



Olfaction

ELL788

Date: 28th Sept. 2016

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

Even so, odors affect many aspects of our behavior:

Food selection

Mate choice

Reproductive cycles

Just how good are we at detecting odors?

Just how good are we at detecting odors?

- 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

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

Rats are 8 to 50 times more sensitive to odors than humans

Dogs are 300 to 10,000 times more sensitive

Why is a dog's sense of smell so much better than a human's?

Why is a dog's sense of smell so much better than a human's?

- 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

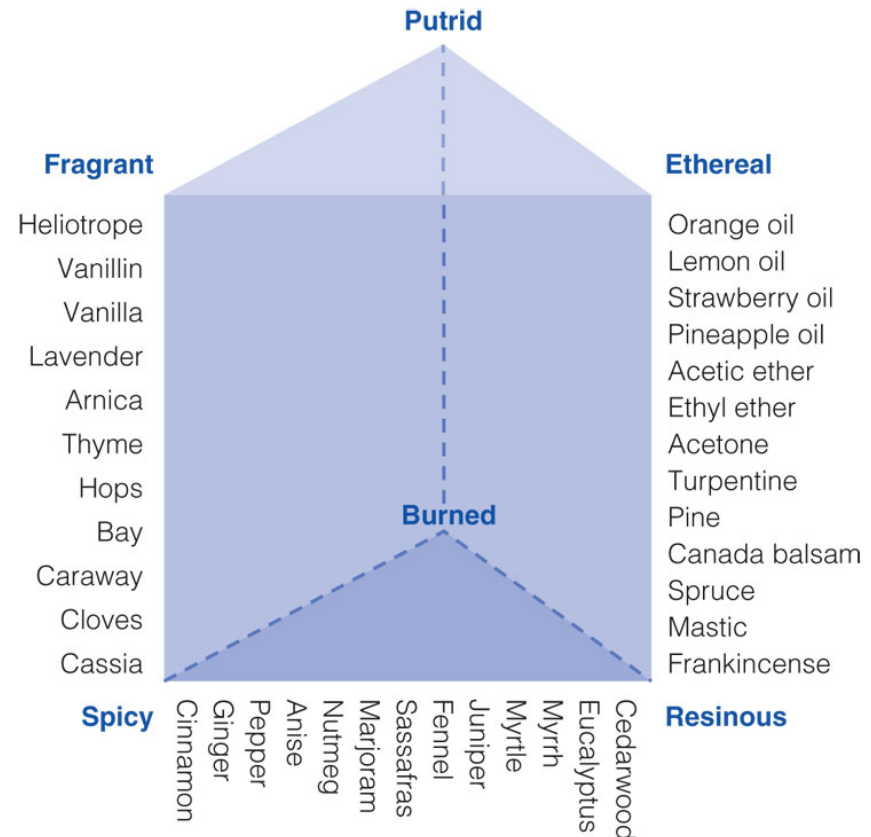
How well can we identify odors, beyond just detecting them?

How well can we identify odors, beyond just detecting them?

- Humans can discriminate among $> 10,000$ odors but they cannot label them accurately
- This appears to be caused by an inability to retrieve the name from memory
- We also do not seem to have the appropriate vocabulary for describing the quality of different odors.

Systems for describing odors

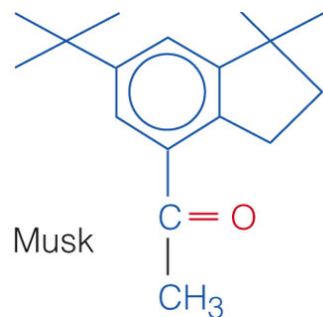
- Researchers have found it difficult to map perceptual experience onto physical attributes of odorants
- Henning's odor prism (1916)
 - 6 corners with the qualities putrid, ethereal, resinous, spicy, fragrant, and burned
 - Other odors located in reference to their perceptual relation to the corner qualities



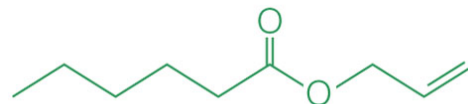
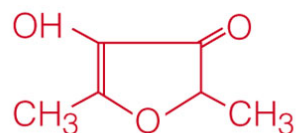
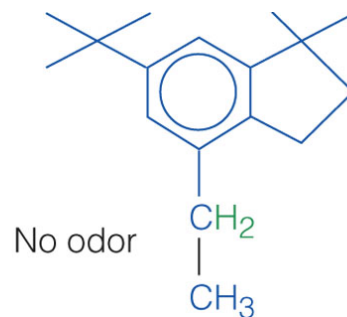
Systems for describing odors – contd.

- Unfortunately, Henning's prism has proven of little use in olfactory research because of inter-subject variability
- Can we directly link chemical structure to types of smells?
 - Initial attempts showed difficulties since:
 - Some molecules with similar shapes had very different smells
 - Some similar smells came from molecules with different shapes

Systems for describing odors – contd.



(a)



Both pineapple

(b)

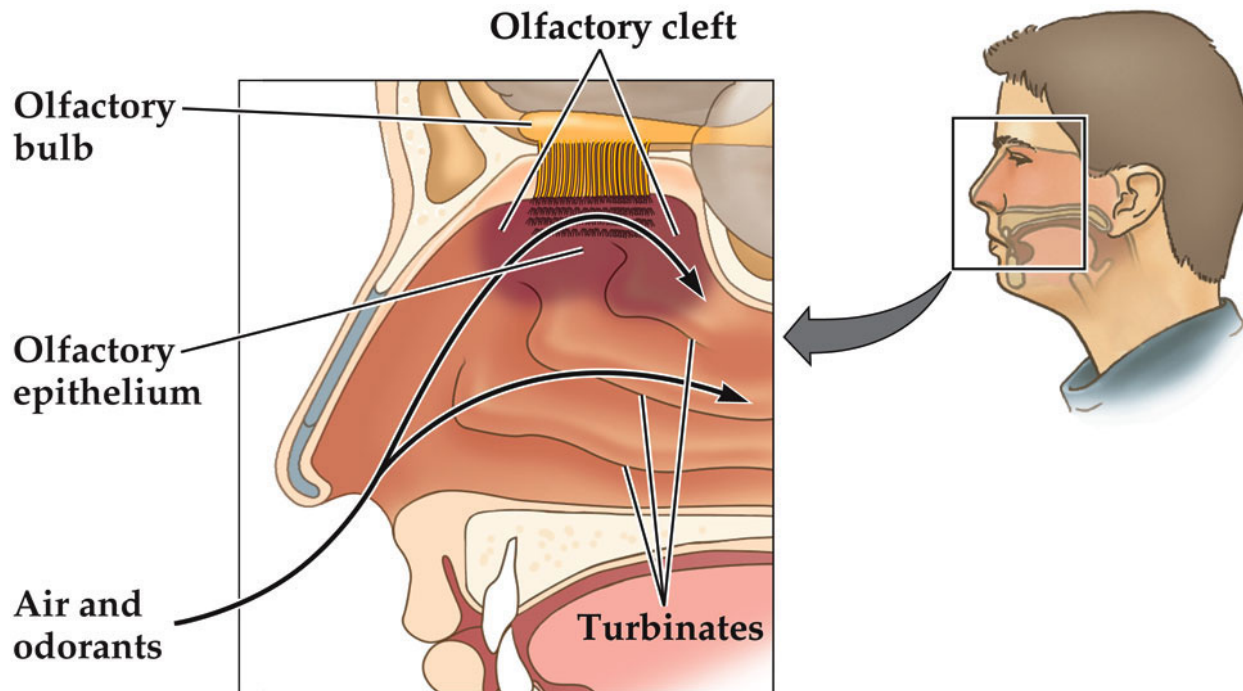
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(a) Two molecules that have similar structures, but one smells like musk and the other is odorless. (b) Two molecules with different structures but similar odors.

