14

Olfaction

- Olfactory Physiology
- Neurophysiology of Olfaction
- From Chemicals to Smells
- Olfactory Psychophysics, Identification, and Adaptation
- Olfactory Hedonics
- Associative Learning and Emotion: Neuroanatomical and Evolutionary Considerations

Introduction

Olfaction: The sense of smell

Gustation: The sense of taste

Olfactory Physiology

Odor: The translation of a chemical stimulus into a smell sensation.

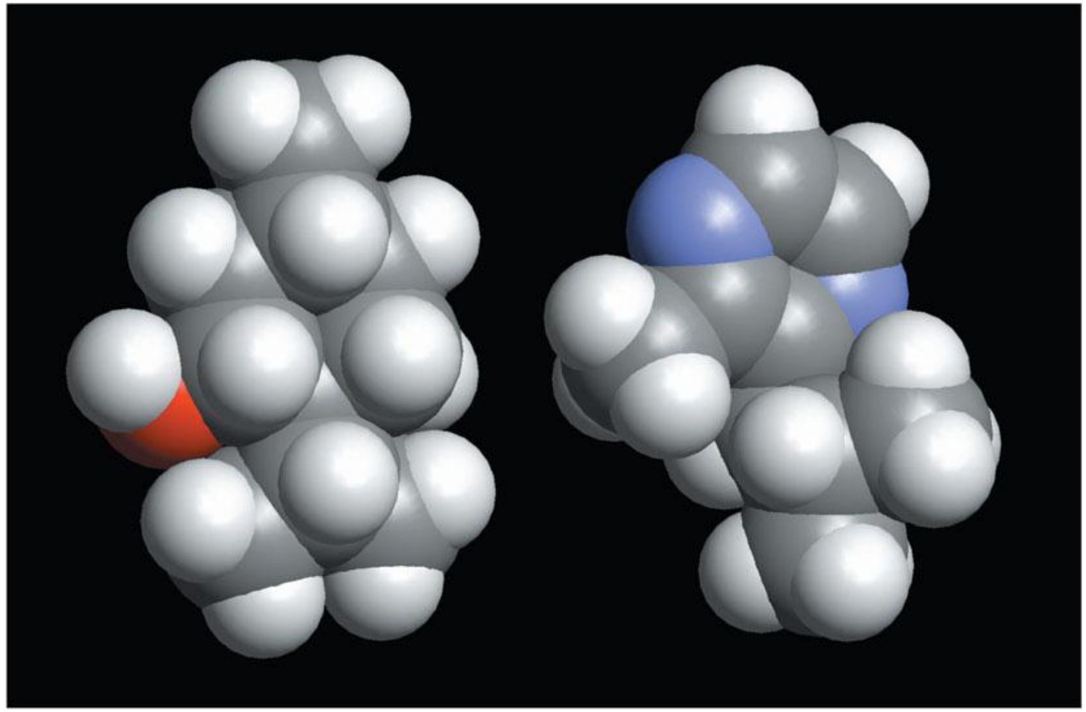
Odorant: A molecule that is defined by its physiochemical characteristics, which are capable of being translated by the nervous system into the perception of smell.

To be smelled, odorants must be:

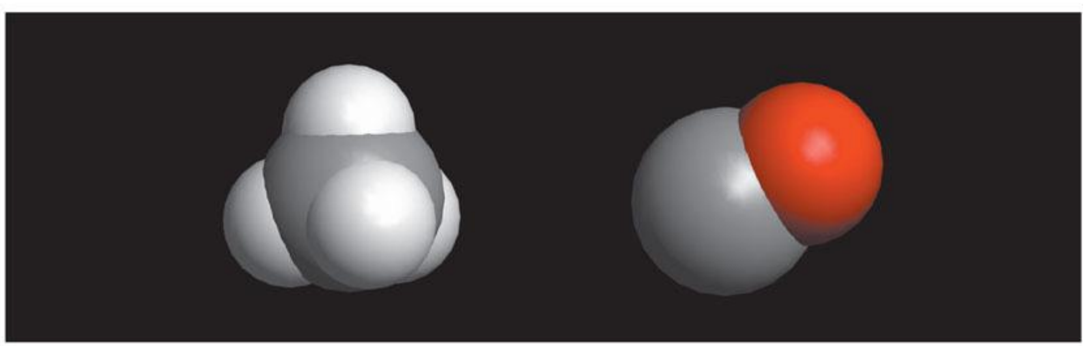
- Volatile (able to float through the air)
- Small
- Hydrophobic (repellent to water)

Figure 14.1 Odorants

(*a*) Menthol — Isobutylmethoxypyrazine (green bell pepper)



(*b*) Methane — Carbon monoxide



***SENSATION & PERCEPTION 4e*, Figure 14.1**

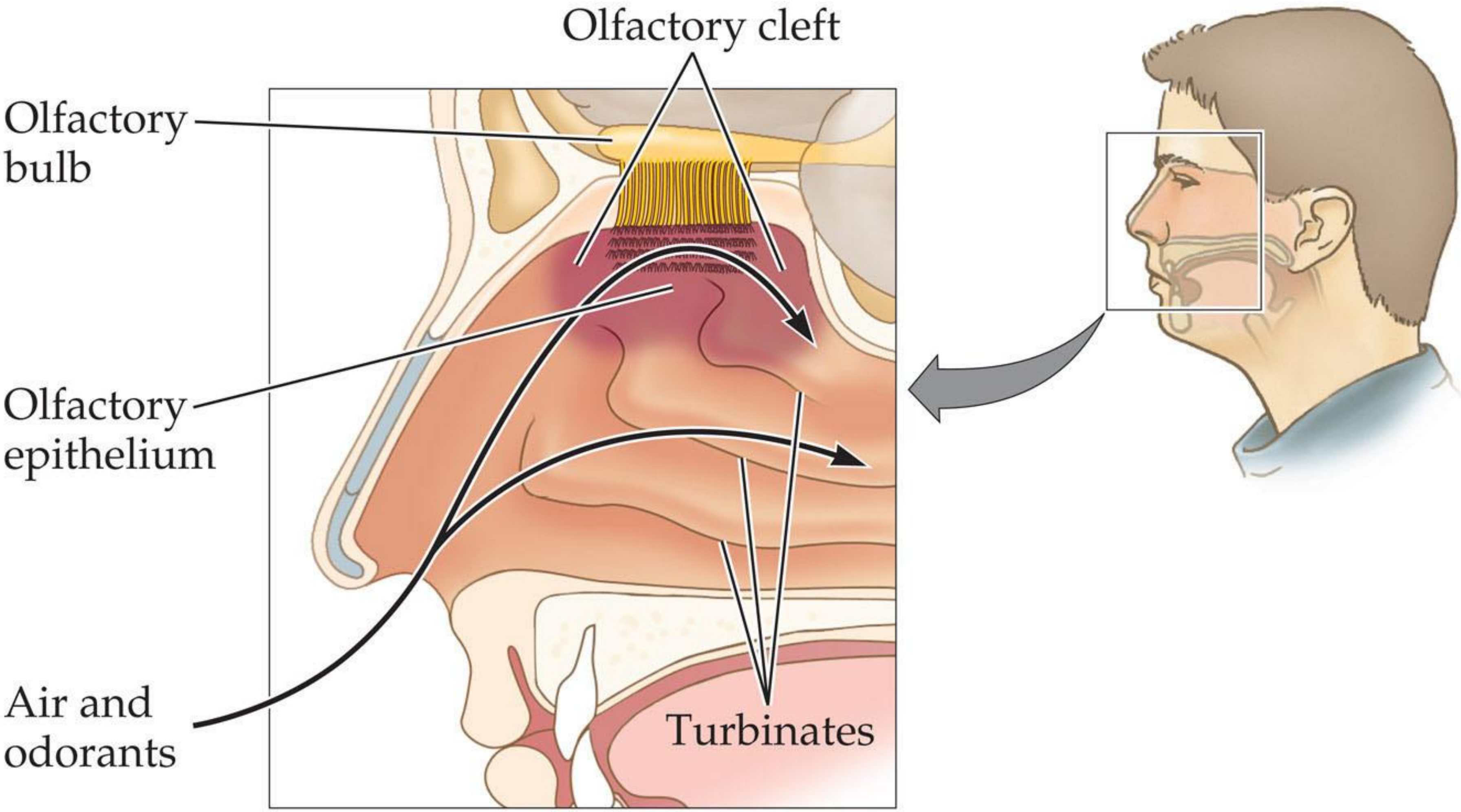
The human olfactory apparatus

- Unlike other senses, smell is tacked onto an organ with another purpose—the nose.
  - Primary purpose—to filter, warm, and humidify air we breathe
  - Nose contains small ridges, olfactory cleft, and olfactory epithelium

The human olfactory apparatus (*continued*)

- 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.

