Some Questions

- Why is a dog's sense of smell so much better than a human's?
- Why does a cold inhibit the ability to taste?
- How do neurons in the cortex combine smell and taste?

The Chemical Senses

- “Gatekeepers” of the body which
  - Identify things that could/should be consumed for survival.
  - Detect things that would be harmful and should be rejected.
  - Cause good and bad affective responses.
- Olfaction and taste have constant neurogenesis (receptors die and are replaced).

Functions of Olfaction

- Many animals are *macrosmatic* – they have a keen sense of smell that is necessary for survival.

- Humans are *microsmatic* – we have a less keen sense of smell that is not crucial to survival.

Detecting Odors Tasks

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.

Detecting Odors Results

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

Detecting Odors Results - 2

Thresholds (in parts per billion) vary widely for different substances:

1. 141,000 for methanol
2. 15,000 for acetone
3. 40 for menthol
4. 0.3 (< 1) for T-butyl mercaptan

Detecting Odors (cont.)

Measuring the difference threshold:

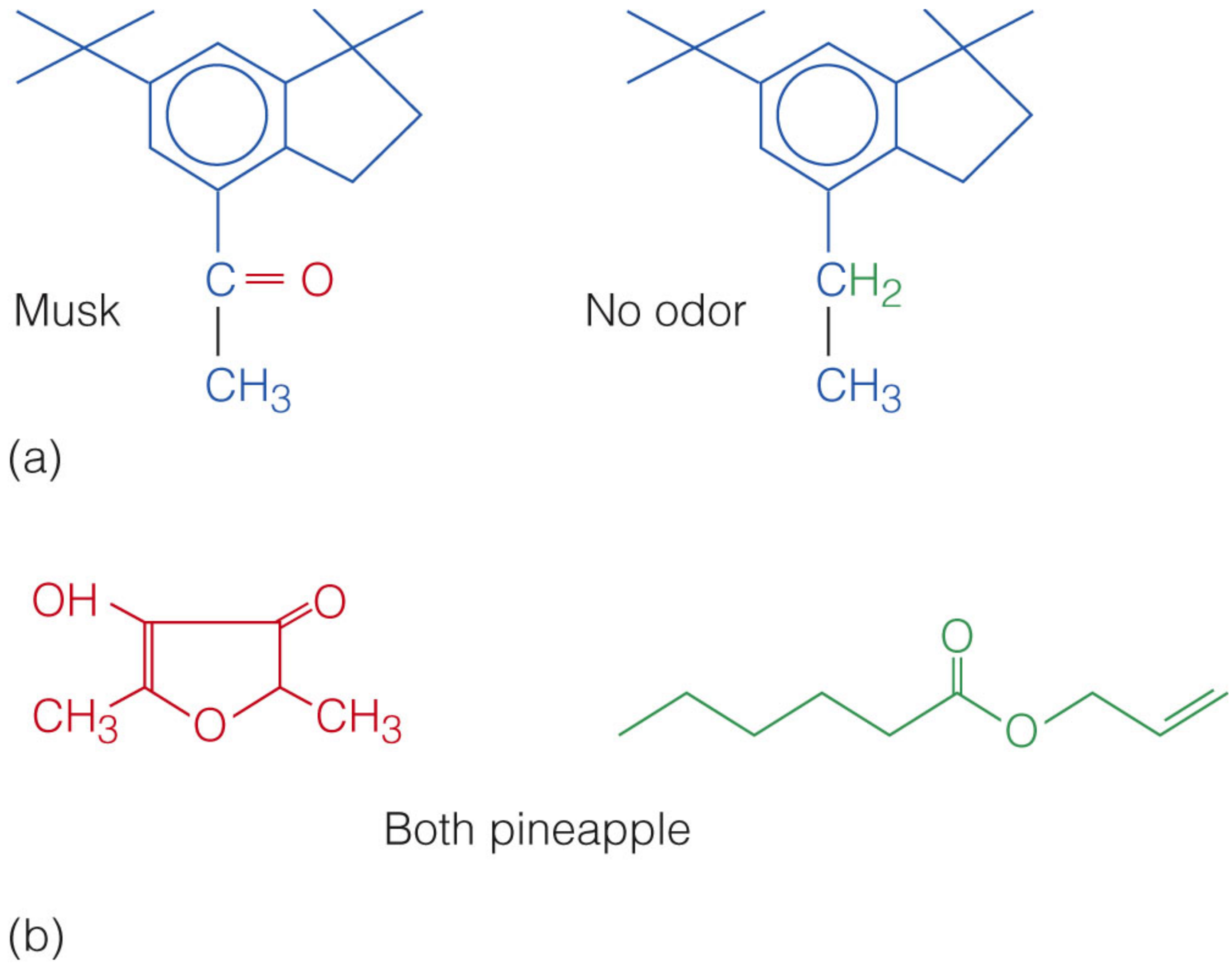
- Smallest difference in concentration that can be detected between two samples.
- This research must be done with carefully controlled concentrations using a device called a *olfactometer.*
- Research has shown the threshold to be approximately 11%.

Identifying Odors

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

The Puzzle of Olfactory Quality

- Researchers have found it difficult to map perceptual experience onto physical attributes of odorants because:
    - there is no specific language for odor quality.
    - some molecules that have similar structure smell different
    - some that have different structures smell the same.
- Links have been found between the structure of molecules, olfactory quality, and patterns of activation in the olfactory system.


Musk
C = O
CH3
No odor
CH2
CH3
(a)
OH
O
CH3
O
CH3
O
O
Both pineapple
(b)

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 olfactory receptor neurons (ORN).
- These neurons contain molecules called olfactory receptors.
- Humans have about 350 types of receptors.

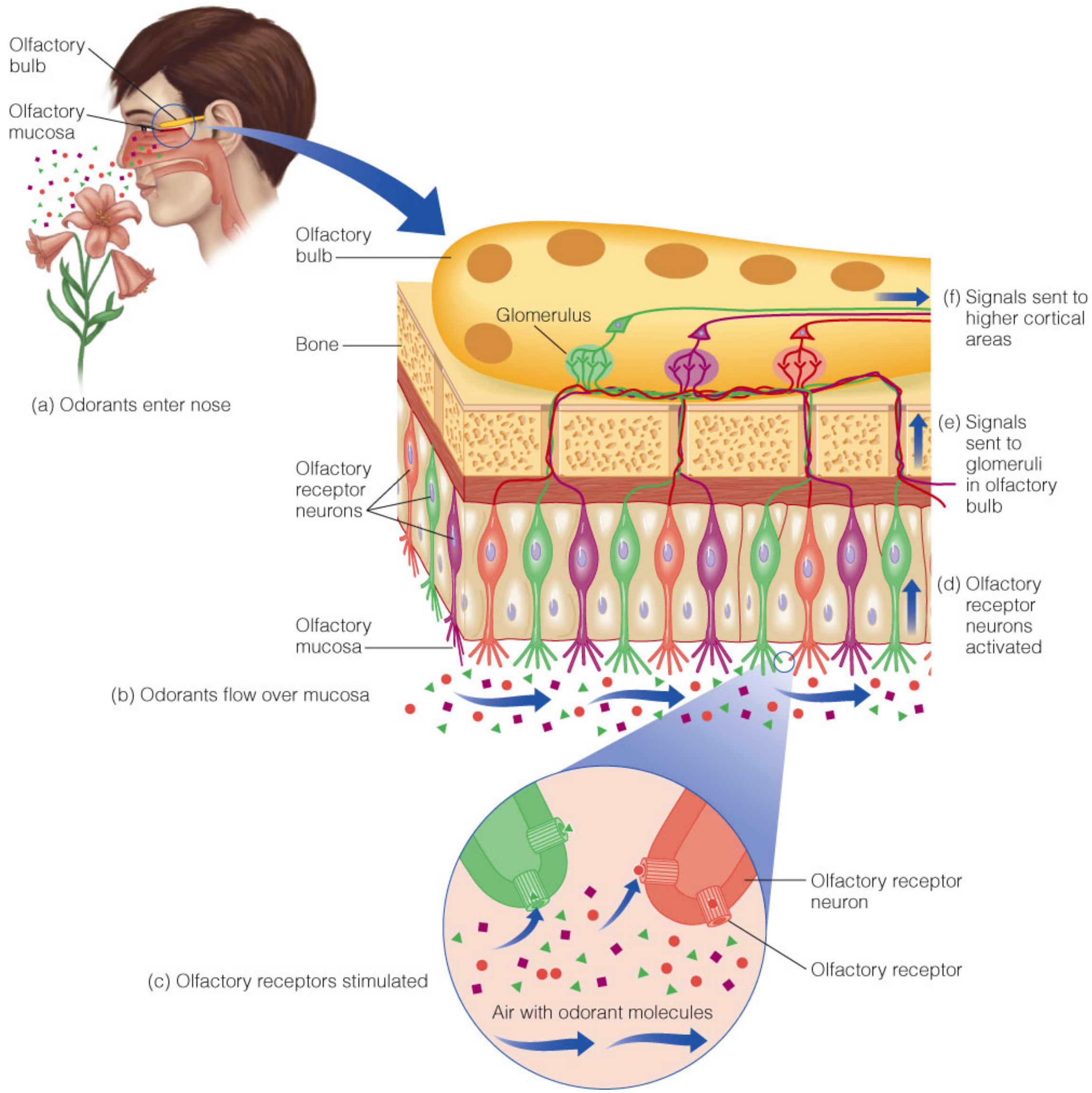


Figure 15.4 The structure of the olfactory system. Odorant molecules flow over the olfactory mucosa, which contains 350 different types of olfactory receptor neurons (ORNs). Three types of ORNs are shown here, indicated by different colors. Each type has its own specialized receptors.