Relating physical properties to subjective smell perception is still an open issue

Olfactory Physiology

- Olfactory cleft: A narrow space at the back of the nose into which air flows, where the main olfactory epithelium is located
- Olfactory epithelium: A secretory mucous membrane in the human nose whose primary function is to detect odorants in inhaled air



Olfactory epithelium: The “retina” of the nose

- 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

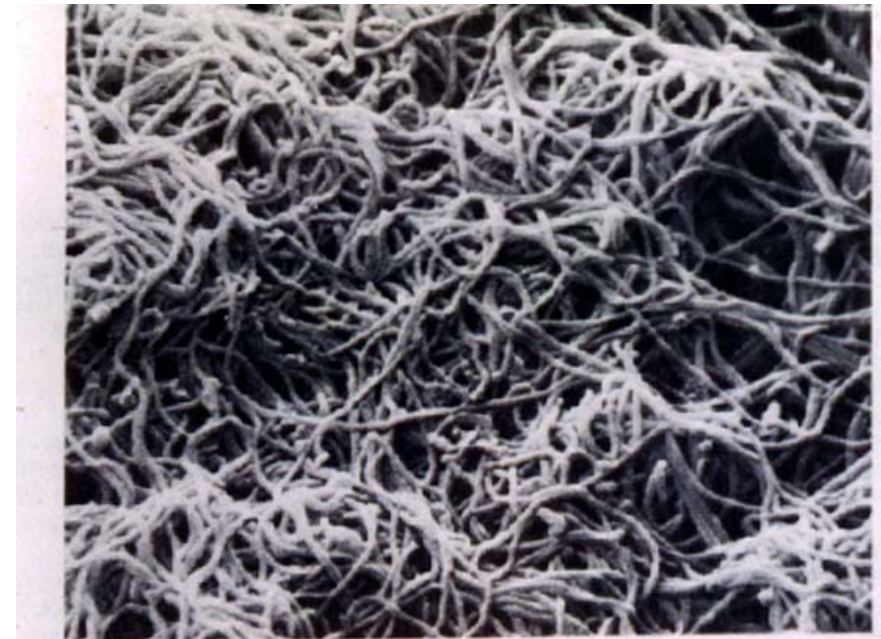
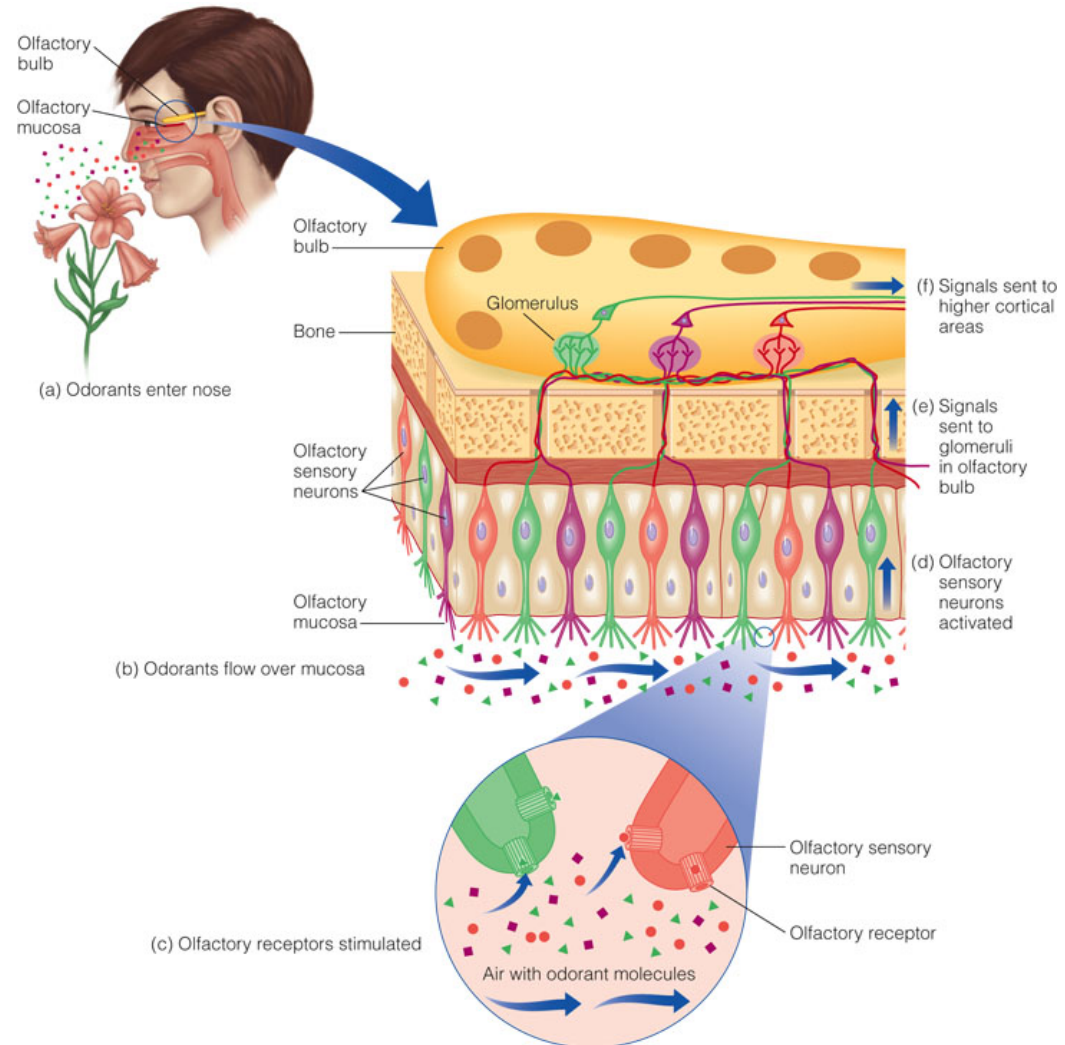


Fig. 17-11. Scanning electron photomicrograph of surface of olfactory epithelium of turtle showing numerous cilia. (Courtesy Dr. D. Tucker.)

