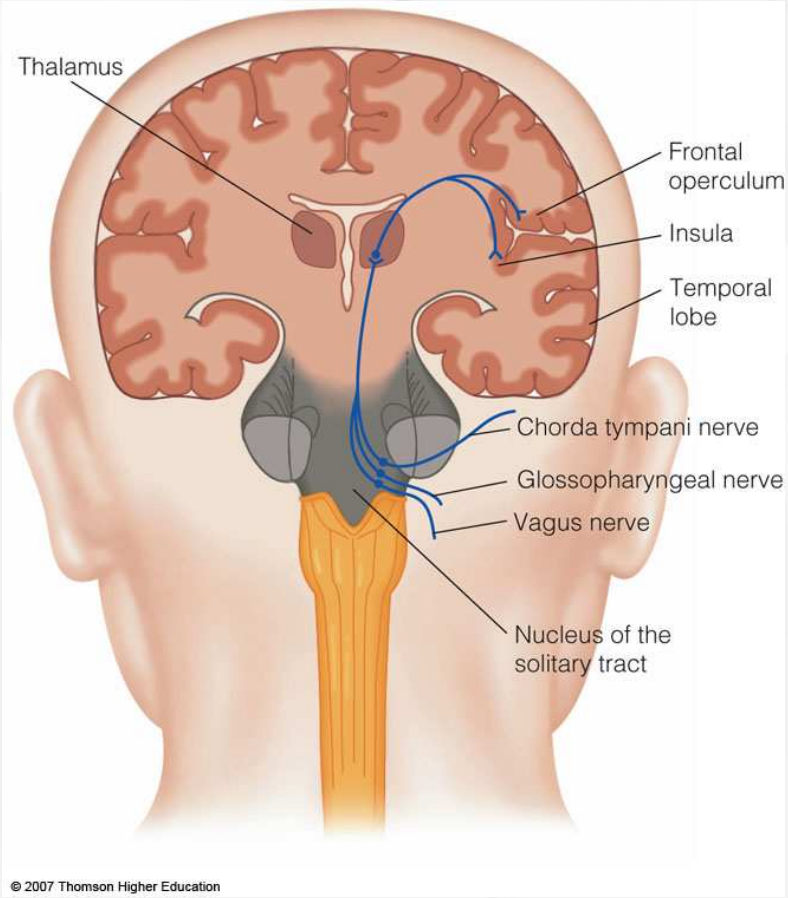
Structure of the Taste System

- Signals from taste cells travel along a set of pathways:
  - Chorda tympani nerve from front and sides of tongue
  - Glossopharyngeal nerve from back of tongue
  - Vagus nerve from mouth and throat
  - Superficial petronasal nerve from soft palate



Structure of the Taste System

- These pathways make connections in the nucleus of solitary tract in the spinal cord
- Then they travel to the thalamus
- Followed by areas in the frontal lobe:
  - Insula
  - Frontal operculum cortex
  - Orbital frontal cortex



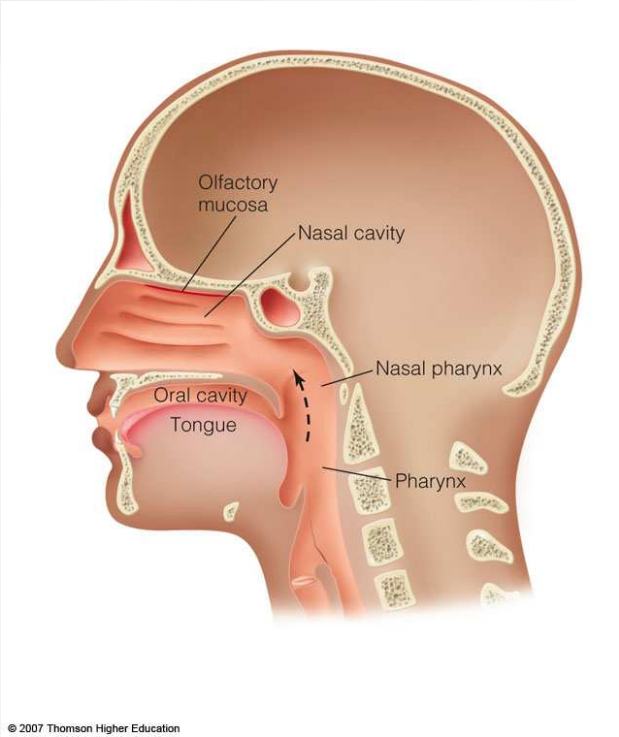
Neural Coding for Taste

- Evidence exists for both specificity and distributed coding
- Some researchers suggest that the neural system for taste may function like the visual system for color
- Currently there is no agreed upon explanation for the neural system for taste