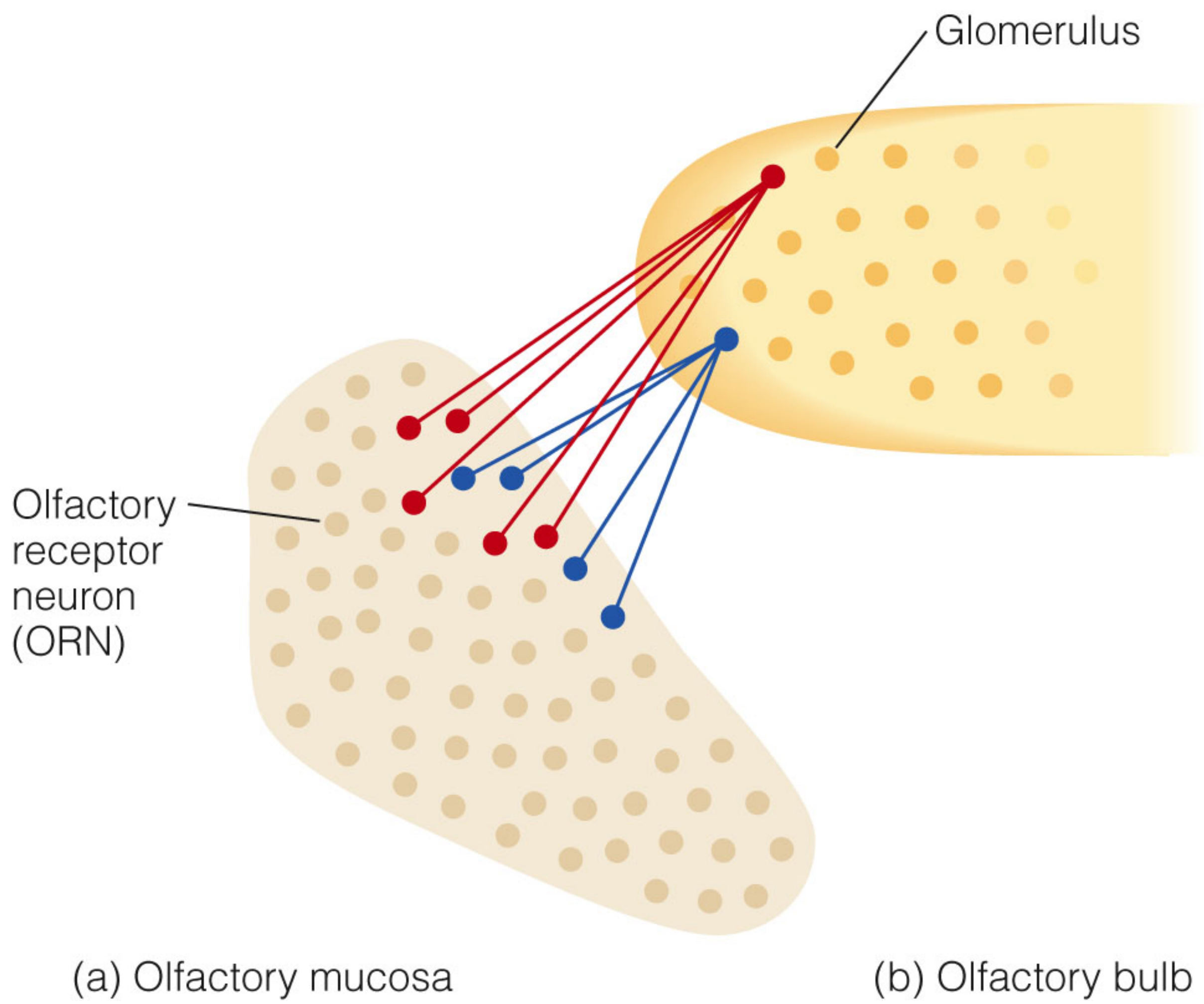


Figure 15.5 (a) A portion of the olfactory mucosa. The mucosa contains 350 types of ORNs and about 10,000 of each type. The red circles represent 10,000 of one type of ORN, and the blue circles, 10,000 of another type. (b) All ORNs of a particular type send their signals to one or two glomeruli in the olfactory bulb.

Activating Receptor Neurons

- Calcium imaging method
  - Concentration of calcium increases inside the ORN when an olfactory receptor responds.
  - Calcium can be detected by using a chemical that makes the neuron fluoresce.
  - Measuring the change in fluorescence indicates the strength of the response.

Activating Receptor Neurons - continued

Combinatorial code for odor:

- Proposed by Malnic et al. from results of calcium imaging experiments.
- Odorants are coded by patterns of activation of olfactory receptors called *recognition profiles.*
- Molecules that have similar structures but smell different have different recognition profiles.

Olfactory Receptors

Odorants	1	18	19	41	46	51	79	83	85	86
Octanoic acid	●	●	●	●	●	●	•	●		
Nonanoic acid	●	●	●	●	●	●		●		●
Octanol		●	●	●		●				
Bromo-hexanoic acid			●	●					●	
Bromo-octanoic acid	●	●	●	●	●	●		●	●	

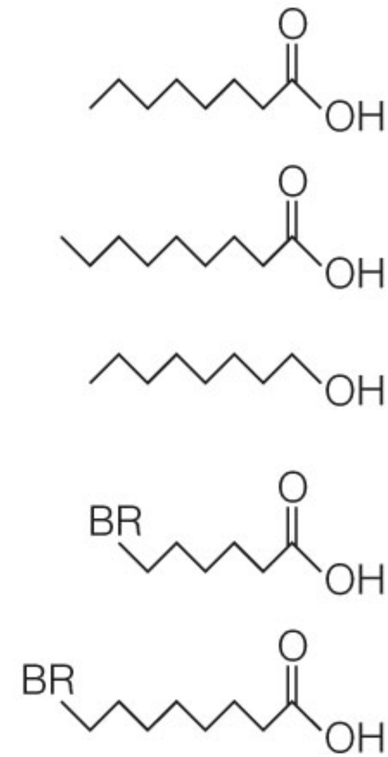


Figure 15.6 Recognition profiles for some odorants. Large dots indicate that the odorant causes a high firing rate for the receptor listed along the top; a small dot indicates a lower firing rate for the receptor. The structures of the compounds are shown on the right. (*Adapted from Malnic et al., 1999.*)

Activating the Olfactory Bulb

Signals are carried to the glomeruli in the olfactory bulb.

- ORNs of a particular type send their signals to one or two glomeruli.

Two techniques have been used to determine how the glomeruli respond to different odorants.

- Optical imaging method
- 2-deoxyglucose (2DG) technique

Activating the Olfactory Bulb (cont.)

Optical imaging method:

- Cortical cells consume oxygen when activated.
- Red light is used to determine the amount of oxygen in the cells.
- Less oxygen reflects less red light
- Measuring the amount of light reflected reveals which areas of cortex are most active.