The structure of the olfactory system

- Cilia: Hairlike protrusions on the dendrites of OSNs. Contain receptor sites for odorant molecules. These are the first structures involved in olfactory signal transduction
- Olfactory receptor (OR): The region on the cilia of OSNs where odorant molecules bind
 - Takes seven or eight odor molecules binding to a receptor to initiate an action potential



Olfactory Physiology

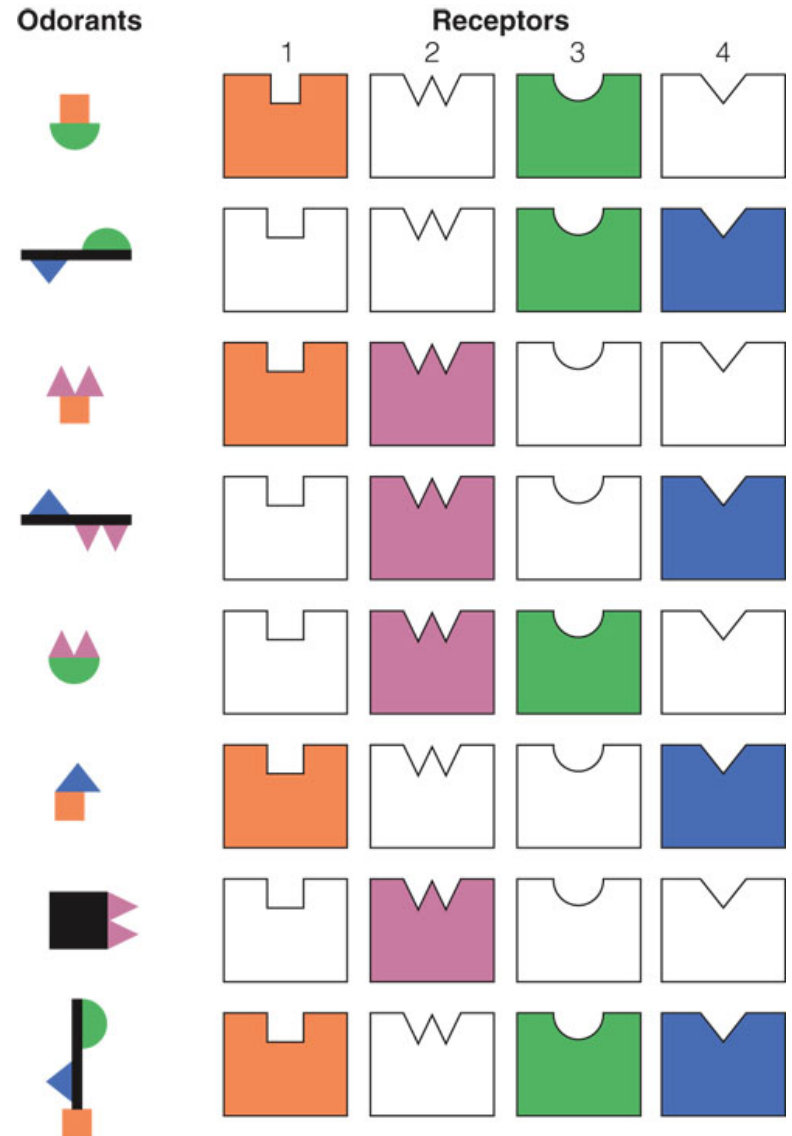
- Genetic basis of olfactory receptors:
 - Buck and Axel (1991): Genome contains about 1000 different olfactory receptor genes; each codes for a single type of OR
 - All mammals have pretty much the same set of 1000 genes. However, some genes are non-functional pseudogenes
 - Dogs and mice: About 20% are pseudogenes
 - Humans: Between 60%–70% are pseudogenes
 - ❖ Each person has a different number of pseudogenes, resulting in individual differences in sensitivity to smells
 - There may be an evolutionary trade-off between vision and olfaction

Olfactory Physiology

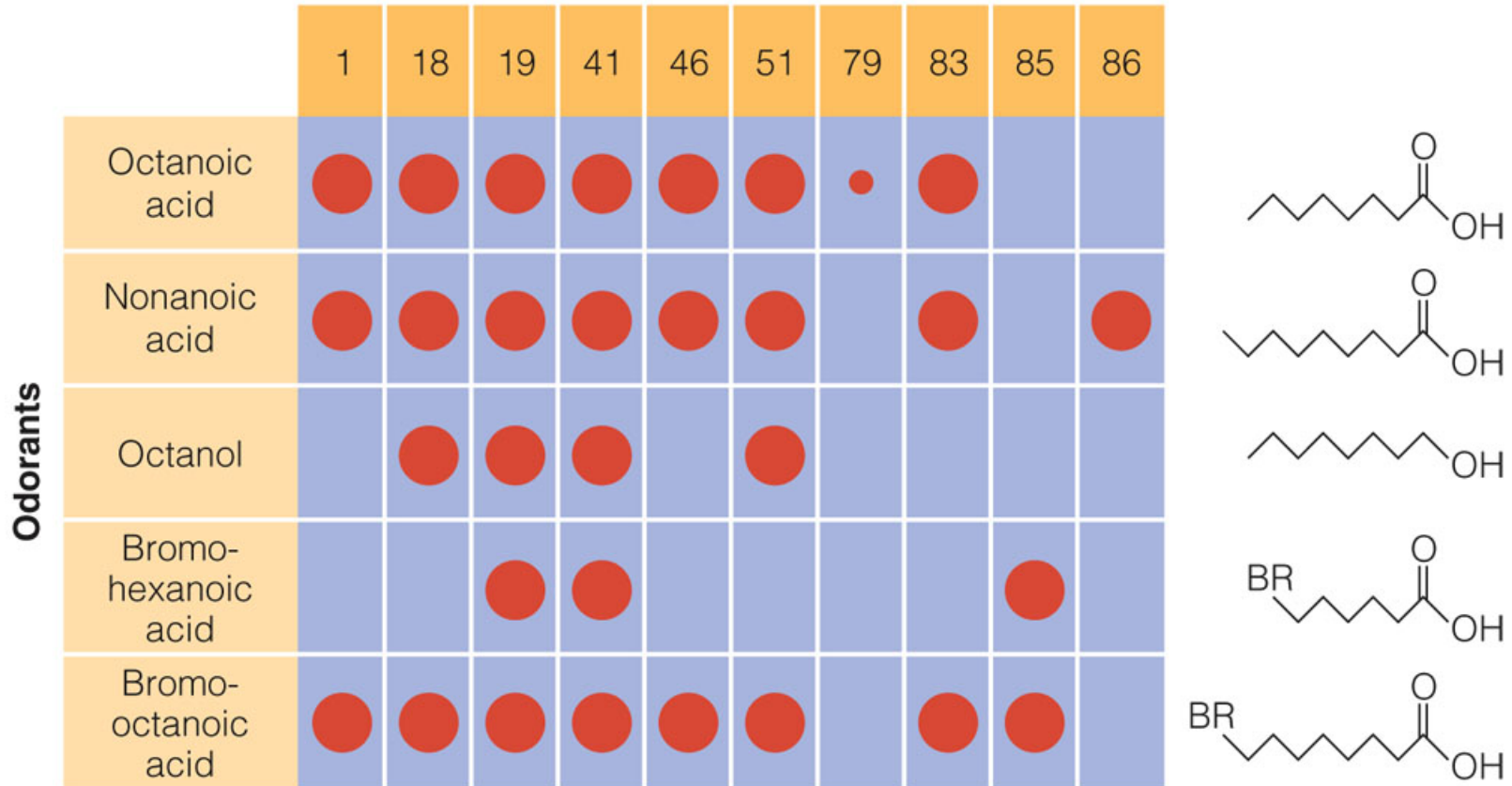
- Olfactory receptor cells are different from all other sensory receptor cells: They are not mediated by any protective barrier and make direct contact with the brain
 - Contrast with visual receptors that are protected by cornea, hearing receptors protected by eardrum, taste buds are buried in papillae
 - Therefore, many drugs can be inhaled
 - OSN axons are among the thinnest and slowest in the body
 - Takes longer to perceive odors compared to other senses