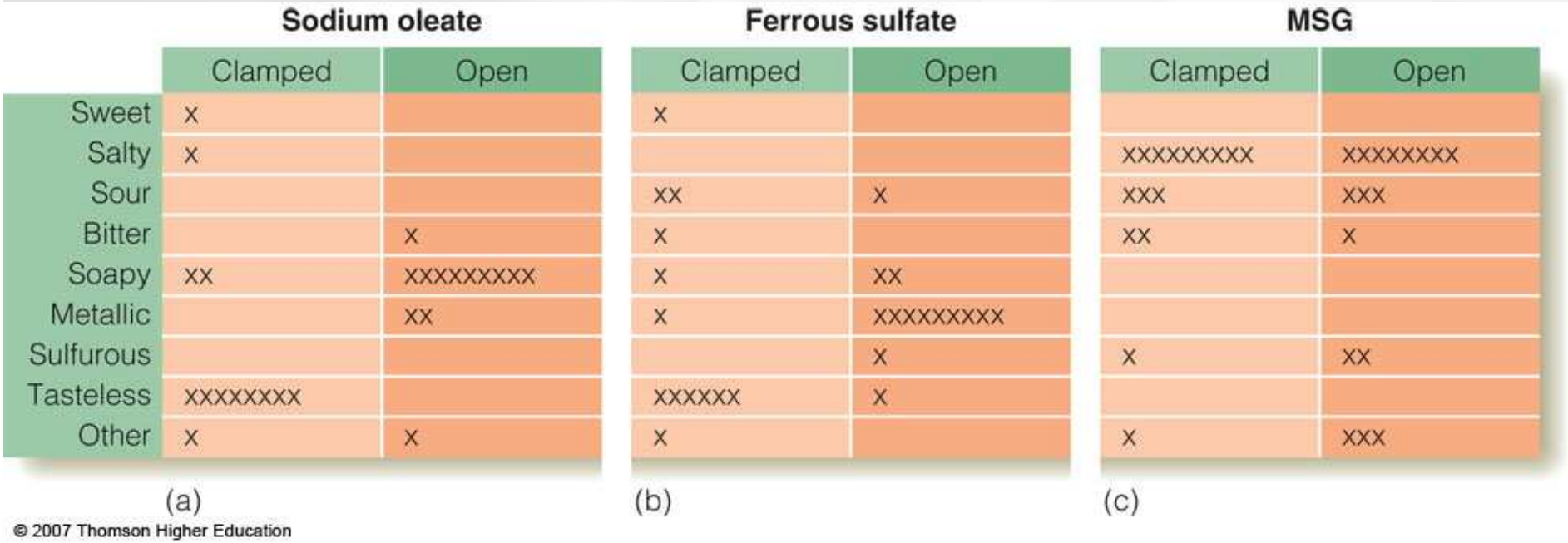
The Perception of Flavor

Taste + Smell = Flavor

- Combination of smell, taste, and other sensations (such as burning of hot peppers)
- Odor stimuli from food in the mouth reaches the olfactory mucosa through the retronasal route
- The taste of most compounds is influenced by olfaction, but a few, such as MSG are not



Flavor is affected by blocking the nose.