Figure 14.2 The nose

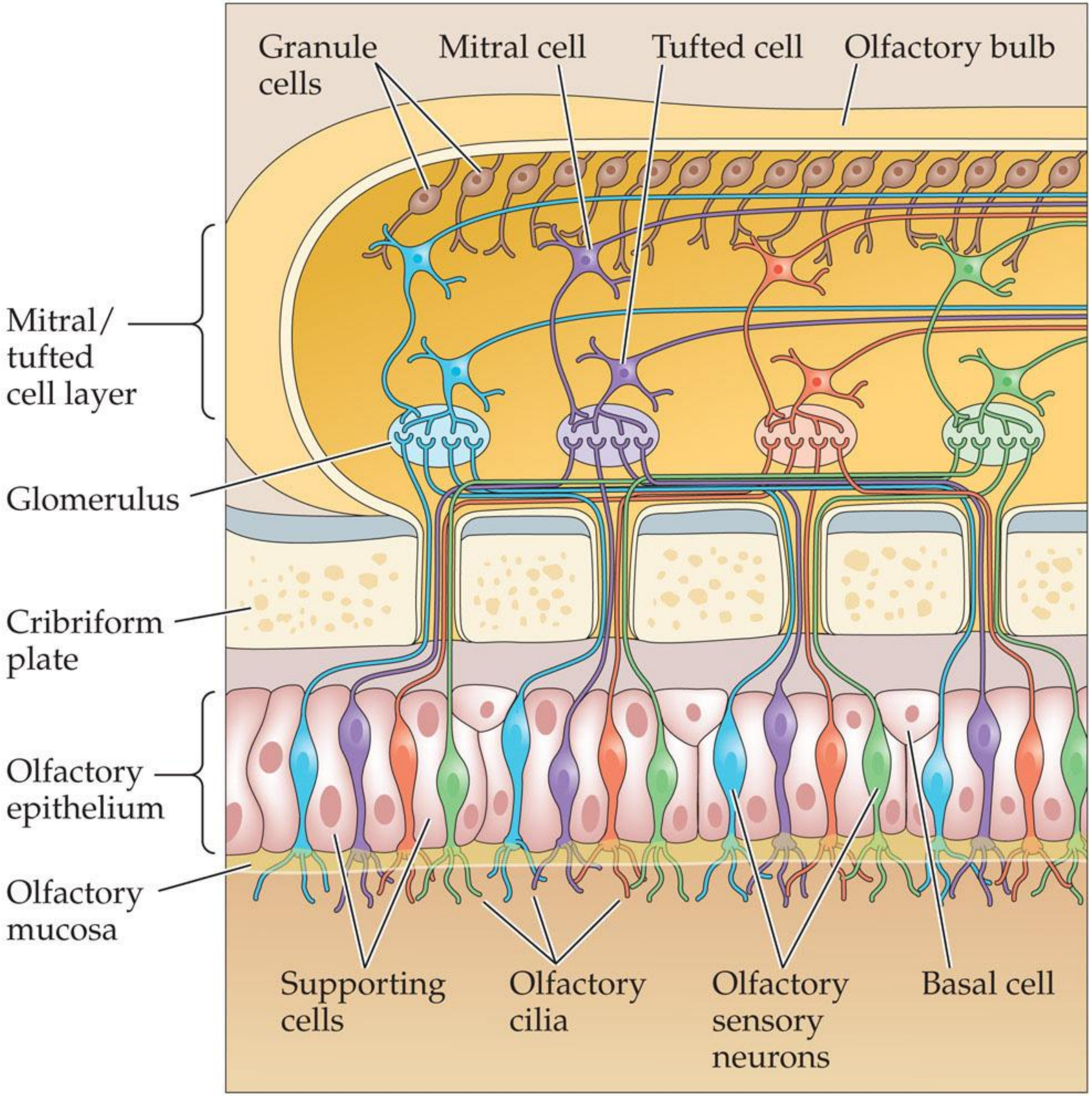


SENSATION & PERCEPTION 4e, Figure 14.2

Olfactory epithelium: The “retina” of the nose

- Three types of cells
  - Supporting cells: Provide metabolic and physical support for the olfactory sensory neurons.
  - Basal cells: Precursor cells to olfactory sensory neurons.
  - Olfactory sensory neurons (OSNs): The main cell type in the olfactory epithelium.
    - OSNs are small neurons located beneath a watery mucous layer in the epithelium.

Figure 14.3 The retina of the nose



SENSATION & PERCEPTION 4e, Figure 14.3

Olfactory Physiology

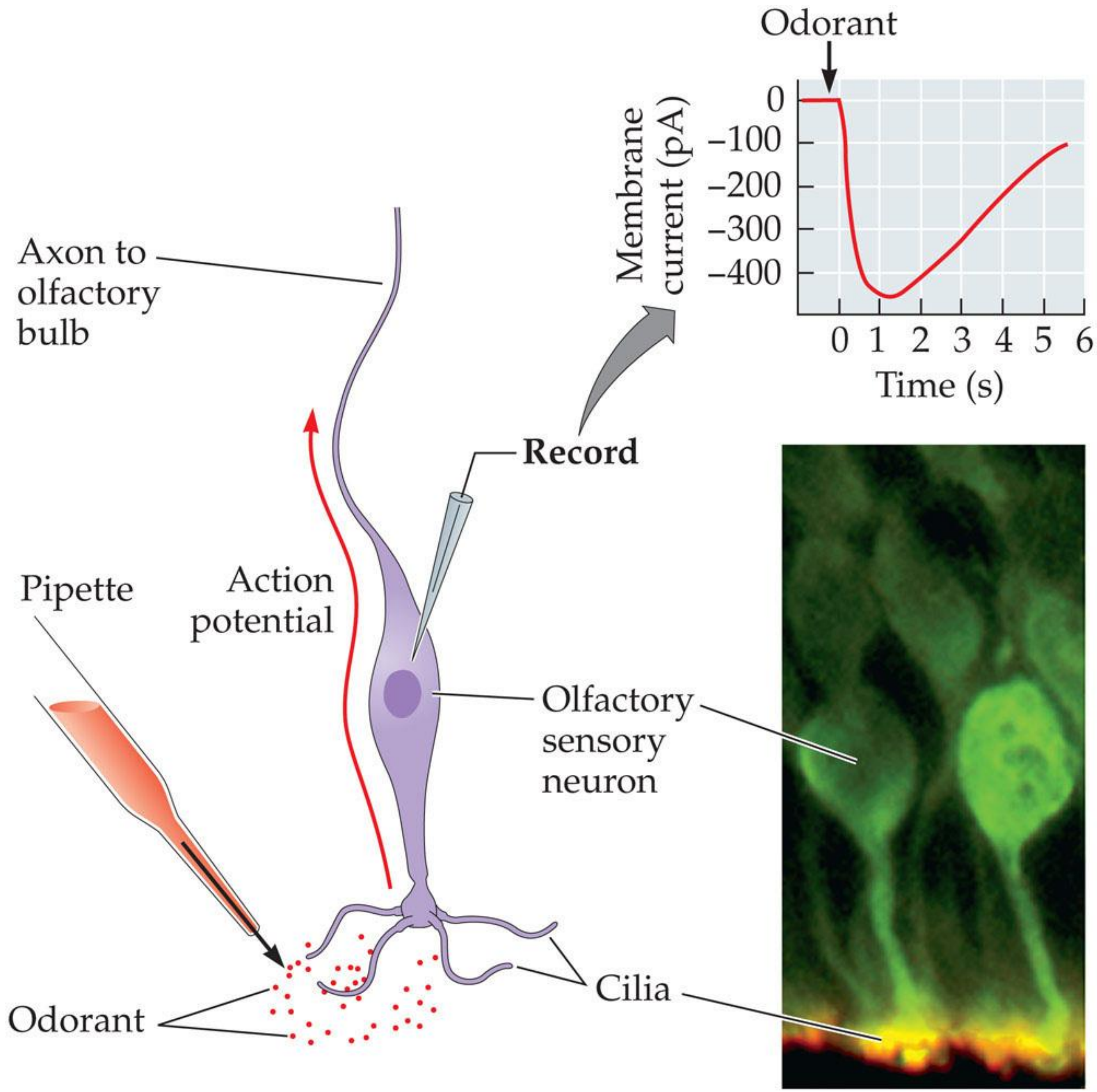
Cilium (plural Cilia): Any of the hairlike protrusions on the dendrites of OSNs.