Activating Receptor Neurons

- Combinatorial code for odor
 - Odorants are coded by combinations of olfactory receptors called *recognition profiles*
 - Specific receptors may be part of the code for multiple odorants



Olfactory Receptors

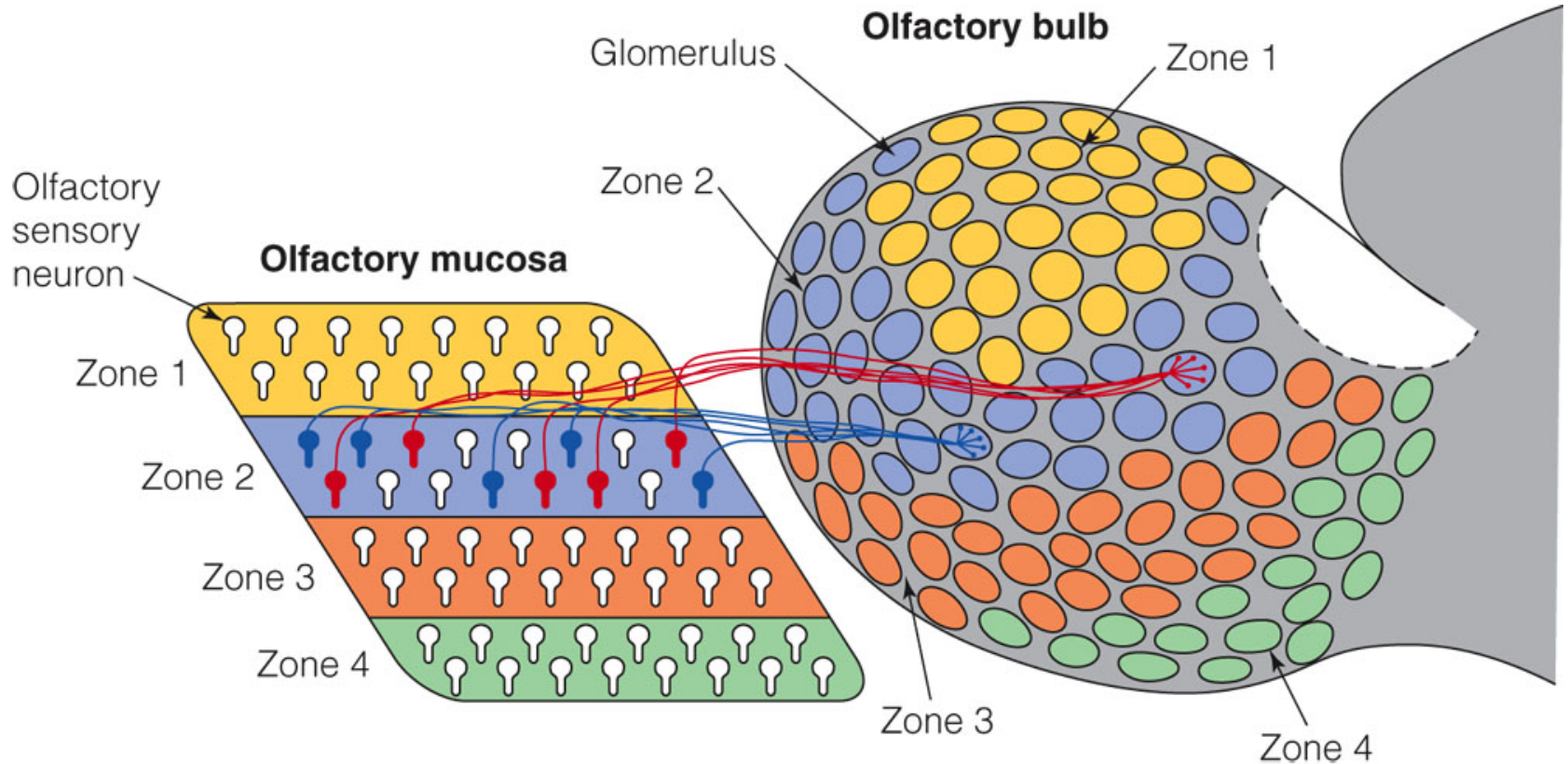


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Recognition profiles for some odorants. Large dots indicate that the odorant causes a high firing rate for the receptor listed along the top; small dots indicate lower firing rates for the receptor. The structures of the compounds are shown on the right.

The spatial pattern of activation is also reflected in the olfactory bulb

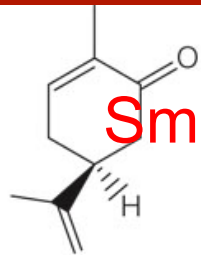
Activating the Olfactory Bulb



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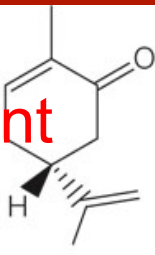
Organization of the olfactory mucosa. The olfactory mucosa, on the left, is divided into four zones. Each zone contains a mixture of different kinds of sensory neurons, as indicated by the red and blue neurons in Zone 2. However, a particular kind of sensory neuron is found only in one zone. The olfactory bulb, on the right, is also divided into zones. Each type of sensory neuron in the olfactory mucosa sends its axons to just one or two glomeruli in the olfactory bulb.

- 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

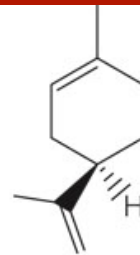


Smell different

(+)-Carvone

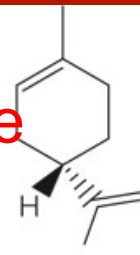


(-)-Carvone

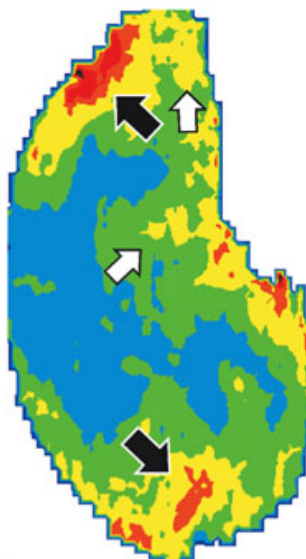


Smell same

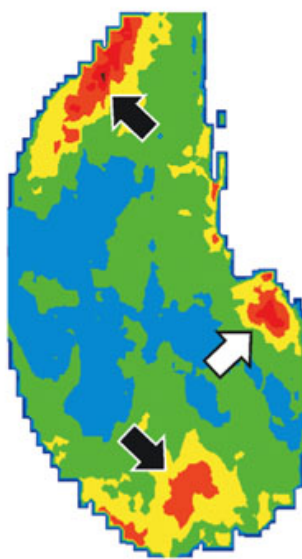
(+)-Limonene



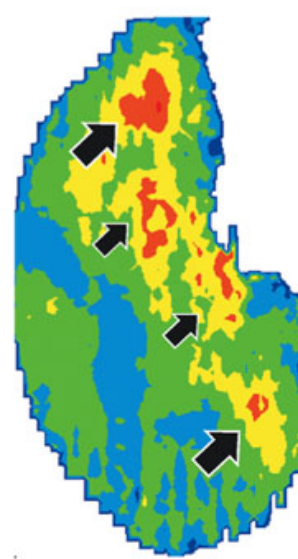
(-)-Limonene



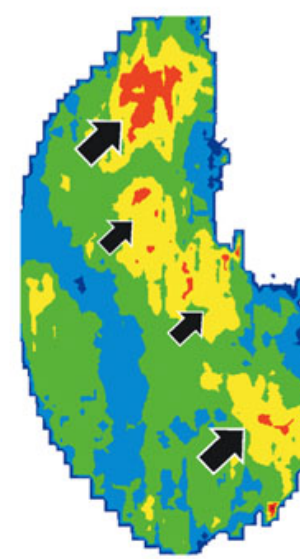
+Carvone



-Carvone



+Limonene



-Limonene

(a)