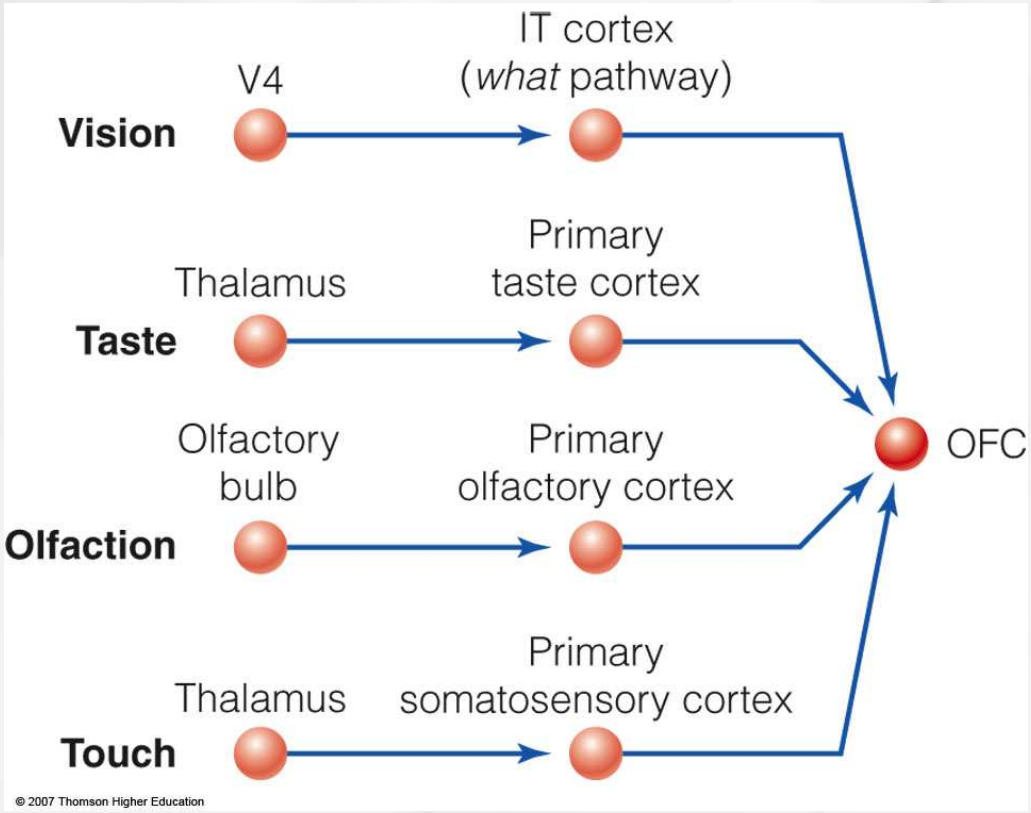


	Sodium oleate		Ferrous sulfate		MSG	
	Clamped	Open	Clamped	Open	Clamped	Open
Sweet	x		x			
Salty	x				xxxxxxxxx	xxxxxxxx
Sour			xx	x	xxx	xxx
Bitter		x	x		xx	x
Soapy	xx	xxxxxxxxx	x	xx		
Metallic		xx	x	xxxxxxxxx		
Sulfurous				x	x	xx
Tasteless	xxxxxxxx		xxxxxx	x		
Other	x	x	x		x	xxx

(a) (b) (c)

The Physiology of Flavor Perception

- Responses from taste and smell are first combined in the orbital frontal cortex (OFC)
- OFC also receives input from the primary somatosensory cortex and the inferotemporal cortex in the visual *what* pathway