- Contain receptor sites for odorant molecules
- 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
- Takes about 40 nerve impulses for a smell sensation to be reported

Figure 14.4 A fluorescence image of an olfactory sensory neuron, with a schematic graph of an action potential sequence following odorant application

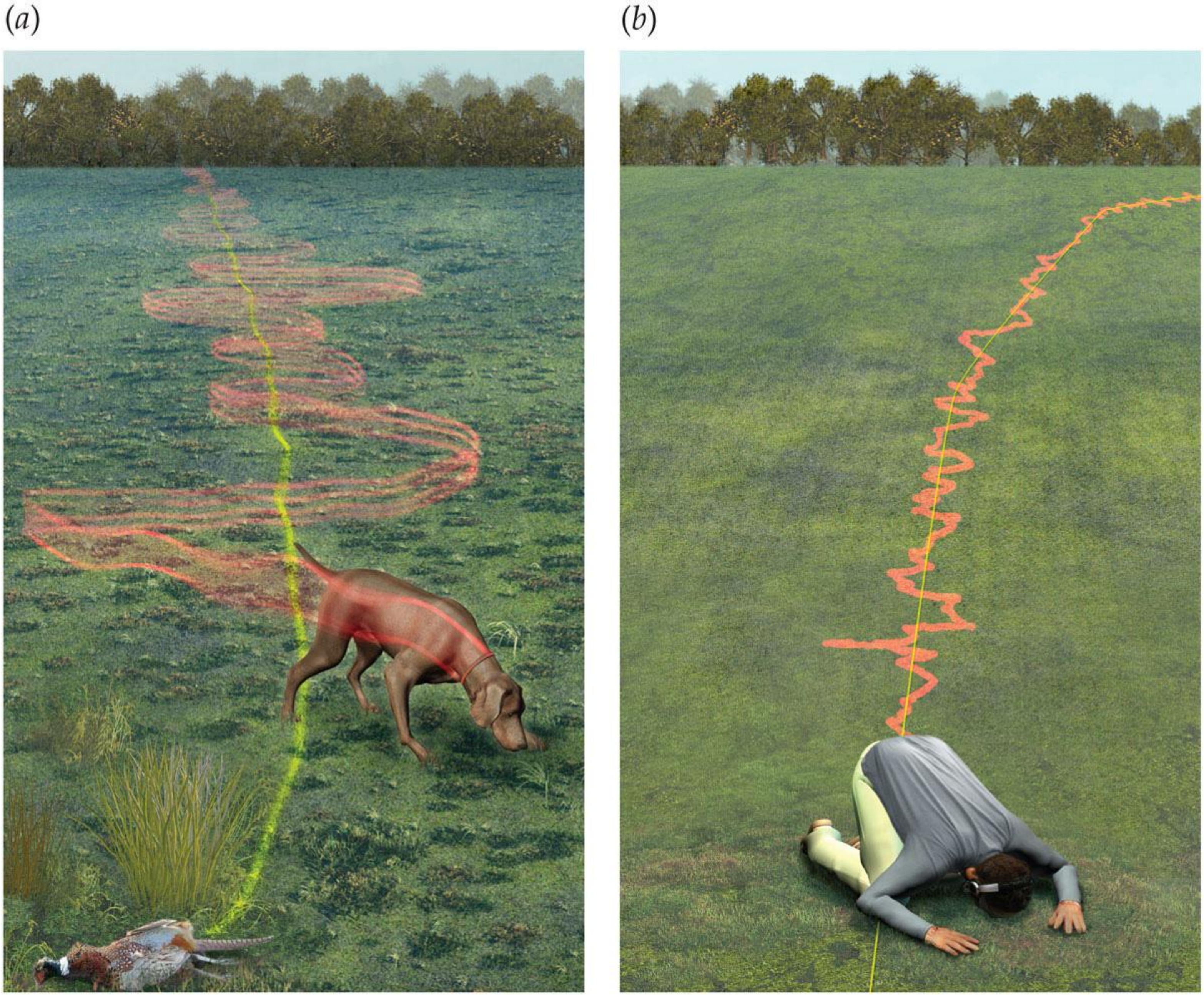


SENSATION & PERCEPTION 4e, Figure 14.4

How good is our sense of smell?

- Latest findings suggest we can detect over one trillion smells!
- We can only detect about 7.5 million colors.
- Humans have about 5–10 million OSNs.
- Dogs have 100 times more OSNs and more of their brain is dedicated to olfaction. They can sense smells in much lower concentrations than humans.

Figure 14.5 Tracking scents



SENSATION & PERCEPTION 4e, Figure 14.5

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.
- Estimated that as many as 1 in 20 suffer from a reduced sense of smell.

Neurophysiology of Olfaction

Olfactory nerves: The first pair of cranial nerves. The axons of the OSNs bundle together after passing through the cribriform plate to form the olfactory nerve.

Olfactory bulb: The blueberry-sized extension of the brain just above the nose, where olfactory information is first processed.

- There are two olfactory bulbs, one in each brain hemisphere, corresponding to the left and right nostrils. Connections are ipsilateral (same side of body).

Neurophysiology of Olfaction

Glomeruli: The spherical conglomerates containing the incoming axons of the OSNs.

- Each OSN converges on two glomeruli (one medial, one lateral).
  - First relay for the OSNs in the olfactory bulb
- Patterns of activity in the glomeruli determine which odor is experienced.

Glomeruli are surrounded by several layers of cells: juxtaglomerular neurons, tufted cells, mitral cells, and granule cells.

Juxtaglomerular neurons: The first layer of cells surrounding the glomeruli. Mixture of excitatory and inhibitory cells that respond to a wide range of odorants.

Tufted cells: The next layer of cells after the juxtaglomerular neurons. They respond to fewer odorants than the juxtaglomerular cells, but more than neurons at the deepest layer of cells.

Mitral cells: The deepest layer of neurons in the olfactory bulb. Each mitral cell responds to only a few specific odorants.