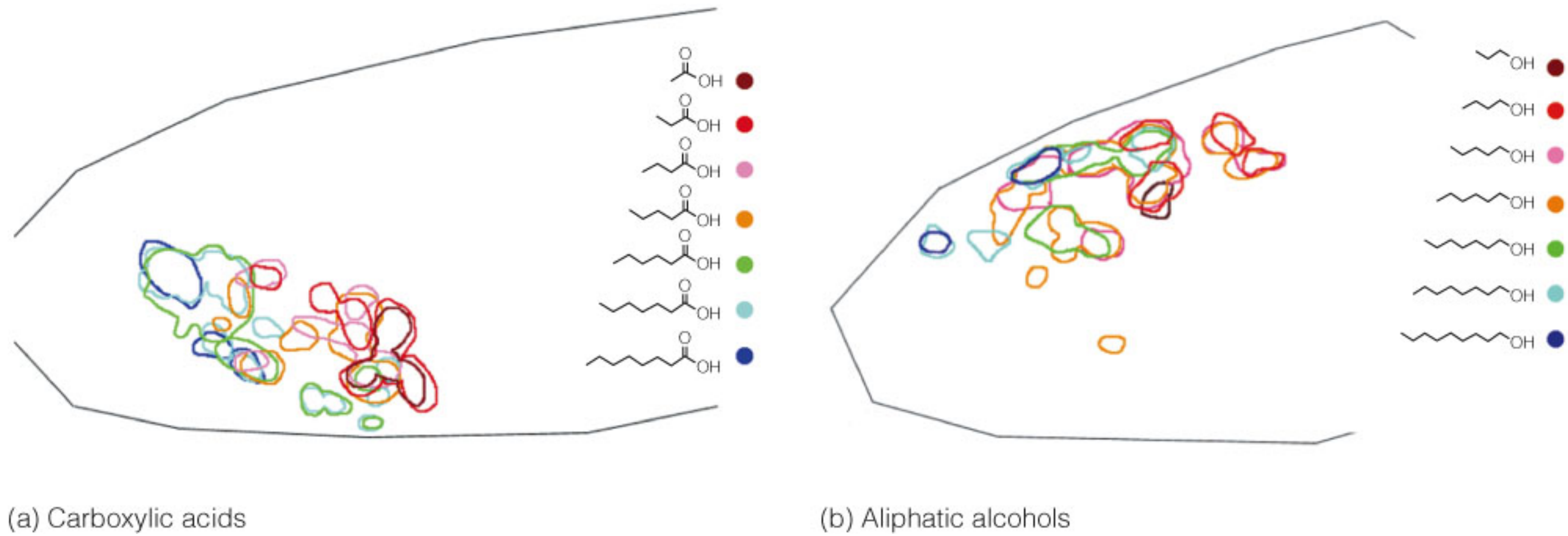


Figure 15.7 Areas in the olfactory bulb that are activated by various chemicals: (a) a series of carbolic acids; (b) a series of aliphatic alcohols. *(From Uchida et al., 2000.)*

Activating the Olfactory Bulb (cont.)

2-deoxyglucose (2DG) technique:

- 2DG, which contains glucose, is injected into an animal.
- Animal 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.

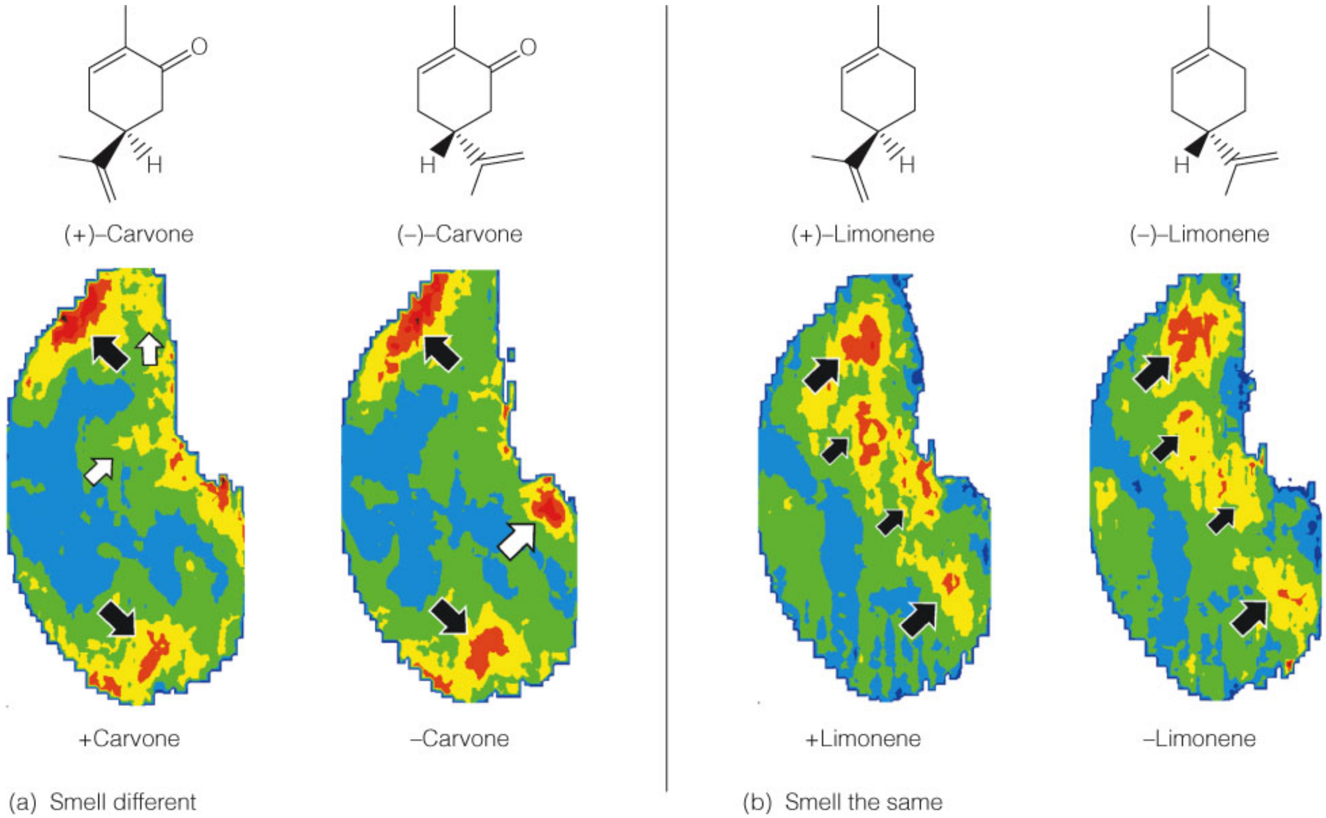


Figure 15.8 Patterns of activation in the rat olfactory bulb. Red, orange, and yellow indicate high activation. (a) Top: Two forms of carvone. These molecules have the same chemical formula, but the molecular group at the bottom is rotated to a different position. Bottom: Activation patterns. Black arrows indicate areas in which activation was the same for the two compounds. The white arrows indicate areas activated by one compound but not the other. They show that the two forms of carvone activate different areas in the olfactory bulb. (b) Top: Two forms of limonene. These molecules also have the same chemical formula, with the molecular group at the bottom rotated to a different position. Bottom: Activation patterns. The black arrows indicate that the two forms of limonene activate similar areas in the olfactory bulb. *Adapted from Linster et al., 2001.*

Hardwired Responses to Odors

- Rats that are bred in laboratories and have not been exposed to cats for generations show a fear response to cat odor.
- Female rabbits release phermones that trigger nursing responses in newborn rabbits.

Higher Level Olfactory Processing

Signals from the olfactory bulb are sent to:

- primary olfactory (piriform) cortex in the temporal lobe and to the amygdala.
  - Amygdala plays a role in emotional reactions to odors.
- then to secondary olfactory (orbitofrontal) cortex in the frontal lobe.