(b)

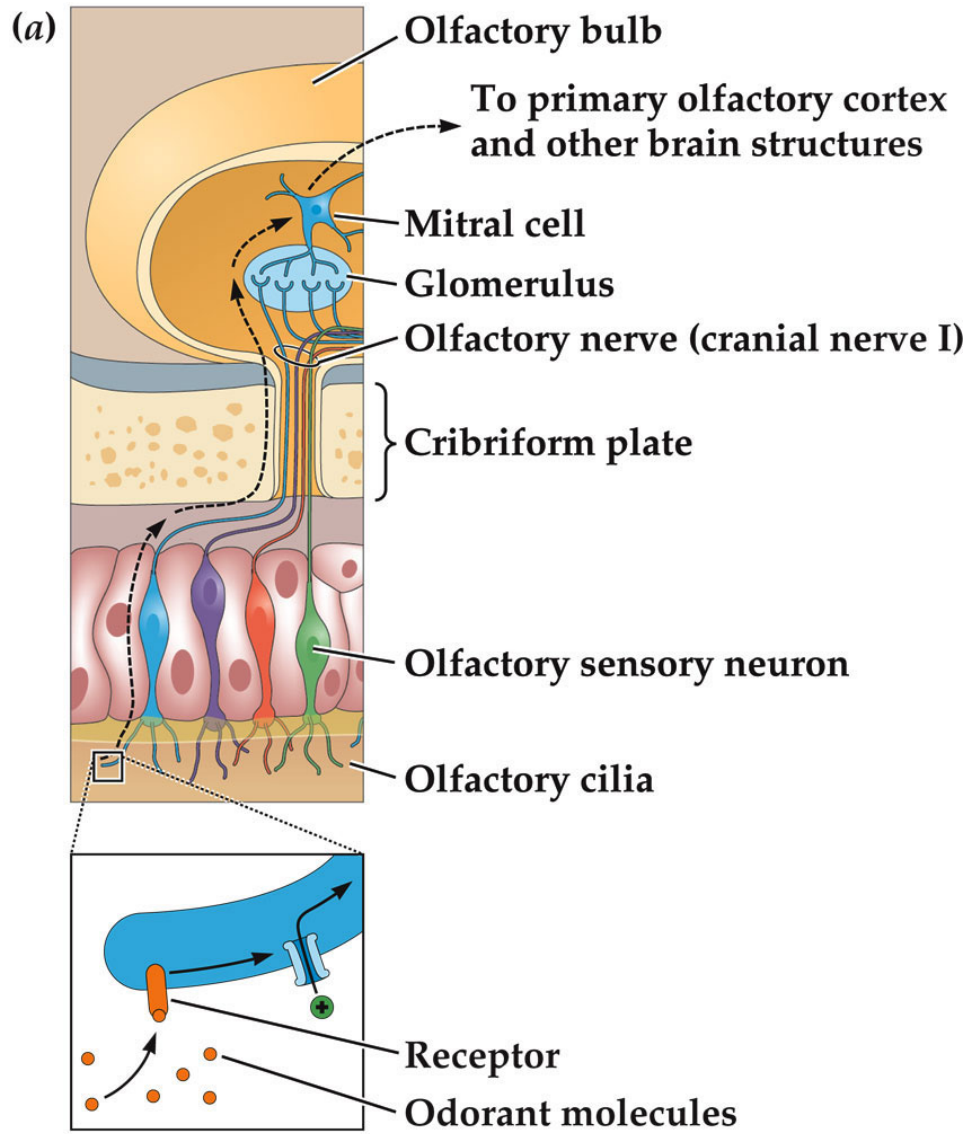
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Patterns of activation in the rat olfactory bulb. Red, orange, and yellow indicate high activation. (a) Top: two forms of carvone. These molecules have the same chemical formula, but the molecular group at the bottom is rotated to a different position. Bottom: activation patterns. The black arrows indicate areas activated by both compounds. The white arrows, which indicate areas activated by one compound but not the other, show that the two forms of carvone activate different areas in the olfactory bulb. (b) Top: two forms of limonene. Bottom: activation patterns. The black arrows indicate that the two forms of limonene activate similar areas in the olfactory bulb.

From Chemicals to Smells

- The importance of patterns
 - How can we detect so many different scents if our genes only code for about 1000 olfactory receptors?
 - We can detect the *pattern* of activity across receptors
 - Intensity of odorant also changes which receptors will be activated
 - Weak concentrations of an odorant may not smell the same as strong concentrations
 - Specific time order of activation of OR receptors is important

From the olfactory epithelium to the olfactory bulb



SENSATION & PERCEPTION 3e, Figure 14.6 (Part 1)
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What happens beyond the olfactory bulb?

(b)