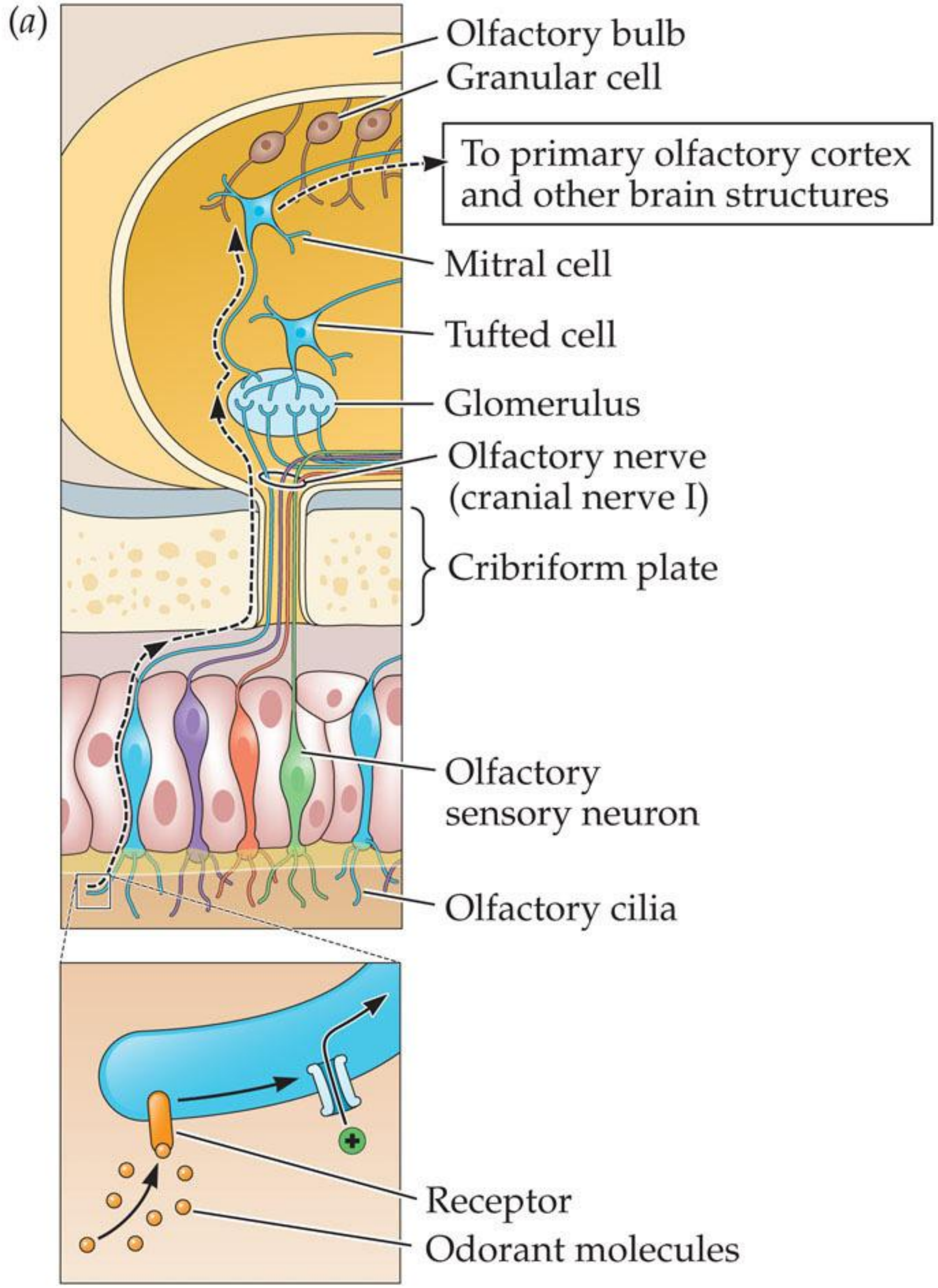
Granule cells: Also in the deepest layer of neurons in the olfactory bulb, along with the mitral cells. Granule cells comprise an extensive network of inhibitory neurons, integrate input from all the earlier projections, and are thought to be the basis of specific odorant identification.

Neurophysiology of Olfaction

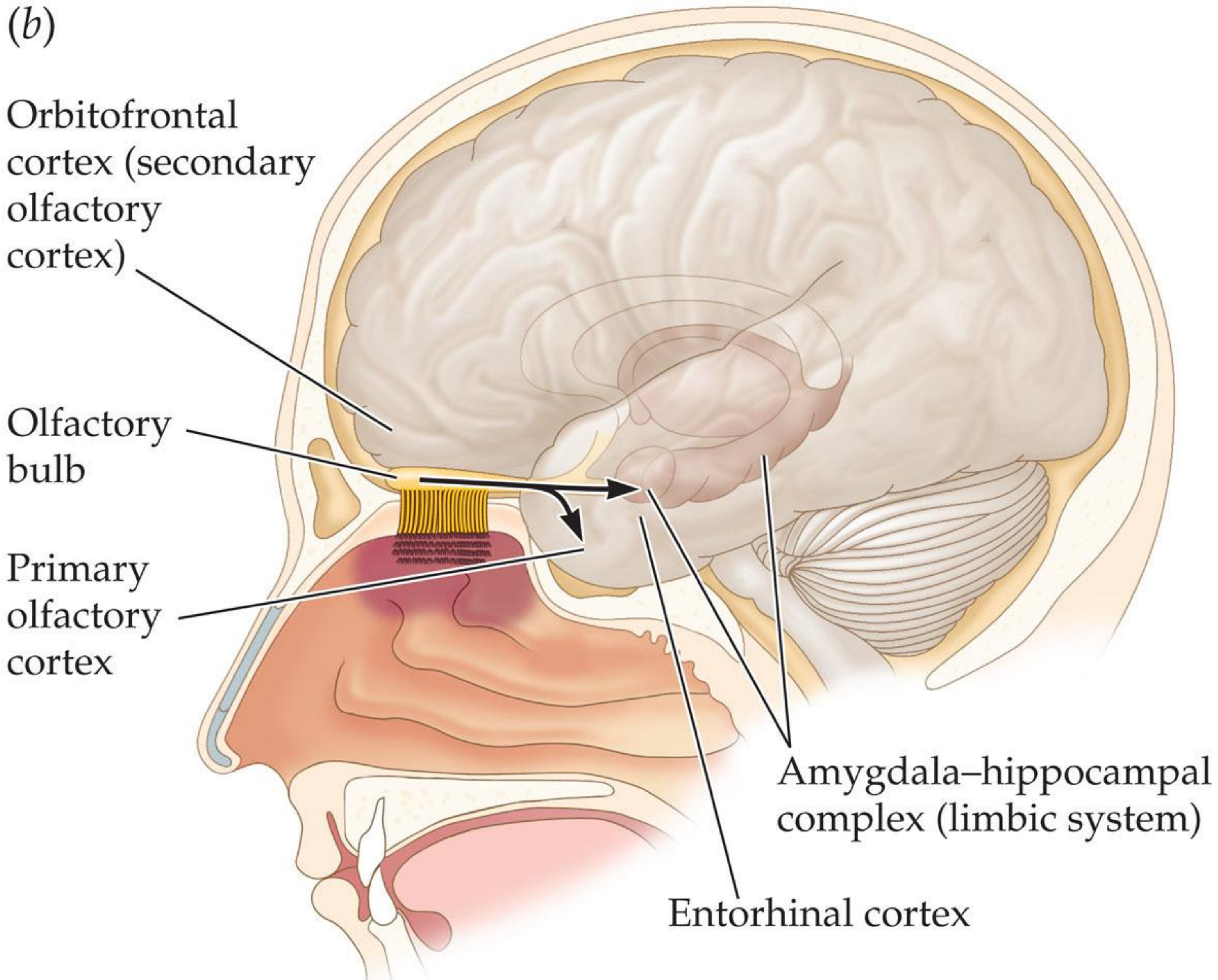
Primary olfactory cortex: The neural area where olfactory information is first processed, which includes the amygdala, parahippocampal gyrus, and interconnected areas, and also entorhinal cortex.

Entorhinal cortex: A phylogenetically old cortical region that provides the major sensory association input into the hippocampus. Also receives direct projections from olfactory regions.

Figure 14.7 How smells are perceived (Part 1)



SENSATION & PERCEPTION 4e, Figure 14.7 (Part 1)



SENSATION & PERCEPTION 4e, Figure 14.7 (Part 2)

Neurophysiology of Olfaction

Limbic system: The encompassing group of neural structures that includes the olfactory cortex, the amygdala, the hippocampus, the piriform cortex, and the entorhinal cortex.

- Involved in many aspects of emotion and memory
- Olfaction—unique among the senses for its direct and intimate connection to the limbic system

Olfaction's unique connection to the limbic system explains why scents tend to have such strong emotion associations.