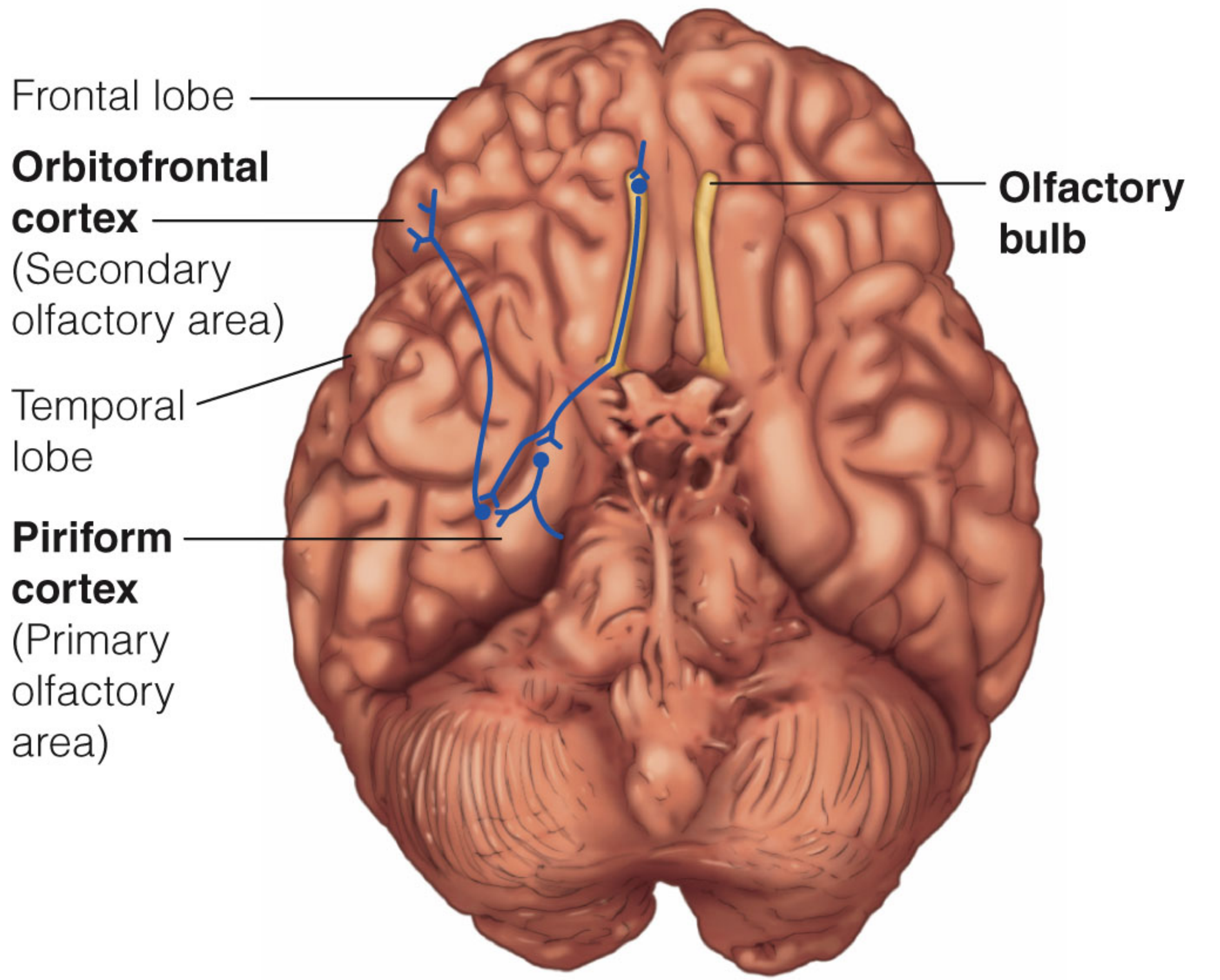


Figure 15.9 (a) The underside of the brain, showing the neural pathways for olfaction. On the left side, the temporal lobe has been deflected to expose the olfactory cortex. (Adapted from Frank & Rabin, 1989).

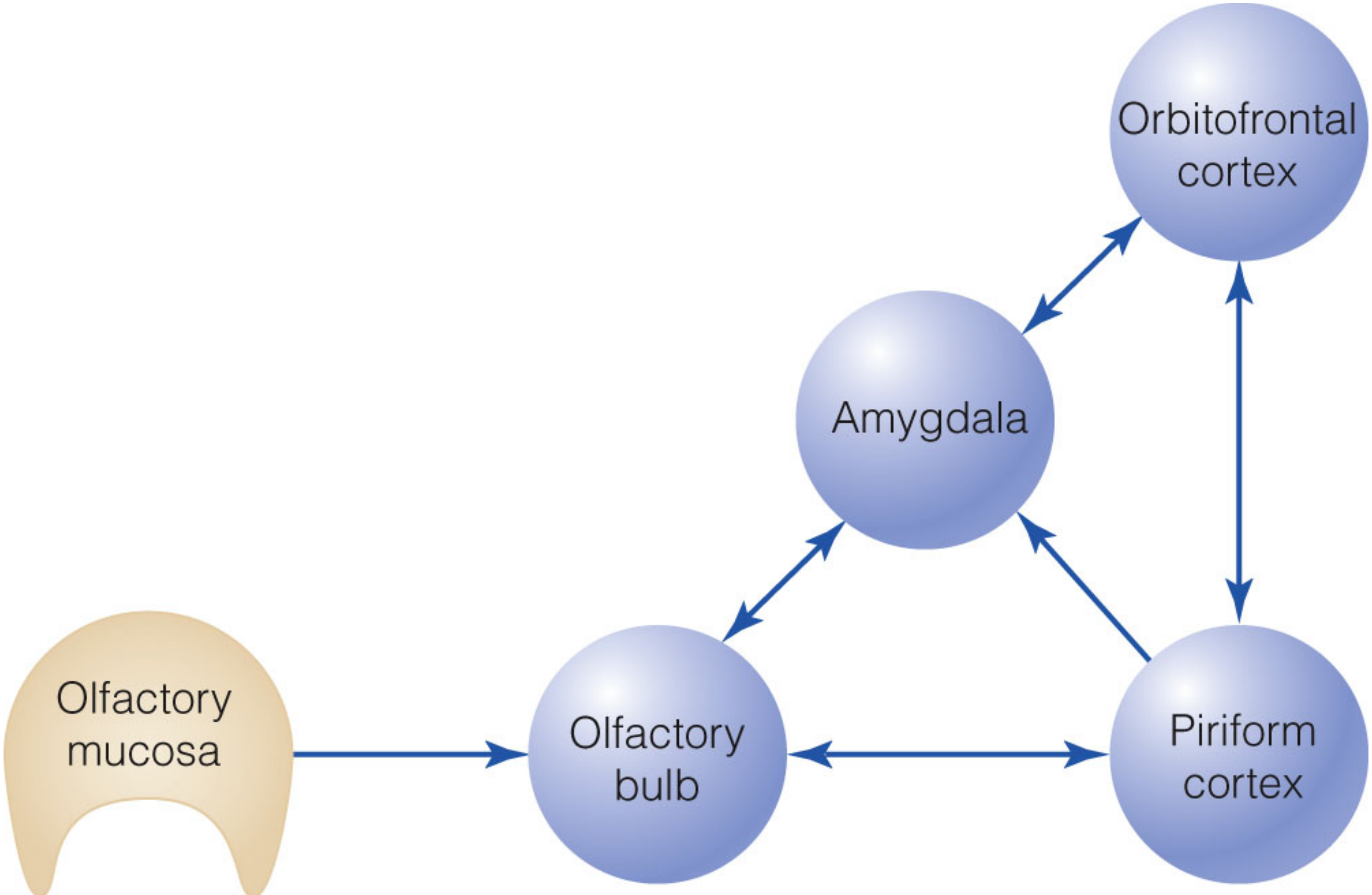


Figure 15.10 Flow diagram of the pathways for olfaction. (From Wilson and Stevenson, 2006)

The Physiology of Higher Level Olfactory Processing

Experiment by Wilson.

- Measured response of neurons in the rat's piriform cortex to two odorants:
  - A mixture - isoamyl acetate and peppermint
  - A compound - isoamyl acetate alone
- Results showed that with enough exposure, the piriform cortex could discriminate between the mixture and the compound.

The Physiology of Higher Level Olfactory Processing (cont.)

Experiment by de Araujo et al.

- People were exposed to a mixture of a sweat-like smell and a cheddar cheese flavoring.
- On some trials, they saw the label “cheddar cheese,” and on others, the label “body odor.”
- Pleasantness ratings were higher for the cheddar cheese trials.
- fMRI scans showed activity in the orbitofrontal cortex to be associated with the pleasantness ratings.