Adjectives for describing the flavors of Wine

Acetic: A vinegary taste fault that results when a wine is excessively exposed to air.
Acidity: A sharp radiance and pleasing quality that naturally enhances wine's flavor. Wines in which acidity is lacking or out of balance with the fruit and other elements are most likely boring and unexciting.
Aftertaste: The taste or "finish" that remains in the mouth after swallowing a sip of wine. The finer the wine, the longer lingering the aftertaste.
Aroma: The fragrance or smell of a wine, ranging from smoky to herby to flowery and more.
Aromatic: A wine with a prominent aroma, particularly those fragrant with herbs or spices.
Astringent: A quality caused by high tannins that produces a drying sensation of the gums and tongue.
Balance: When a wine's elements, including fruit, tannins, acidity, and alcohol are in perfect proportioned agreement with one another.
Big: Robust or full-bodied in flavor and aroma.
Bitter: A twinge or strong sensation noticeable at the back of the tongue. Usually a taste fault but an attribute in certain Italian reds.
Body: The texture and weight of a wine as perceived in the mouth. A wine may have light, medium, or full body.
Botrytis cinerea: A fungus or mold that grows on ripening grapes, which can produce sweet dessert wines when cultivated properly.
Bouquet: The complex fragrance that develops in fine aged wines.
Brix: A scale of measurement used to determine the sugar content of grape juice and its ripeness and readiness to harvest and begin fermentation.
Brut: A very dry style of champagne or sparkling wine.
Buttery: A rich and oily heaviness in the mouth and buttery flavor that's found in many oak-aged whites, like Chardonnay.
Chewy: Unusual thickness of texture or tannins.
Clean: The quality of a thin, fresh wine that finishes smooth in the mouth and has nothing unfavorable about it.
Closed: Withheld character common in young, immature, or undeveloped wines.
Complete: A satisfying and mature quality of wine with a solid finish.
Complex: Flavors and aromas that have multiple layers of sensation.
Cooked: A heavy flavor suggestive of prunes.
Corky: A taste fault suggestive of cork or mildew caused by a defective or damaged cork.
Crisp: A clean and fresh characteristic that is sometimes tart, not soft.
Deep: Having layers of flavor complexity that progressively open up with oxygenation.
Delicate: Restrained flavors and aromas that are neither strong nor intense.
Developed: A drinkable and mature quality of wine.
Distinctive: A wine that sets itself apart with refined character qualities.
Dry: A wine that finishes parched or dehydrated in the mouth, not sweet.
Dull: A flat, lackluster wine, deficient in acidity and liveliness.
Dumb: Withheld flavor or aroma common in young or improperly chilled, stored, or aged wines.
Earthy: The pleasant aroma or flavor of moist soil or earth.
Fat: Robust or full-bodied in flavor and aroma.
Fine: A quality wine in terms of flavor, aroma, and overall positive characteristics.
Finish: The aftertaste that remains in the mouth after swallowing a sip of wine. The finer the wine, the longer lingering the finish.
Firm: A well-balanced wine in terms of its structure and components, not soft or harsh.
Flat: A dull, lackluster wine, deficient in acidity and liveliness.
Flavor: The taste or notes found in a wine, which may vary from smoky to spicy to flowery and more.
Fleshy: Robust and ripe in fruit flavor, texture, and aroma.
Flinty: A dry, mineral flavor that's suggestive of limestone.
Flowery: An aroma suggestive of flowers.
Forward: Full of robust fruit flavor.
Foxy: The distinctive flavors of wines made from native American grapes.
Fruity: A sweet aroma or flavor suggestive of peaches, cherries, apples, pears, raspberries, citrus, currants, strawberries, and more.
Full-bodied: Indicating strong character, in terms of flavor and alcohol.
Green: A tart and fruit-deficient flavor found in wines made from unripe grapes.
Hard: Taut with high tannins.
Harmonious: A perfectly balanced wine in terms of all its components—fruit, acid, and tannin.
Harsh: A negative characteristic describing a bitter, unpleasant, or offensive taste or sensation, usually from excessive tannins or acidity.
Heady: A robust, full-bodied wine that is high in alcohol.
Herbaceous: An herbal aroma or flavor suggestive of herbs, leaves, or plants.
Herby: An herbal aroma or flavor suggestive of herbs like sage, mint, or thyme.
Honest: The quality of a clean, simple wine that has nothing unfavorable about it.