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

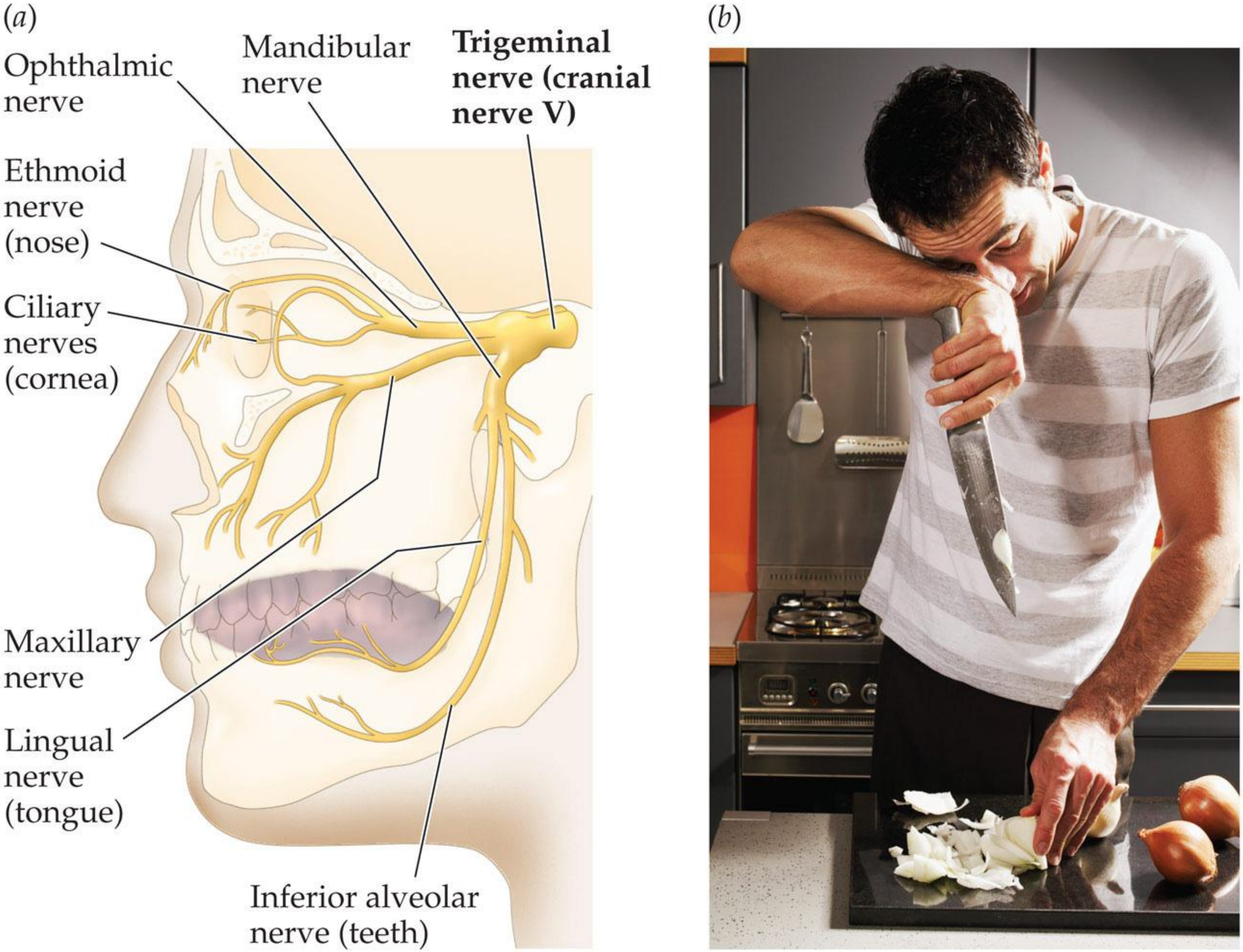
Genetic basis of olfactory receptors (*continued*)

- Humans: Between 60% and 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.

The feel of scent

- Odorants can stimulate somatosensory system through polymodal nociceptors (touch, pain, temperature receptors).
- These sensations are mediated by the trigeminal nerve (cranial nerve V).
- Often, it is impossible to distinguish between sensations traveling up cranial nerve I from olfactory receptors and those traveling up cranial nerve V from somatosensory receptors.

Figure 14.8 The trigeminal nerve's role in the perception of odors



SENSATION & PERCEPTION 4e, Figure 14.8

From Chemicals to Smells

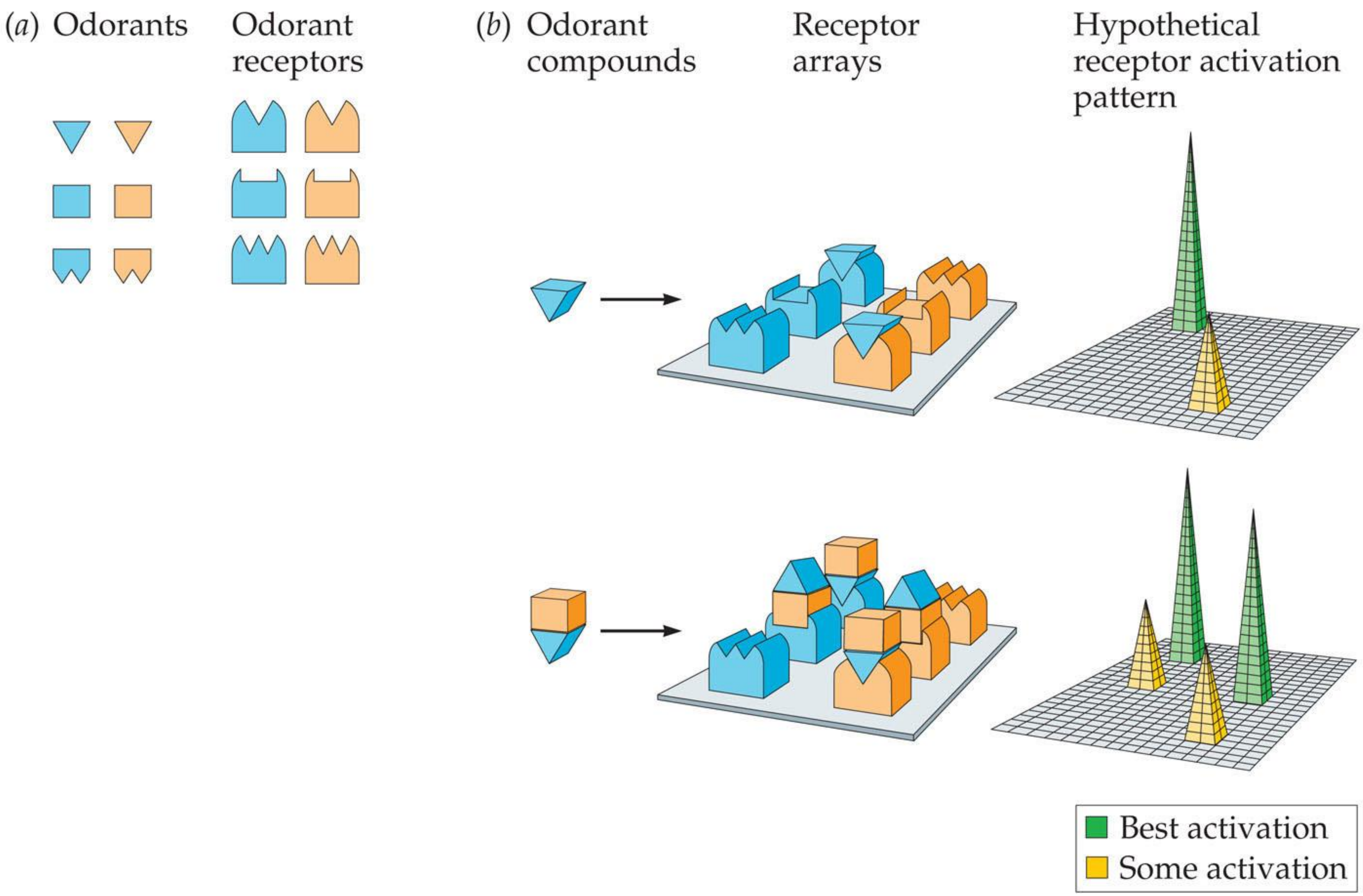
Theories of olfactory perception

- Shape-pattern theory: The current dominant biochemical theory for how chemicals come to be perceived as specific odors. Contends that different scents—as a function of odorant-shape to OR-shape fit—activate different arrays of olfactory receptors in the olfactory epithelium.
  - These various arrays produce specific firing patterns of neurons in the olfactory bulb, which then determine the particular scent we perceive.

Theories of olfactory perception (*continued*)

- Vibration theory: Proposes that every perceived smell has a different vibrational frequency, and that molecules that produce the same vibrational frequencies will smell the same.

Figure 14.9 Odorant-receptor binding and odorant activation, as predicted by shape-pattern theory



SENSATION & PERCEPTION 4e, Figure 14.9

Specific anosmia: The inability to smell one specific compound amid otherwise normal smell perception.

- 20–40% of population has specific anosmia to androstenone, a molecule found in armpit sweat and pork.
  - Of those who can smell it, most perceive it as an unpleasant “urinous” odor; the remainder perceive it as a “sweet musky-floral” scent.