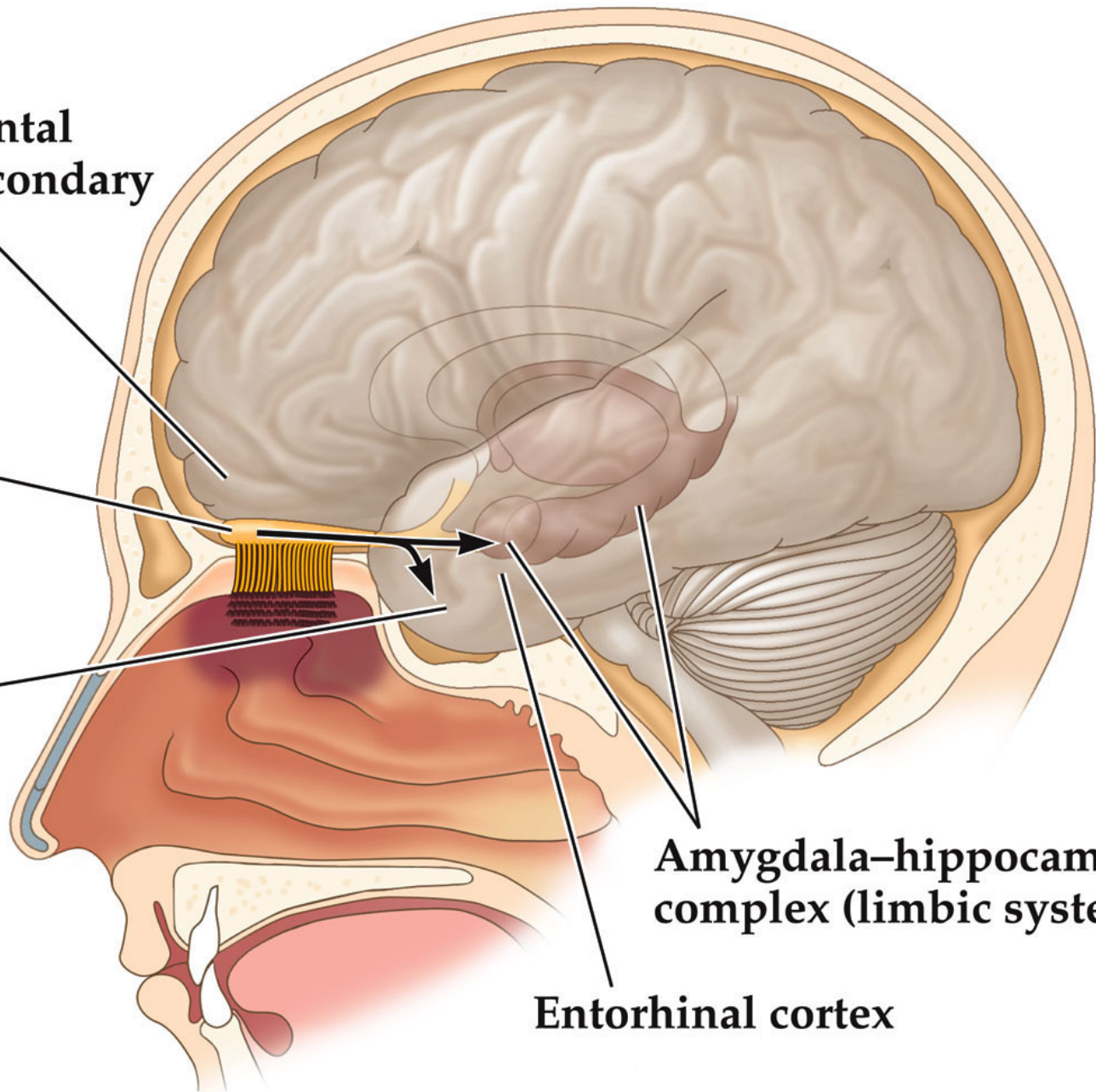
Orbitofrontal
cortex (secondary
olfactory
cortex)

Olfactory
bulb

Primary
olfactory
cortex

Amygdala–hippocampal
complex (limbic system)

Entorhinal cortex

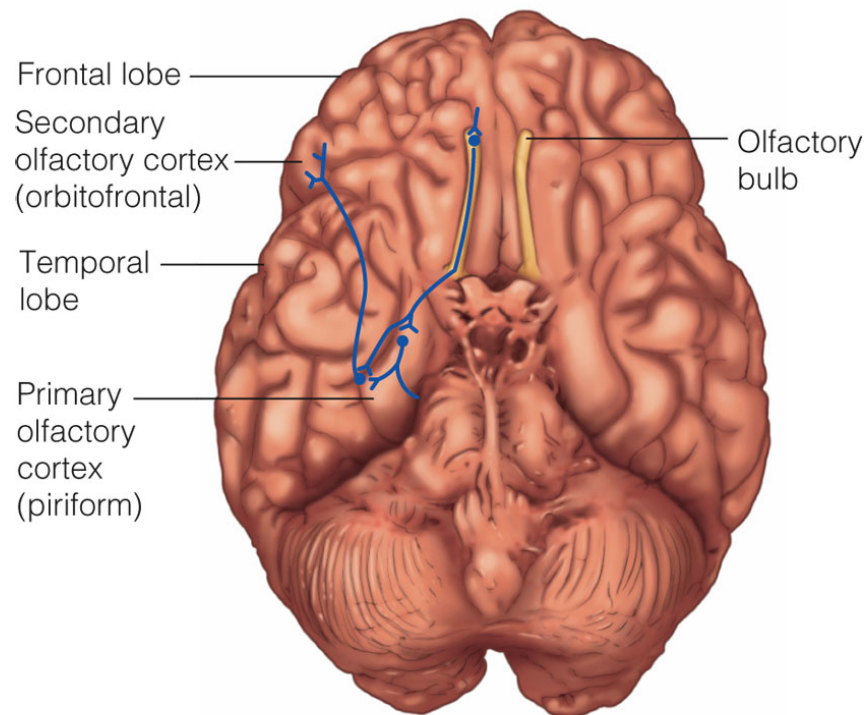


Olfactory Physiology

- Cribriform plate: A bony structure riddled with tiny holes, at the level of the eyebrows, that separates the nose from the brain
 - Axons from OSNs pass through the tiny holes to enter the brain
- Anosmia: The total inability to smell, most often resulting from sinus illness or head trauma
 - A hard blow to the front of the head can cause the cribriform plate to be jarred back or fractured, slicing off the fragile olfactory neurons
 - Anosmia causes a profound loss of taste as well as smell

Beyond the olfactory bulb

- 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



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Olfaction's direct connection to the limbic system, which is involved in many aspects of memory and emotion, explains why scents tend to have such strong emotion associations and also why aromatherapy can be effective.

(Aromatherapy: The contention that odors can influence, improve, and alter mood, performance, and well-being, as well as the physiological correlates of emotion such as heart rate, blood pressure, and sleep.)

Olfaction summary:

Odors are detected by receptors in the mucosa and are represented via a combinatorial code across the 350 different kinds of receptors.

Different smells lead to different patterns of activation in the olfactory bulb.