Honeyed: A flavor or aroma suggestive of honey, often found in late-harvest wines affected by Botrytis cinerea.
Intricate: A wine with subtle aroma and flavor complexities that intermingle
Legs: The syrupy remnants that run down the inside of the wine glass after it is swirled or sipped, which indicate the body and texture of a wine.
Length: A long-lingering taste or “finish” that remains in the mouth after swallowing a sip of wine.
Light: Indicating a thin character, in terms of texture, weight on the tongue, and alcohol.
Lively: Pleasingly vibrant, crisp, and fresh.
Maderized: The stale odor and deep amber color that’s found in many aged and oxidized wines, like the whites from Madeira.
Mature: Fully developed and ready to bottle or drink.
Mellow: A soft and smooth quality, not harsh.
Moldy: An aroma suggestive of mold or rot, often found in aged wines or wines affected by Botrytis cinerea.
Muscular: A big, bold, and fruitful flavor quality.
Musty: A stale or pungent aroma.
Noble Rot: See Botrytis cinerea.
Nose: The smell of a wine.
Nutty: A roasty aroma or flavor suggestive of hazelnuts, almonds, roasted nuts, etc.
Oaky: An aroma or flavor suggestive of oak that’s found in many oak-aged wines, often smoky or spicy.
Off-dry: Wine quality that cannot be deemed sweet or dry.
Open: Fully released character common in mature or fully developed wines.
Oxidized: A flat, stale taste fault that results when a wine is excessively exposed to air.
Pétillant: A lightly sparkling quality.
Rich: A full-bodied wine that finishes with a depth and complexity of flavor and an overall pleasing taste and aroma.
Ripe: A mature wine that tastes of fully ripened fruit.
Robust: A full-bodied, big, and heady quality.
Rough: A harsh and unfavorable flavor quality.
Round: A perfectly structured flavor quality in terms of a wine’s acidity, tannin, alcohol, and sweetness.
Sharp: An intense sensation along the sides of the tongue, attributed to acidity or tannins.
Short: A too-brief taste or “finish” that ends abruptly after swallowing a sip of wine.
Silky: A smooth and graceful texture quality.
Simple: Flavors and aromas that have only a single layer of sensation, not complex.
Smoky: An aroma or flavor suggestive of wood smoke and often associated with oak-aged wines.
Soft: Wines that are heady and sweet more than acidic or tannic, not hard or rough.
Solid: A well-structured wine in terms of its components, not soft or harsh.
Sommelier: A professional wine steward.
Sour: An intense acidic or vinegary sensation along the sides of the tongue.
Sparkling: Bubbly wines, like champagnes or sparkling wines.
Spicy: A fragrance or flavor reminiscent of spices like cinnamon, black pepper, clove, or mint.
Spritzy: A slightly sparkling quality, sometimes created when bottling very young wines.
Stiff: See dumb or closed.
Strong: Characteristic of rich, robust, full-bodied wines.
Structure: A wine’s makeup and proportions in terms of alcohol, tannin, acid and sugar.
Supple: A soft flavor and texture quality found in wines that are ready for drinking, not rough or harsh.
Sweet: A ripe and fruity taste quality noticeable at the tip of the tongue, which is usually indicative of residual sugars.
Tannin: A natural substance found in the skins, stems, and seeds of grapes that imparts a puckery mouthfeel to young reds and produces the structure, texture, ageability of most reds.
Tart: An intensely sharp sensation along the sides of the tongue, which is sometimes acceptable if not overly acidic.
Terroir: A French word used to describe the growing region and the aspects of that region that make it unique from any other.
Thick: A heavy, dense texture quality.
Thin: Indicating a deficient character, in terms of body and flavor.
Vigorous: A firm and fruit-forward flavor quality.
Volatile Acidity (VA): An acetone-smelling aroma that indicates a wine is turning to vinegar.
Watery: Indicating a deficient character, in terms of flavor.
Weak: A wine lacking in character.
Weedy: A stalky aroma or flavor suggestive of wet hay or straw.
Weighty: See strong or full-bodied.
Woody: An aroma or flavor suggestive of tree bark or oak.
Yeasty: An aroma or flavor suggestive of bread.
Young: A wine that is fresh and new or in fine wines, a wine that is immature.

Individual Differences in Taste – ‘supertasters’

Around 35% of women are super-tasters, compared with just 15% of men

- There are different responses to phenylthiocarbamide (PTC) and to 6-*n*-propylthiouracil (PROP):
  - Tasters, nontasters, and supertasters
  - Tasters have more taste buds than nontasters
  - Tasters have specialized receptors for these compounds
  - Supertasters appear more sensitive to bitter substances than tasters

Are you a ‘supertaster’?

To test your taste buds, you need some blue food coloring, a piece of paper with a 7mm-wide hole punched through it, and a magnifying glass.