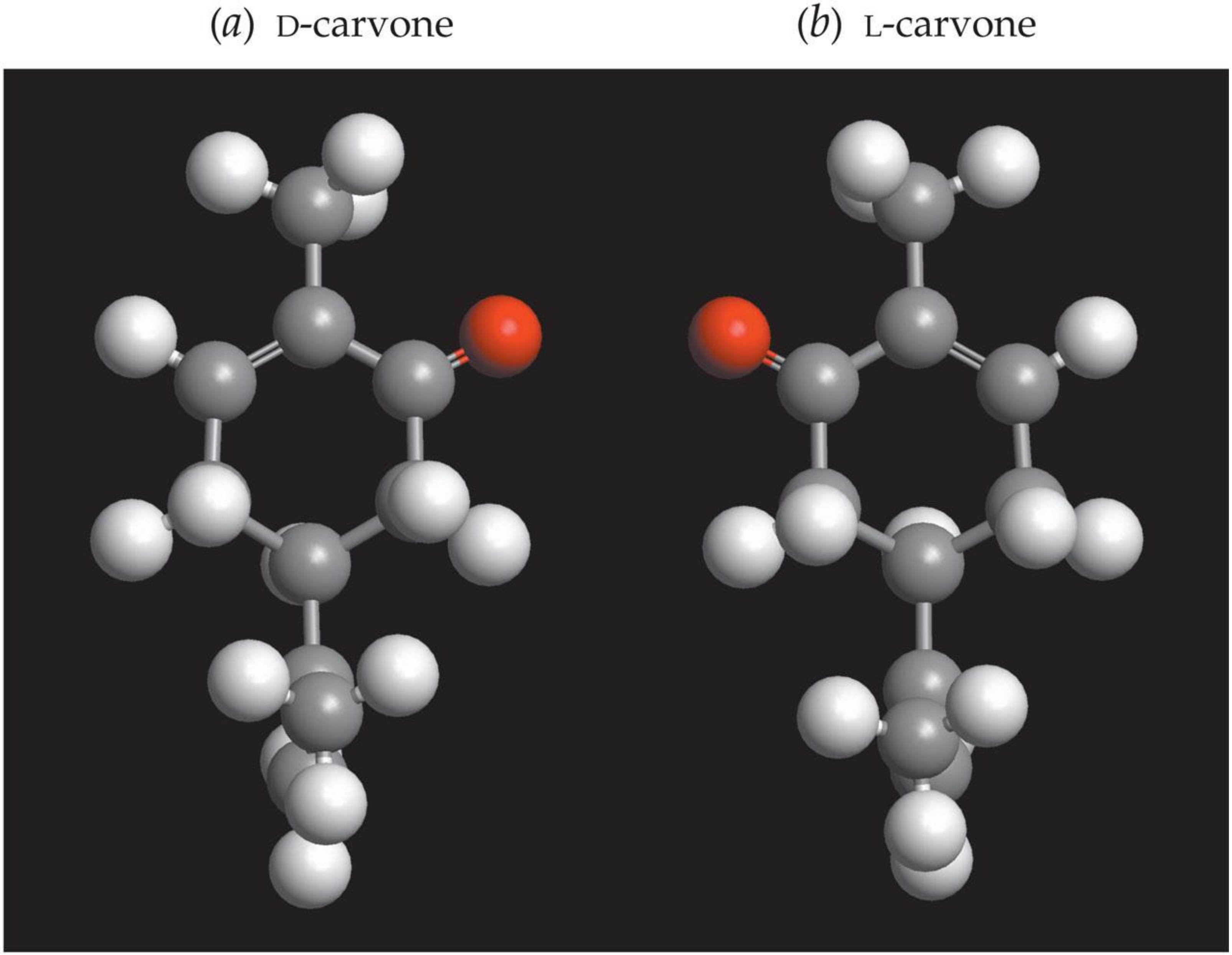
From Chemicals to Smells

- Sensitivity to androstenone can be increased with training.
  - This cannot be explained by vibration theory, nor can the differences in perceived smell.
  - Shape-pattern theory can explain these findings.

Study of stereoisomers

- Molecules that are mirror-image rotations of one another; although they contain the same atoms, they can smell completely different.
- Vibration theory also cannot explain this phenomenon.

Figure 14.10 The stereoisomers D-carvone (*a*) and L-carvone (b) contain the same atoms, yet they smell completely different

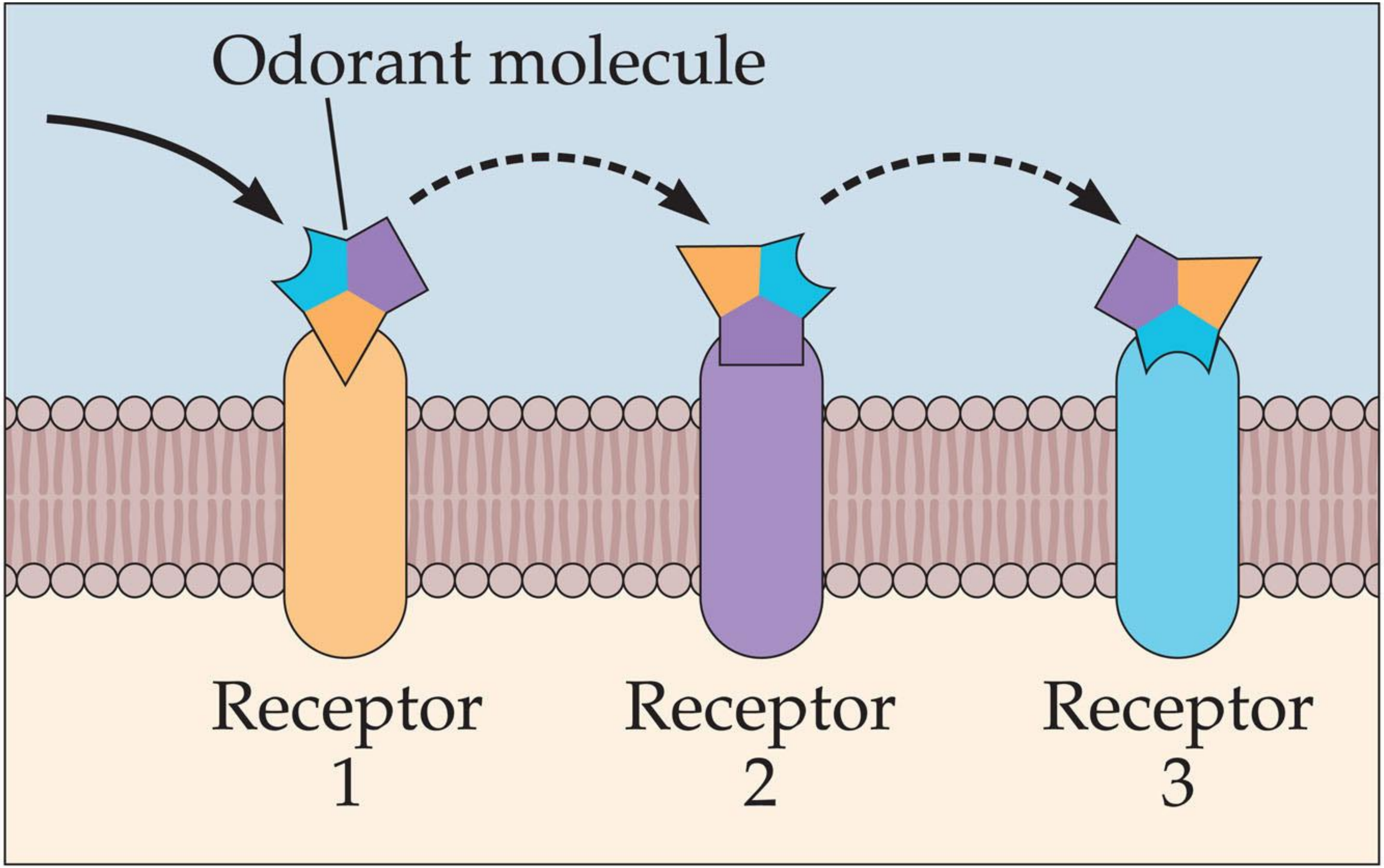


SENSATION & PERCEPTION 4e, Figure 14.10

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.