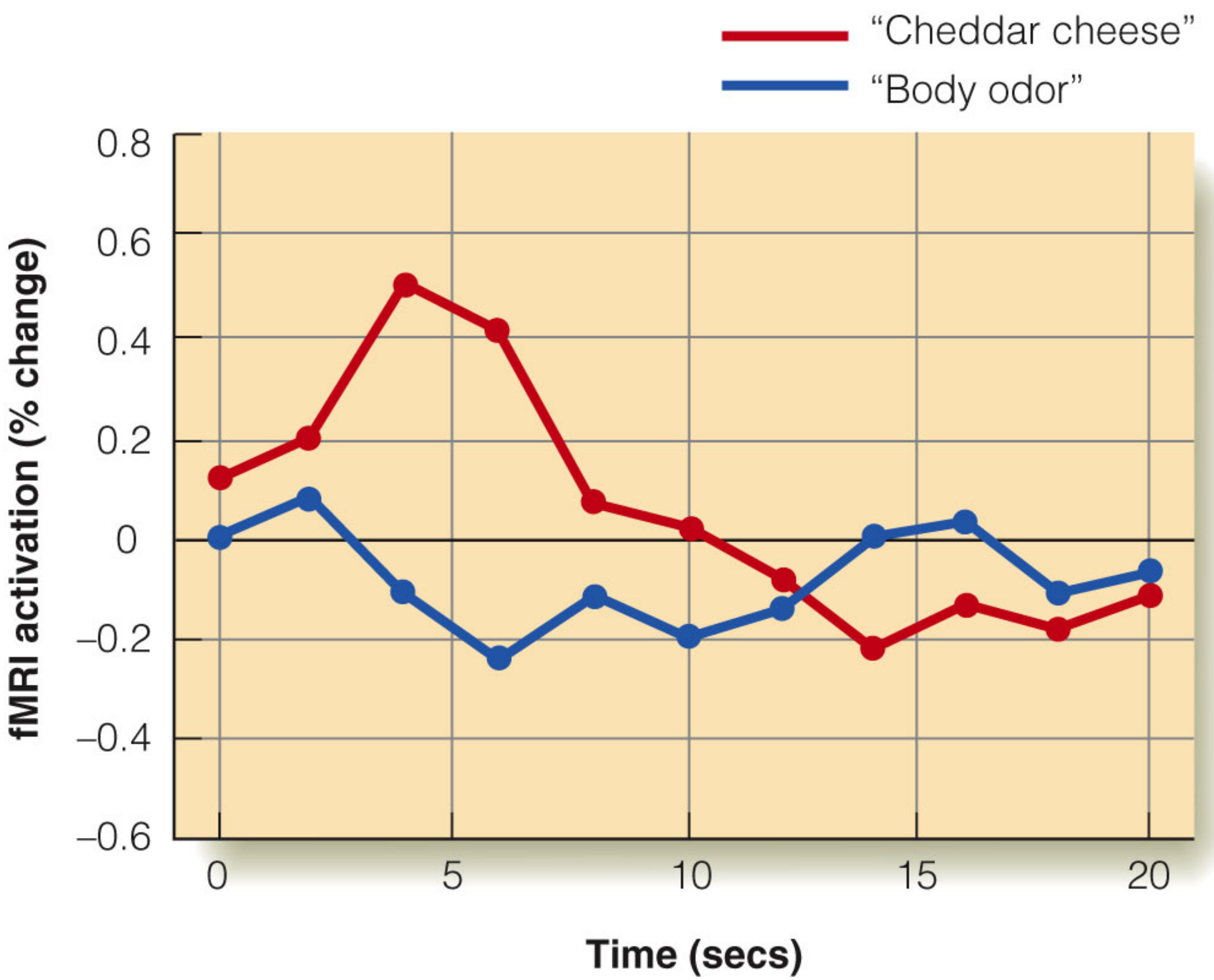


Figure 15.13 Activation in the orbitalfrontal cortex produced by a test odor when labeled "cheddar cheese" and when labeled "body odor." (From de Araujo et al., 2005)

Olfaction in the Environment

- Many molecules create a single perception (e.g. aroma of coffee).
- Odors can occur concurrently (e.g. frying bacon and fresh coffee) but the perceptual system separates them from one another.
- Past experience and expectations have an impact on odor perception.
- Thus, odor perception is both a bottom-up process and top-down process that organizes the information.

Figure 15.11 Hundreds of molecules from the coffee, orange juice and bacon are mixed together in the air, but the person just perceives "coffee", "orange juice, and "bacon." This perception of three odors from hundreds of intermixed molecules is a feat of perceptual organization.

Functions of Taste

- Sweetness is usually associated with substances that have nutritive value.
- Bitter is usually associated with substances that are potentially harmful.
- Salty taste indicates the presence of sodium.
- However, there is not a perfect connection between tastes and function of substances.

Basic Taste Qualities

Five basic taste qualities:

1. Salty
2. Sour
3. Sweet
4. Bitter
5. Umami - described as meaty, brothy or savory and associated with MSG.

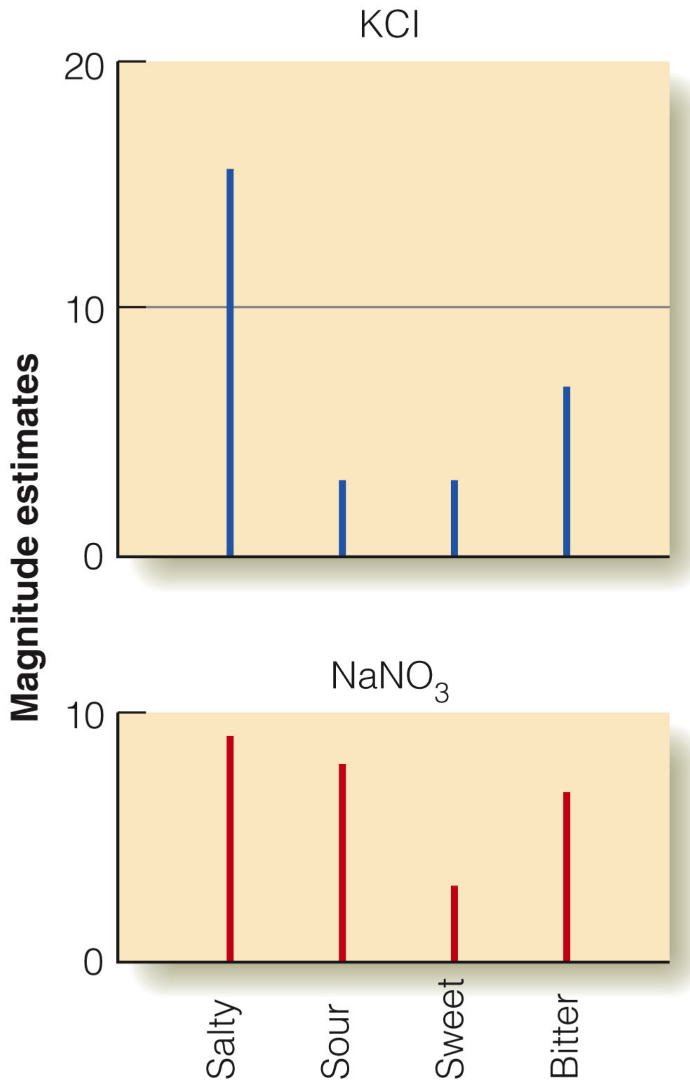


Figure 15.14 The contribution of each of the four basic tastes to the tastes of KCl and $NaNO_3$, determined by the method of magnitude estimation. The height of the line indicates the size of the magnitude estimate for each basic taste. (*From McBurney, 1969.*)

Structure of the Taste System

- Tongue contains papillae
  - 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 (cont.)

- Taste buds are located in papillae (except for filiform).
  - Tongue contains approximately 10,000 taste buds.
  - Each taste bud has 50-100 taste cells with tips that extend into the taste pore.
  - Transduction occurs when chemicals contact the receptor sites on the tips.

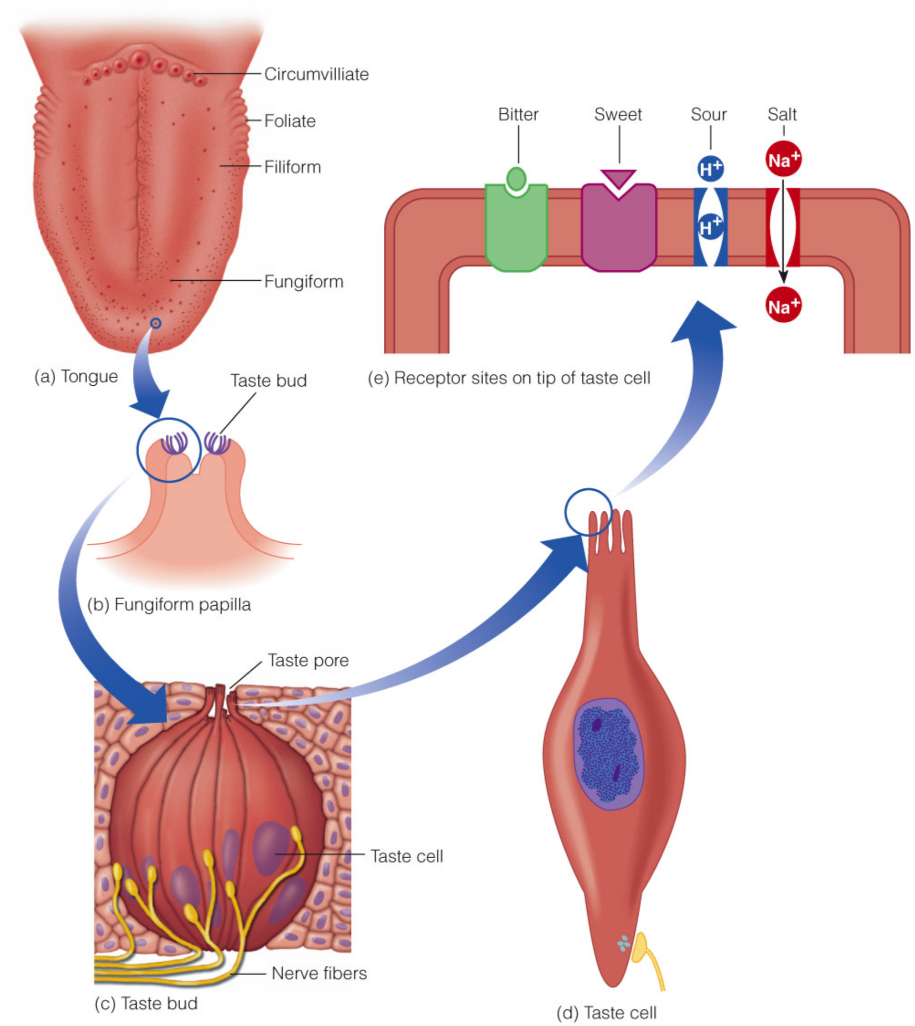


Figure 15.15 (a) The tongue, showing the four different types of papillae. (b) A fungiform papilla on the tongue; each papilla contains a number of taste buds. (c) Cross section of a taste bud showing the taste pore where the taste stimulus enters. (d) The taste cell; the tip of the taste cell is positioned just under the pore. (e) Close-up of the membrane of the tip of the taste cell, showing the receptor sites for bitter, sour, salty, and sweet substances. Stimulation of these receptor sites, as described in the text, triggers a number of different reactions within the cell (not shown) that lead to movement of charged molecules across the membrane, which creates an electrical signal in the receptor.