- Pheromones and chemosignals
- Odor hedonics
- Cross-modal influences

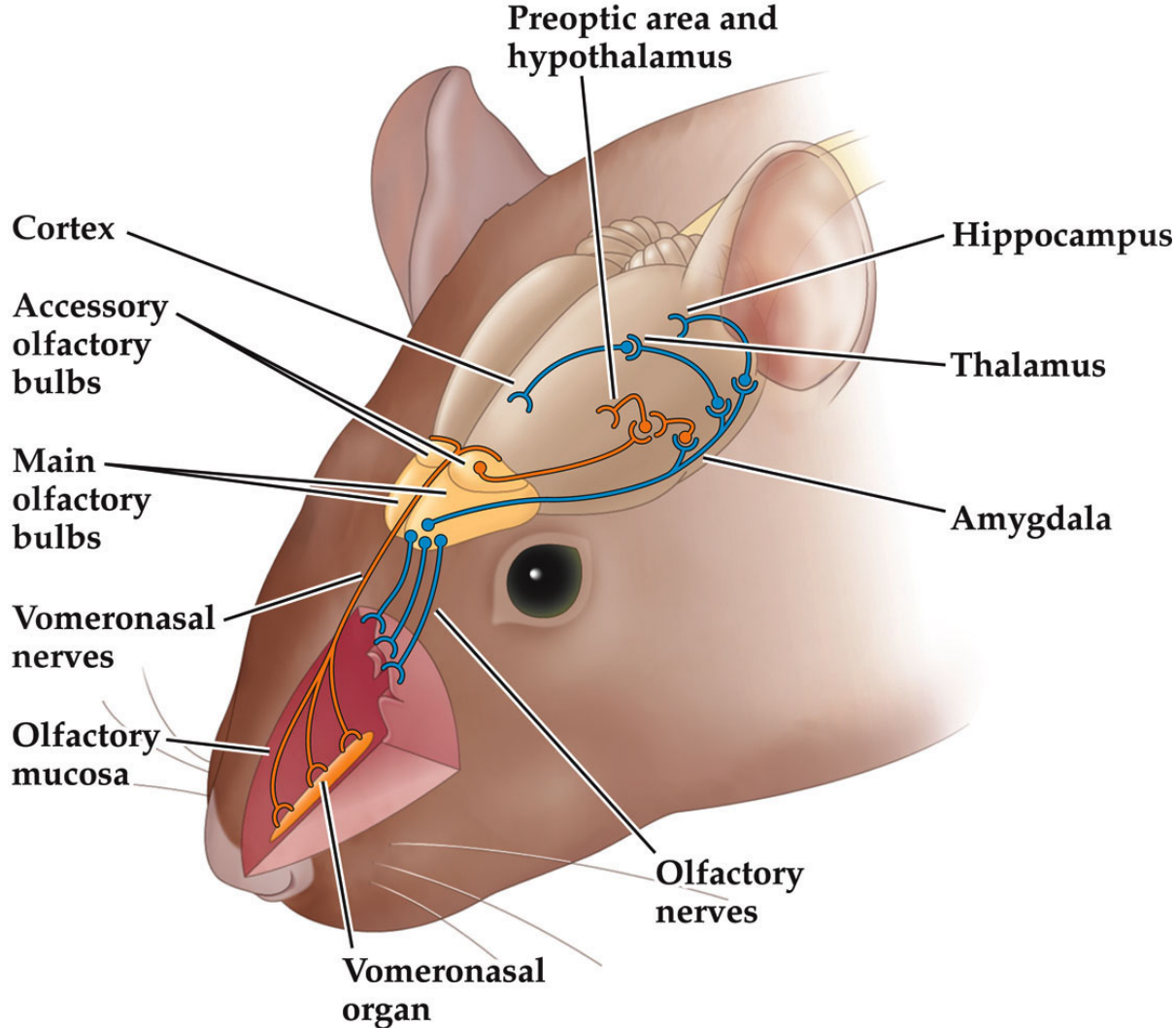
Pheromones and Chemosignals

- Animals that rely on smell for survival: Olfactory system has two subdivisions:
 - Main olfactory bulb (MOB): The structure that we have been referring to as the “olfactory bulb,” but for animals that have two olfactory bulbs we use this term
 - Accessory olfactory bulb (AOB): A smaller neural structure located behind the MOB that receives input from the vomeronasal organ

Pheromones and Chemosignals

- Vomeronasal organ (VNO): A chemical sensing organ at the base of the nasal cavity with a curved tubular shape
 - Evolved to detect chemicals that cannot be processed by the olfactory epithelium, such as large and/or aqueous molecules—the types of molecules that constitute pheromones
- Pheromone: A chemical emitted by one member of a species that triggers a physiological or behavioral response in another member of the same species
 - Pheromones are signals for chemical communication and do not need to have any smell

Pheromones and Chemosignals



SENSATION & PERCEPTION 3e, Figure 14.19
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Pheromones and Chemosignals

- Pheromones are most important for communication in the social insects, like ants, termites, and bees, but also convey important information for many non-insect species, including some primates
 - Often provide signals to males about when a female is fertile and provide signals to males to initiate sexual behavior
 - Male rhesus monkey will ignore a female rhesus monkey in heat if his nose is blocked
 - A female sow will not go into lordosis (the position necessary for impregnation) if she isn't exposed to the male pig pheromone androstenone

Pheromones and Chemosignals

- Do humans respond to pheromones?
 - McClintock effect: Women who are in physical proximity (e.g., live together) over time start to have menstrual cycles that coincide
 - Martha McClintock first identified effect while an undergraduate
 - Women who move into a college dorm together will likely have their menstrual cycles synchronized by winter break



Underarm secretions were collected from 9 donor women

These were wiped on the upper lips of recipient women

Pheromones and Chemosignals

- Results showed that menstrual synchrony occurred in experimental but not control groups
- This suggests that pheromones in the secretions, even though the women did not report smelling them, led to the changes

Pheromones and Chemosignals

- Controversy over the McClintock effect
 - Yang and Schank (2006) failed to observe the phenomenon in Chinese students
 - If the effect does exist, there are doubts about whether the hormonal information is communicated through smell or touch

Pheromones and Chemosignals

- Perhaps a more theory-neutral word than “pheromone” should be used when discussing humans
 - Chemosignal: Any of various chemicals emitted by humans that are detected by the olfactory system and that may have some effect on the mood, behavior, hormonal status, and/or sexual arousal of other humans

Pheromones and Chemosignals

- Do humans respond to chemosignals?
 - Professional exotic lap dancers earn almost twice as much in tips (\$335/night versus \$185/night) during the ovulatory phase of their menstrual cycle
 - Dancers taking birth control pills showed no change in tips over their cycle
 - Dancers not taking birth control pills earned more, overall, than those who did
 - Dancers may have been *perceived* as more attractive to their male customers, increasing their tips

Pheromones and Chemosignals

- Do humans respond to chemosignals? (cont' d)
 - Not all chemosignals increase sexual desire
 - Chemicals present in female tears dampen the sexual desire of men
 - Testosterone levels decreased in the men who smelled the tears, which would also make them less aggressive towards a crying woman
 - Note that the tears were on a strip of paper and the men had no idea what chemical they were sniffing

Pheromones and Chemosignals

<http://www.youtube.com/watch?v=QxTuQI7YtCg>

<http://www.youtube.com/watch?v=aSZajwsq1mM>

Olfactory Hedonics

- Odor hedonics: The liking dimension of odor perception, typically measured with scales pertaining to an odorant's perceived pleasantness, familiarity, and intensity
- Nature or nurture?
 - Are hedonic responses to odors innate or learned?
Debate over this
 - Evidence from infants: Odor preferences often very different from adults
 - Cross-cultural data support associative learning
 - An evolutionary argument: Some animals exhibit an instinctive aversion to smells from predators, etc.
 - Learned taste aversion: Avoidance of a novel flavor after it has been paired with gastric illness

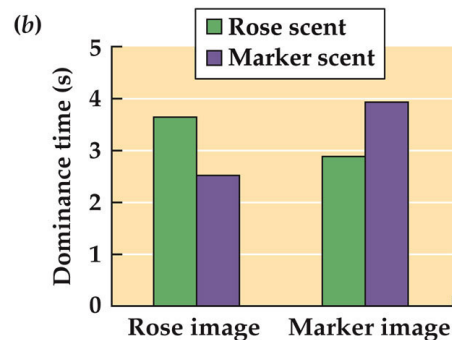
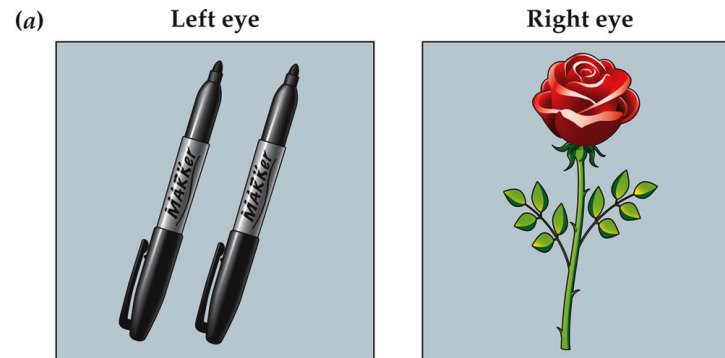
The Japanese eat *natto*, but Westerners do not equate the smell of this food with eating. Cheese, which most Westerners enjoy, is considered disgusting by most Japanese eaters