Figure 14.11 The hypothetical role of OR activation timing and order



SENSATION & PERCEPTION 4e, Figure 14.11

Odor mixtures

- We rarely smell “pure odorants.” Rather, we smell mixtures.
- How do we process the components in an odorant mixture?
  - Analysis—example from auditory mixtures: High note and low note can be played together but we can detect each individual note.

Odor mixtures (*continued*)

- Synthesis—example from color mixtures: Mixing red and green lights results in yellow light, but we cannot separately perceive the red and green in the yellow.

- Olfaction is primarily a synthetic sense, but some analytical abilities can be developed.

Figure 14.12 The roles of analysis and synthesis in sensory perception

(*a*) Auditory mixture: analysis

(*b*) Color mixture: synthesis

(*c*) Olfactory mixture: anaylsis and synthesis

***SENSATION & PERCEPTION 4e*, Figure 14.12**

Binaral rivalry: Competition between the two nostrils for odor perception.

- When a different scent is presented to each nostril, we experience one scent at a time, not a combination of the two scents together.

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.

Olfactory white: The olfactory equivalent of "white noise," or the color white.

- At least 30 odorants of equal intensity that span olfactory physiochemical and perceptual space are mixed together.
- People cannot tell one mixture of 30 odorants from another mixture, even though the various mixtures do not share any common odorants.

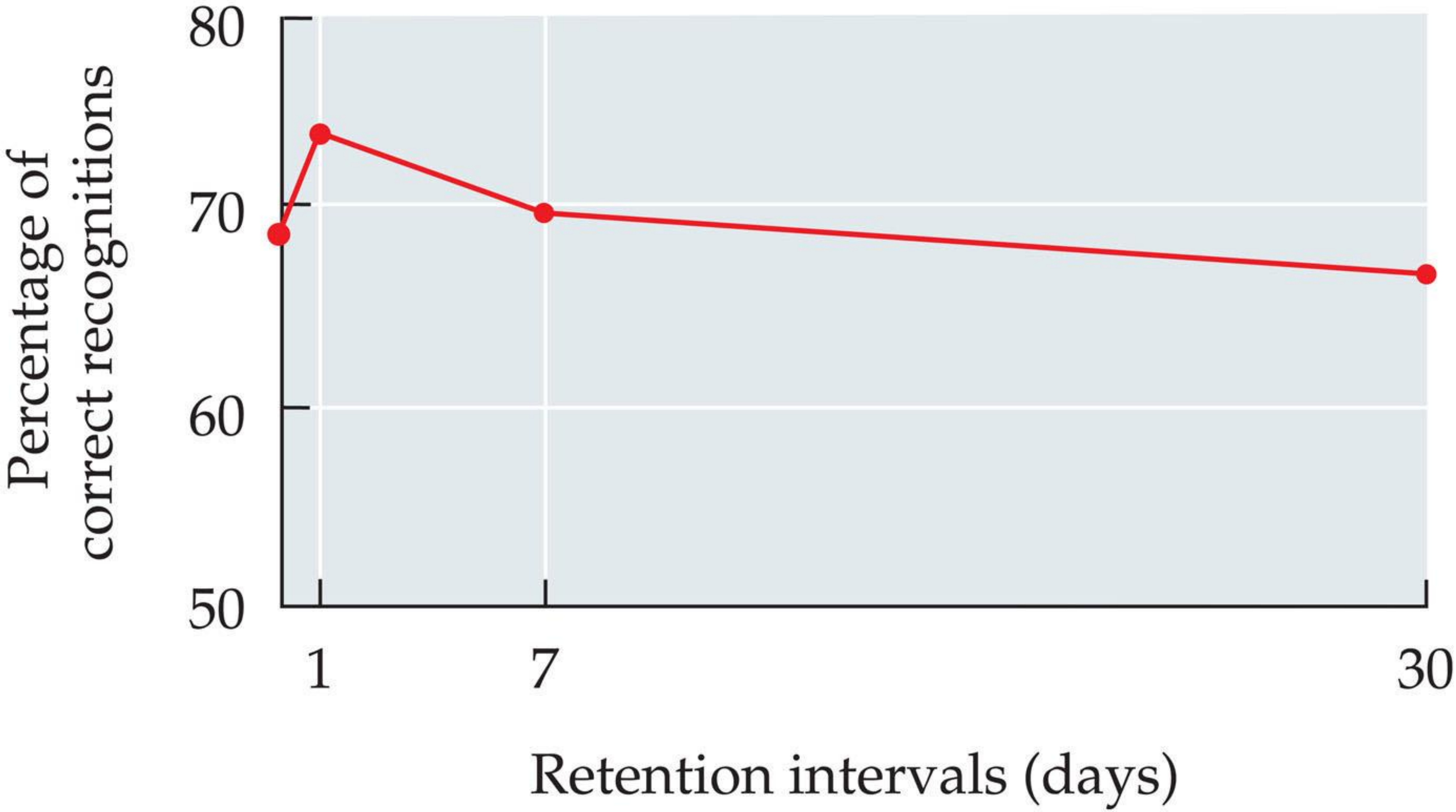
Complex smells like “bacon” and “rose” only stimulate part of the physiochemical and perceptual space, which is why they smell distinct.

Suggests an underlying commonality between olfaction, vision, and audition.

Detection, discrimination, and recognition

- How much stimulation is required before we perceive something to be there?
- Durability: Our recognition of smells is durable even after several days, months, or years.

Figure 14.13 Long-term memory for smells



SENSATION & PERCEPTION 4e, Figure 14.13

Psychophysical methods for detection and discrimination

- Staircase method: Method for determining the concentration of a stimulus required for detection at a threshold level.
  - Stimulus is presented in increasing concentrations until detection is indicated.

Psychophysical methods for detection and discrimination (*continued*)

- Then, concentration is decreased until detection ceases.
- Ascending and descending sequence is repeated several times and concentrations at which reversals occur are averaged to determine threshold detection level.

Psychophysical methods for detection and discrimination (*continued*)

- Triangle test: Participant is given three odors to smell, two of which are the same and one that is different.
  - Participant must identify the odd odor.
  - The order of the three odors is varied and tested several times to increase accuracy.

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.

Identification (*continued*)

- 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.

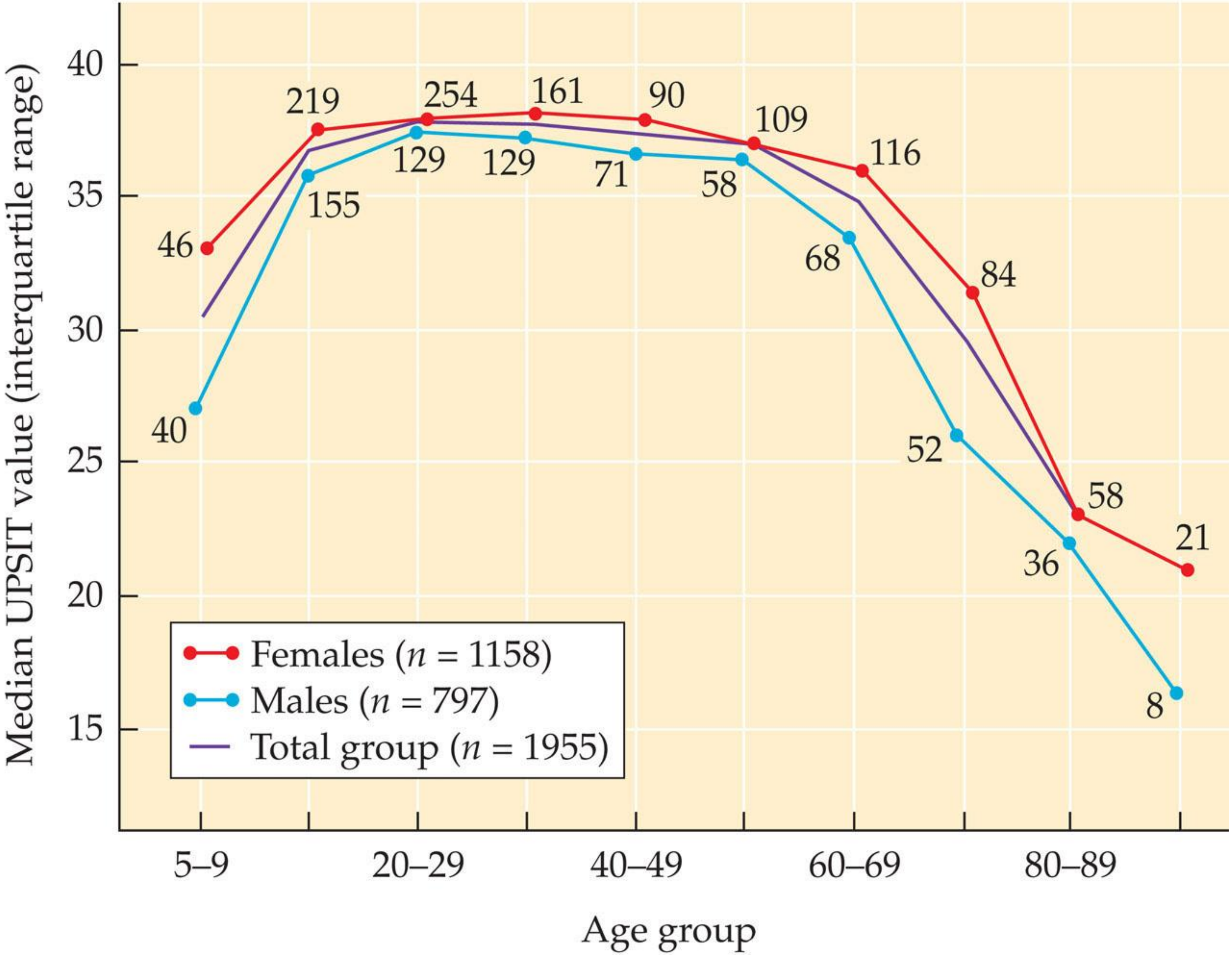
Sense of smell and language are disconnected, possibly because