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.

Table 15.2 Structures in the taste system.

Structure of the Taste System (cont.)

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 (cont.)

- These pathways make connections in the nucleus of the 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

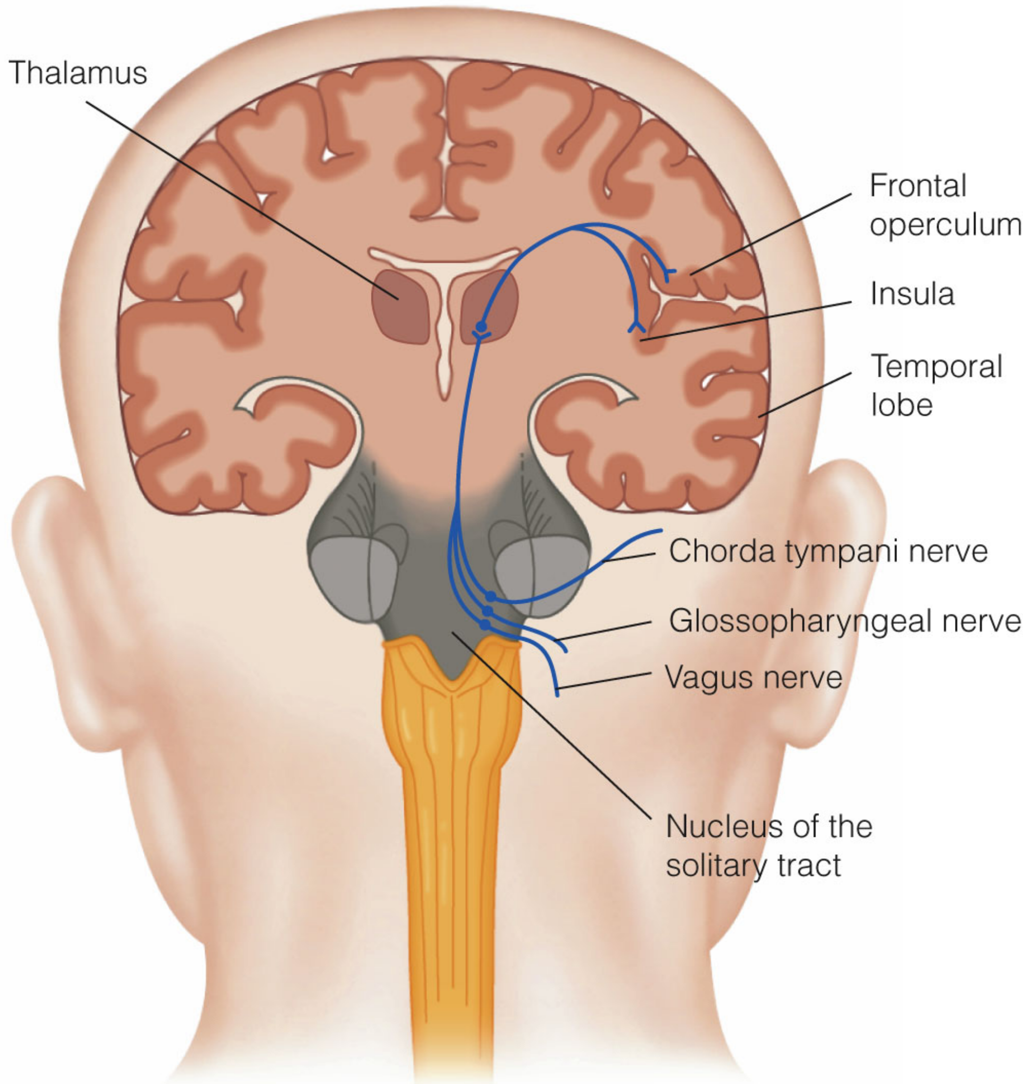


Figure 15.17 The central pathway for taste signals, showing the nucleus of the solitary tract (NST), where the nerve fibers from the tongue and the mouth synapse in the medulla at the base of the brain. From the NST, these fibers synapse in the thalamus and the frontal lobe of the brain. (*From Frank & Rabin, 1989.*)

Neural Coding for Taste

- Distributed coding (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 but different from sodium chloride (salt).

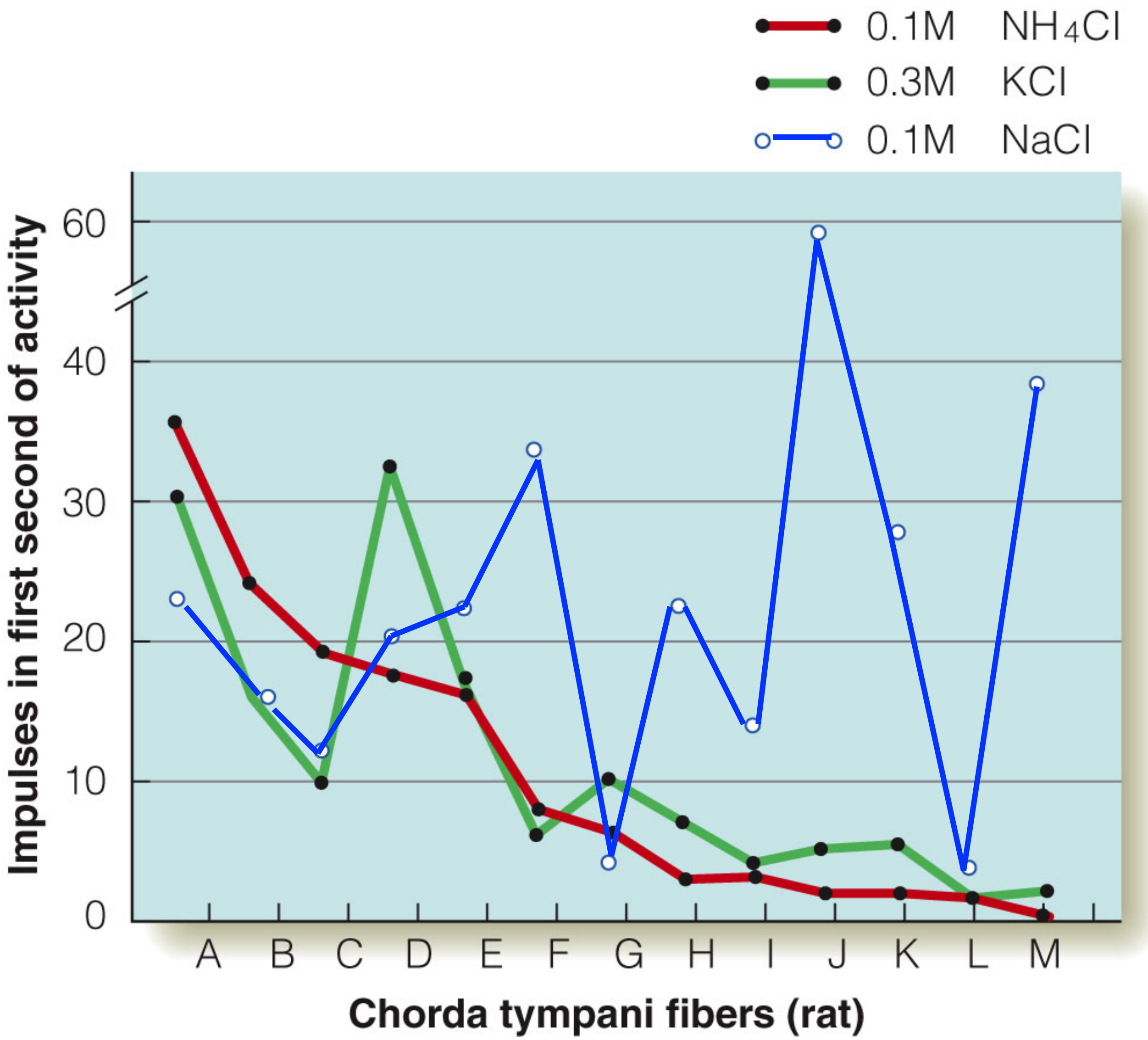


Figure 15.18 Across-fiber patterns of the response of fibers in the rat's chorda tympani nerve to three salts. Each letter on the horizontal axis indicates a different single fiber. (*From Erickson, 1963).*

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 (same pattern of neural response) and drank sodium chloride.
- The experiment provides convergent physiological and behavioral evidence for distributed coding.

Neural Coding for Taste (cont.)

- Specificity coding (Mueller et al.)
  - Genetic cloning was used to determine if mice could be created that possessed a human receptor that responds to PTC (bitter).
  - Normally, mice don't have this receptor or respond to this substance.
  - The experiment was successful. Further, it did not affect neural or behavioral response to other sweet, sour, salty or umami.