SENSATION & PERCEPTION 3e, Figure 14.16
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Cross-modal influences

- What we smell can affect what we see (Zhou et al., 2010)
 - Binocular rivalry stimulus of markers in one eye and rose in the other
 - Subjects switch back and forth between seeing one or the other stimulus
 - When the smell of markers or roses was presented to their nostrils, subjects saw the corresponding stimulus more often



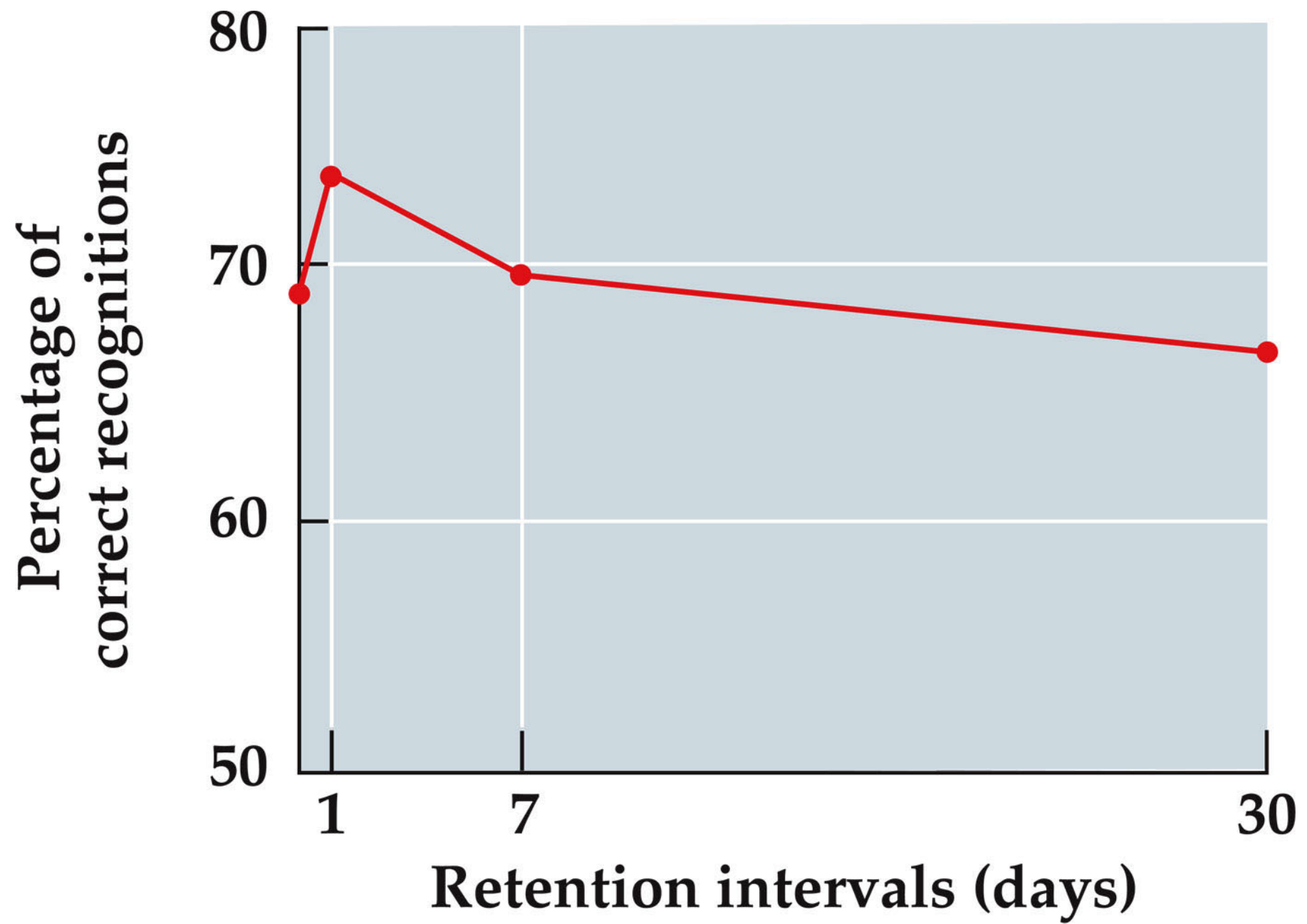
From Chemicals to Smells

- Odor imagery
 - Humans have little or no ability to conjure odor “images”
 - We do not think in smell very well
 - We do not imagine smells very well—dreams with olfactory sensations are very rare
 - Other animals for whom smell plays a more central role, such as rats, may very well think and dream smells

Olfactory Psychophysics, Identification, and Adaptation

- Detection, discrimination, and recognition
 - How much stimulation is required before we perceive something to be there?
 - Olfactory detection thresholds: Depend on several factors
 - Women: Generally lower thresholds than men, especially during ovulatory period of menstrual cycles, but sensitivity is *not* heightened during pregnancy
 - Professional perfumers and wine tasters can distinguish up to 100,000 odors
 - Age: By 85, 50% of population effectively anosmic
 - Durability: Our recognition of smells is durable even after several days, months, or years

Figure 14.13 Long-term memory for smells



Olfactory Psychophysics, Identification, and Adaptation

- Identification
 - Attaching a verbal label to a smell is not always easy
 - Tip-of-the-nose phenomenon: The inability name an odorant, even though it is very familiar
 - Contrary to tip-of-the-tongue phenomenon, one has no lexical access to the name of the odorant, such as first letter, rhyme, number of syllables, etc.
 - One example of how language and olfactory perception are deeply disconnected
 - Anthropologists have found that there are fewer words for experiences of smells compared to other sensations

Olfactory Psychophysics, Identification, and Adaptation

- Sense of smell and language: Disconnected, possibly because:
 - Olfactory information is not integrated in thalamus prior to processing in cortex
 - Majority of olfactory processing occurs in right side of brain while language processing occurs in left side of brain

Olfactory Psychophysics, Identification, and Adaptation

- Adaptation
 - Sense of smell is essentially a change detector
 - Examples: Walking into a bakery and can only smell fresh bread for a few minutes; someone who wears perfume every day cannot smell it and might put on a lot
 - Receptor adaptation: The biochemical phenomenon that occurs after continuous exposure to an odorant, whereby the receptors stop responding to the odorant and detection ceases

Olfactory Psychophysics, Identification, and Adaptation

- Adaptation
 - Cross-adaptation: The reduction in detection of an odorant following exposure to another odorant
 - Presumed to occur because the two odors share one or more olfactory receptors for their transduction, but the order of odorants also plays a role

Figure 14.14 Do these five fragrances smell the same?



SENSATION & PERCEPTION 3e, Figure 14.14

Olfactory Psychophysics, Identification, and Adaptation

- Cognitive habituation: The psychological process by which, after long-term exposure to an odorant, one is no longer able to detect that odorant or has very diminished detection ability
 - Example: Going out of town, coming back and noticing how your house smells
- Three mechanisms involved:
 - Olfactory receptors internalized into cell bodies during odor adaptation may be hindered after continuous exposure, take longer to recycle
 - Odorant molecules may be absorbed into bloodstream, causing adaptation to continue
 - Cognitive-emotional factors