Swab some of the food coloring onto the tip of your tongue. The tongue will take up the dye, but the papillae, tiny structures that house the taste buds, will stay pink.

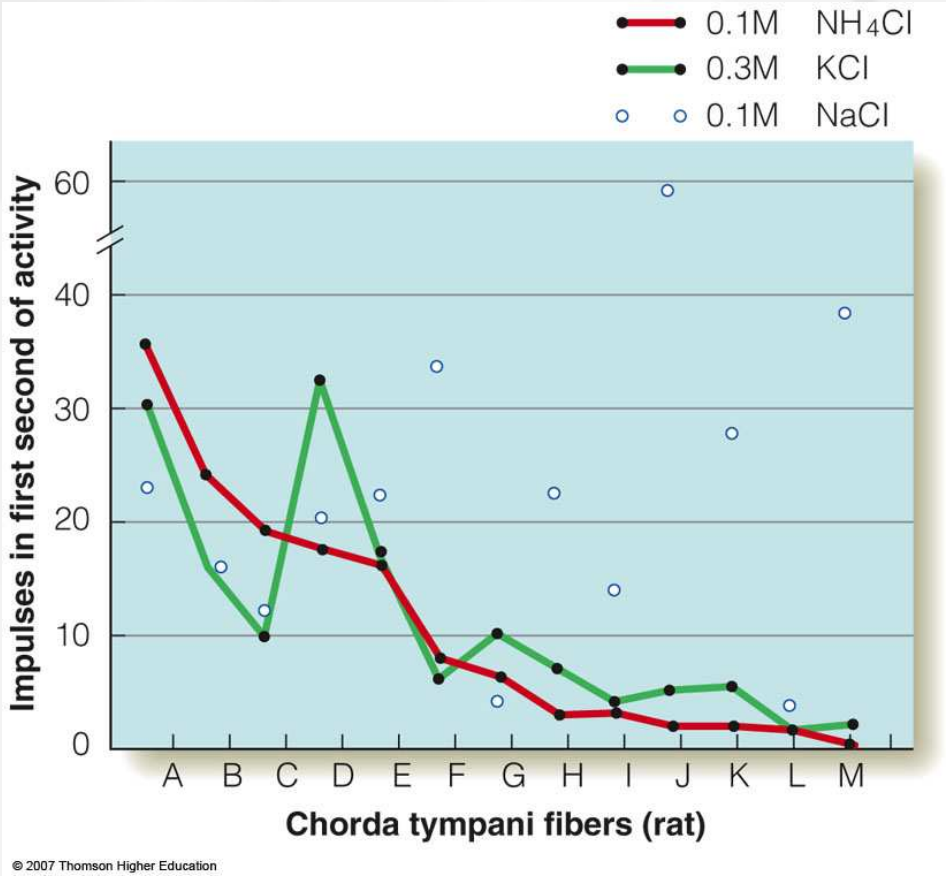
Put the piece of paper on the front part of the tongue and, using the magnifying glass, count how many pink dots are inside the hole.

Fewer than 15 papillae mean you are an insensitive "non-taster", between 15 and 35 indicates an average "taster" and over 35 papillae then you are a "super-taster".

Quoted from interview with Yale researcher Linda Bartoshuk on BBC News
http://news.bbc.co.uk/1/hi/health/2880471.stm

Neural Coding for Taste

- Distributed coding
  - Experiment by Erickson
  - Different taste stimuli were presented to rats and recordings were made from the chorda tympani
  - Across-fiber patterns showed that two substances (ammonium chloride and potassium chloride) are similar to each other.



Experiment by Erickson

- Rats were then trained by shocking them when they drank potassium chloride
- When they were given the choice, they subsequently avoided ammonium chloride
- The experiment provides physiological and behavioral evidence for distributed coding

Neural Coding for Taste

- Experiment by Sato et al.
  - Recordings were made from 66 fibers in the monkey's chorda tympani
  - Results showed that there were fibers that responded best to one of the basic tastes (sweet, salty, sour, and bitter) but poorly to the others
  - Thus, there are fibers that respond specifically to particular chemicals