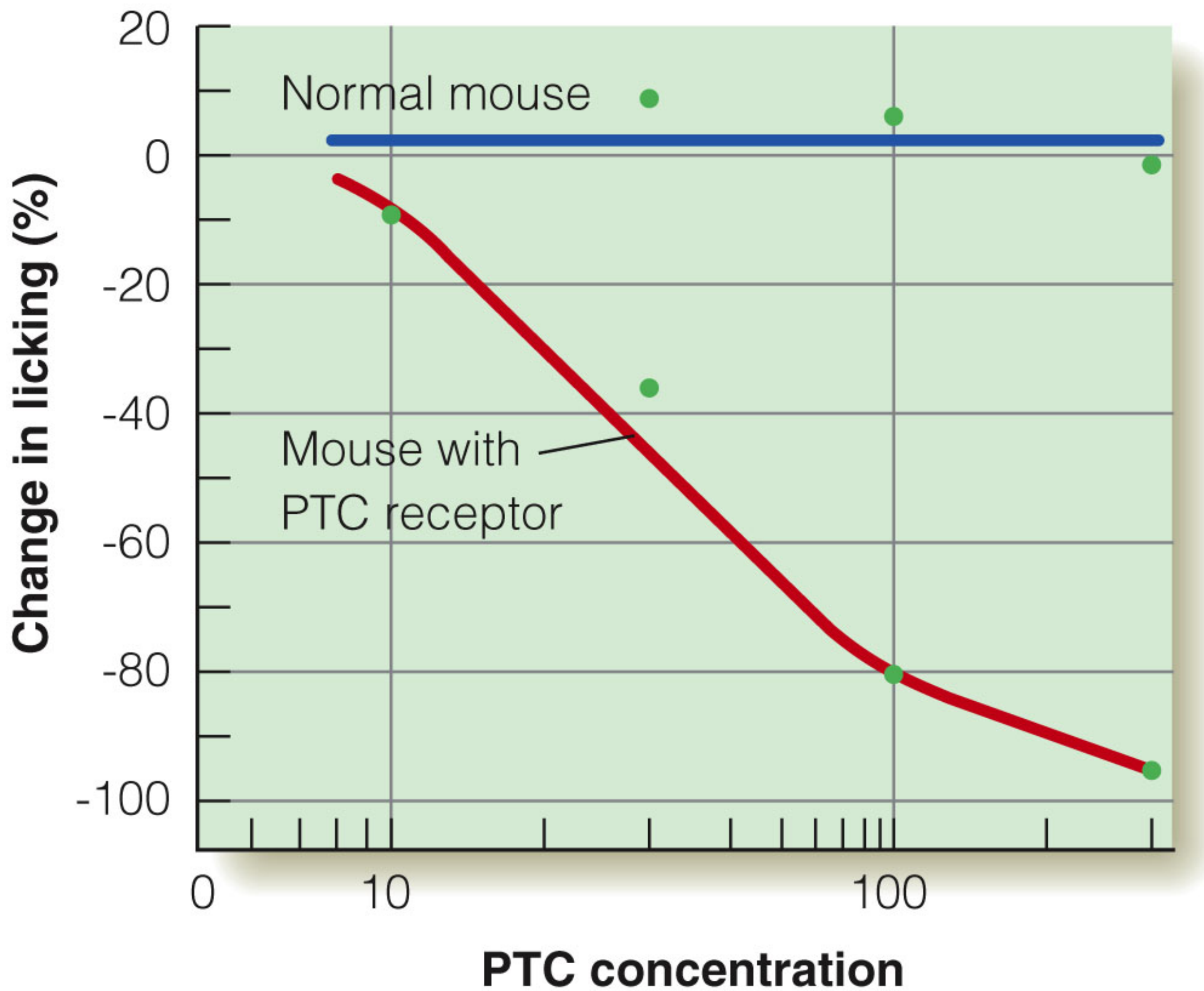


Figure 15.19 Mouse behavioral response to PTC. The blue curve indicates that a normal mouse will drink PTC even in high concentrations. The red curve indicates that a mouse that has a human bitter-PTC receptor avoids PTC, especially at high concentrations. (*Adapted from Mueller et al., 2005.*)

Neural Coding for Taste (cont.)

- 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.

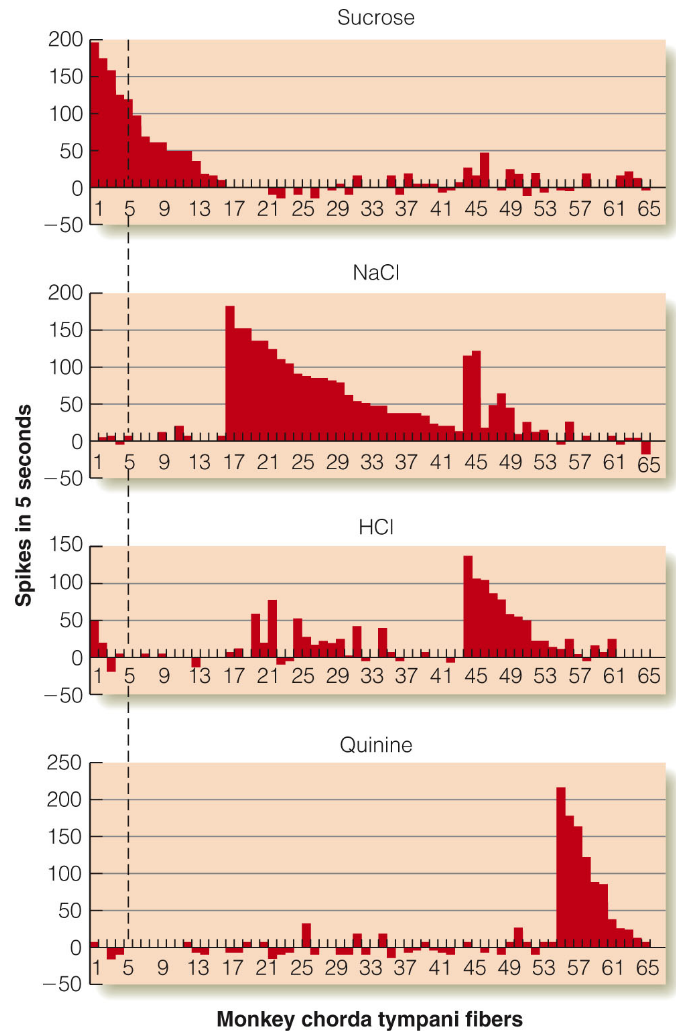


Figure 15.20 Responses of 66 different fibers in the monkey's chorda tympani nerve to four types of stimuli. To determine the response of a particular fiber, pick its number and note the height of the bars for each compound. For example, fiber 5 (dashed line) fired well to sucrose but didn't fire to any of the other compounds. Fiber 5 is therefore called a sucrose-best fiber. *(Adapted from Sato & Ogawa, 1993).*

Neural Coding for Taste - Summary

- 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

- 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. A few, such as MSG are not.

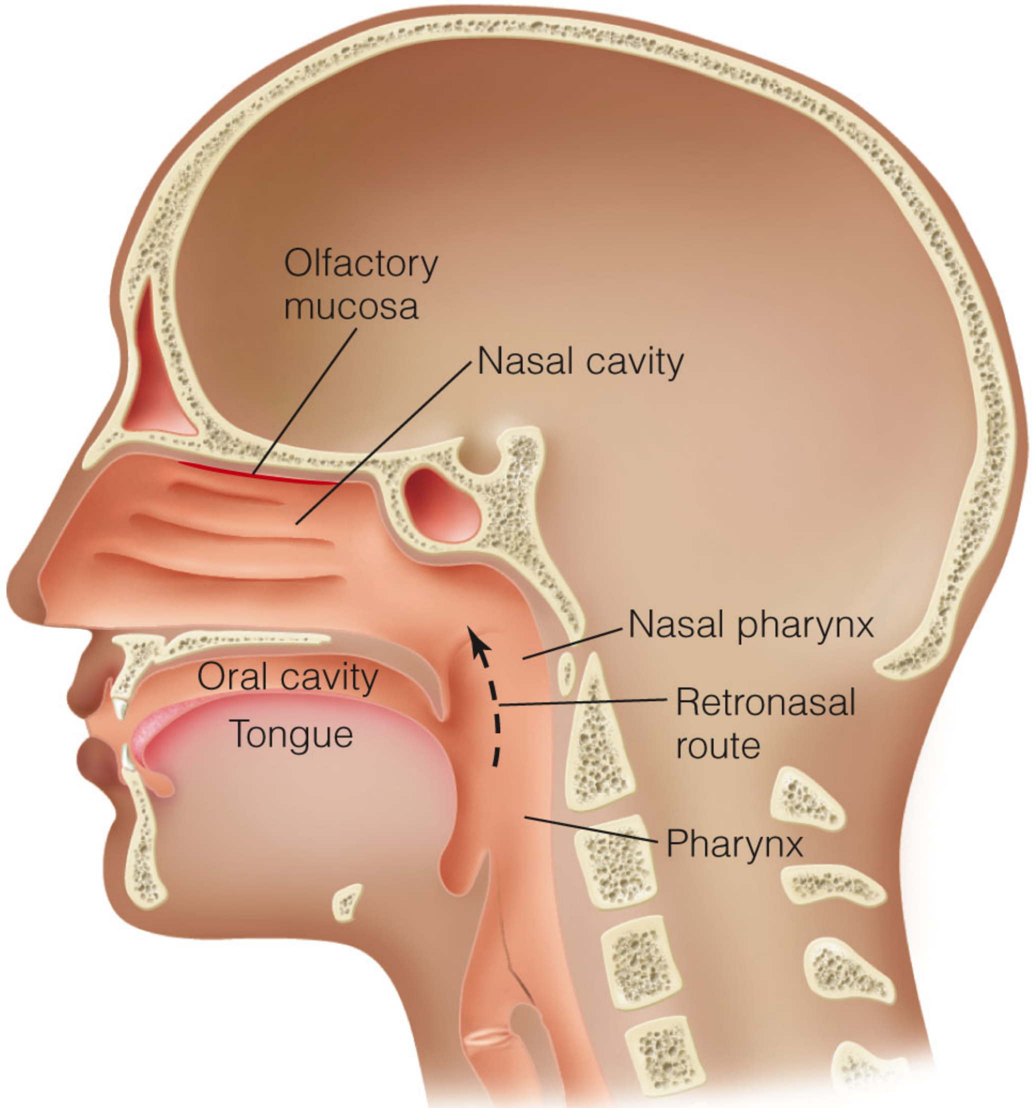


Figure 15.22 Odorant molecules released by food in the oral cavity and pharynx can travel though the nasal pharynx (dashed arrow) to the olfactory mucosa in the nasal cavity. This is the retronasal route to the olfactory receptors.

	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)	

Figure 15.23 How people described the flavors of three different compounds when they tasted them with nostrils clamped shut and with nostrils open. Each X represents the judgment of one person. (Adapted from Hettinger, Myers, & Frank, 1990)

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.
  - Bimodal neurons in this area respond to taste and smell, as well as taste and vision.
  - Firing of these neurons is also affected by the level of hunger of the animal for a specific food.

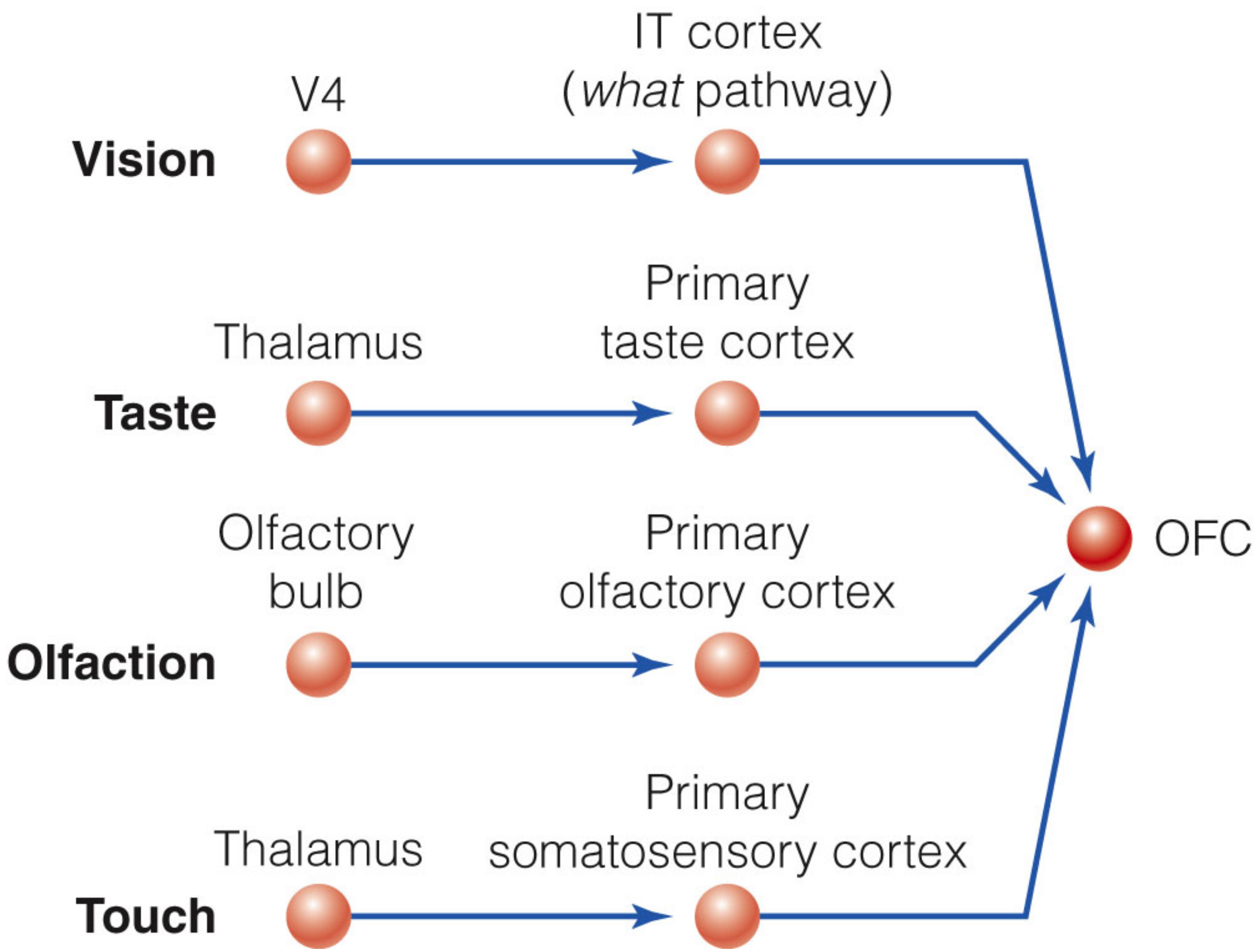


Figure 15.24 The orbital frontal cortex (OFC) receives inputs from vision, olfaction, and touch, as shown. It is the first area where signals from the taste and smell systems meet. (Adapted from Rolls, 2000)

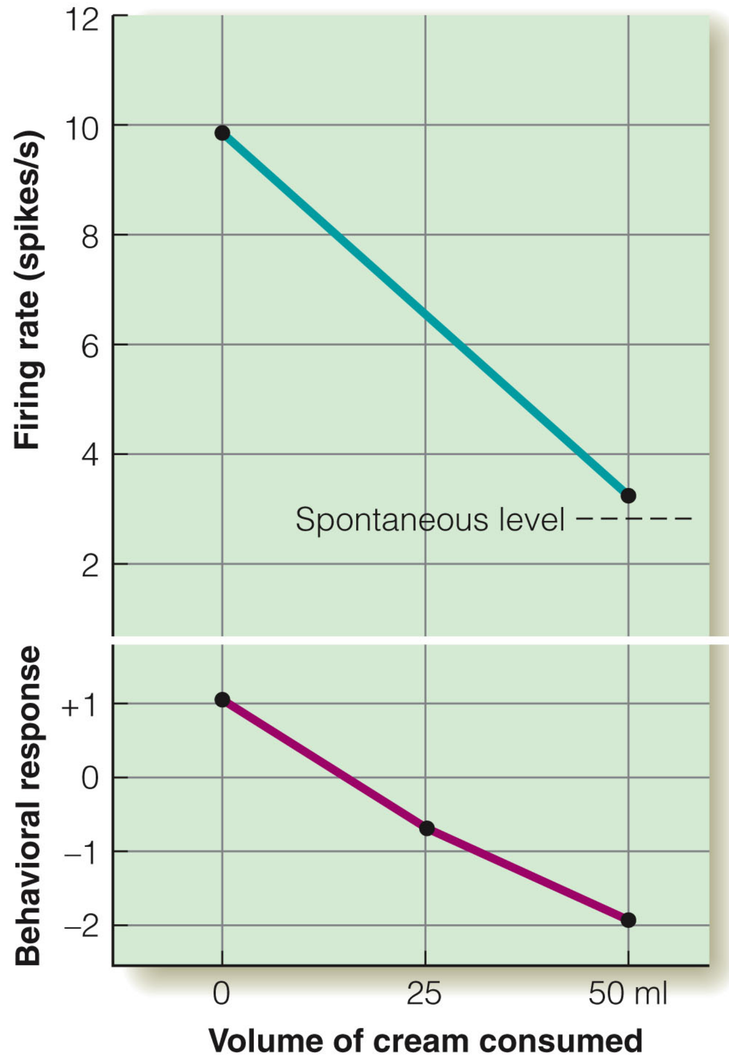


Figure 15.25 How consuming dairy cream affects the firing rate of neurons in the monkey's OFC (top panel) and the monkey's response to the cream (bottom panel). Consuming the cream causes a decrease in the neuron's response to the cream, but not to other substances (not shown). It also causes the monkey to become less interested in drinking the cream, and eventually to actively reject it. (*Adapted from Critchley & Rolls, 1996.*)

Individual Differences in Taste

- 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.