- 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.

Individual differences in olfaction

- Olfactory detection thresholds depend on several factors
  - Women: generally lower thresholds than men, especially during ovulatory period of menstrual cycles, but their sensitivity is *not* heightened during pregnancy
  - Professional perfumers and wine tasters can distinguish up to 100,000 odors
  - Age: By 85, 50% of population is effectively anosmic

Figure 14.14 Changes in olfactory identification ability as a function of age



SENSATION & PERCEPTION 4e, Figure 14.14

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.

Adaptation (*continued*)

- 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 14.15 Olfactory cross-adaptation

SENSATION & PERCEPTION 4e, **Figure 14.15**

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

The importance of attention and conscious perception

- We cannot smell while we are asleep.
- Attention increases our ability to detect odors.
- Attention is cut off during sleep, so is our ability to respond to odors.

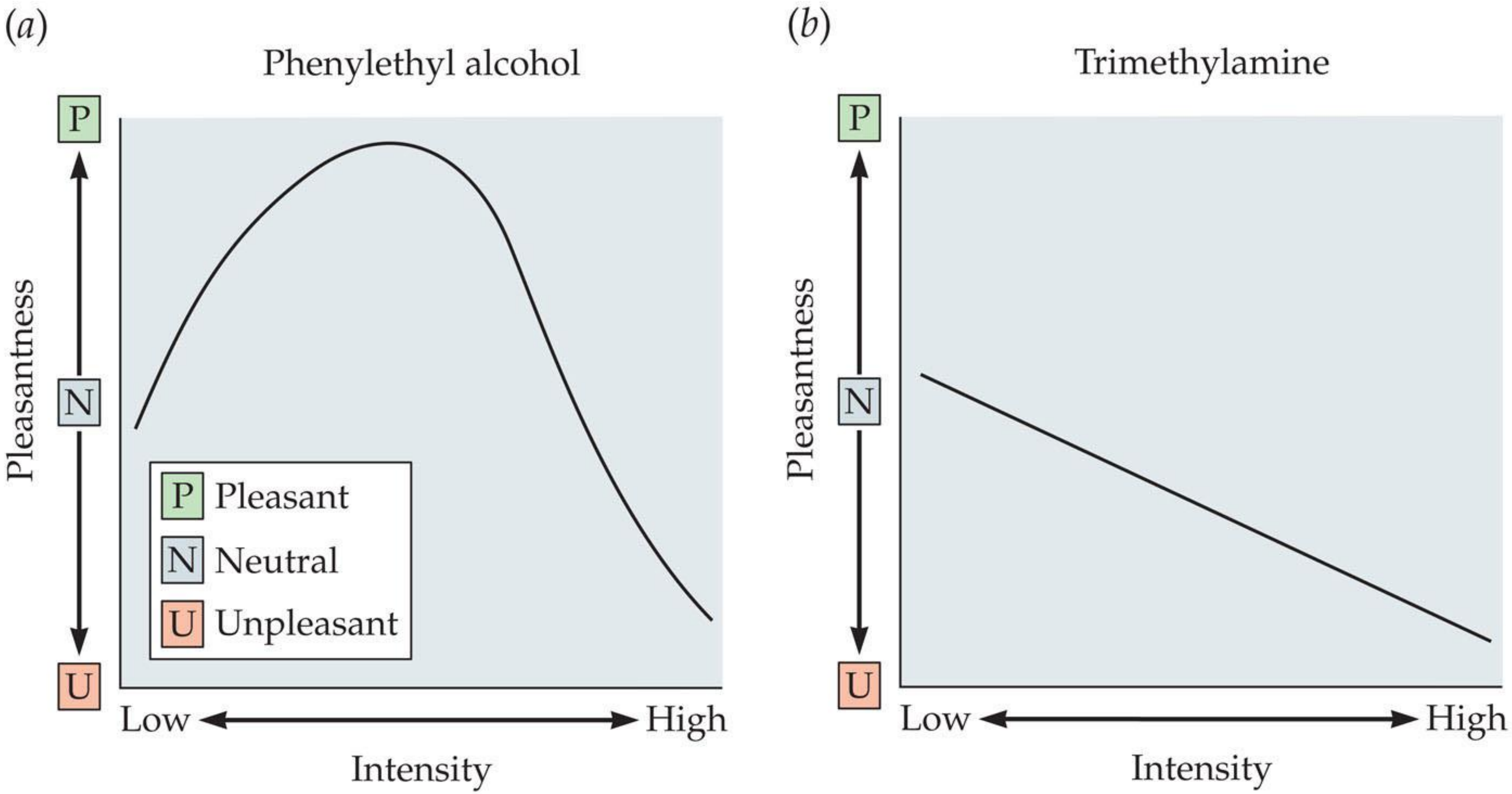
Olfactory Hedonics

Odor hedonics: The liking dimension of odor perception, typically measured with scales pertaining to an odorant's perceived pleasantness, familiarity, and intensity.

Familiarity and intensity

- We tend to like odors we have smelled many times before.
- Intensity has a more complicated relationship with odor liking:
  - Inverted U-shape function
  - Linearly decreasing function

Figure 14.16 Pleasantness ratings of odorants plotted against intensity



SENSATION & PERCEPTION 4e, Figure 14.16

Olfactory Hedonics

Nature or nurture?

- Are hedonic responses to odors innate or learned? Debated
- Evidence from infants: Odor preferences often very different from adults
- Cross-cultural data support associative learning

Nature or nurture? (*continued*)

- 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.

Figure 14.17 Cultural food preferences and smell - the Japanese regularly eat *nattō* for breakfast; Westerners enjoy cheese

SENSATION & PERCEPTION 4e, Figure 14.17

Olfactory Hedonics

Two caveats for theory that odor hedonics are mostly learned:

- Trigeminally irritating odors may elicit pain responses, and all humans have an innate drive to avoid pain.
- There is potential variability in receptor genes and pseudogenes that are expressed across individuals.

Are odors really the best cues to memory?

- Other modalities can elicit memory as well (e.g., vision, touch, taste).
- Memories triggered by odor cues are distinctive in their emotionality.
- Emotion and evocativeness of odor-elicited memories lead to false impression that such memories are especially accurate.

Associative Learning and Emotion: Neuroanatomical and Evolutionary Considerations

Neuroanatomical and evolutionary connections between odor and emotion

- Orbitofrontal cortex—olfaction is processed here.
  - Also the cortical area for assigning affective value (i.e., hedonic judgment)
- These two factors help explain the increased emotionality of smells as opposed to other senses.

The vomeronasal organ, human 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.

Vomeronasal organ (VNO): A chemical sensing organ at the base of the nasal cavity with a curved tubular shape.

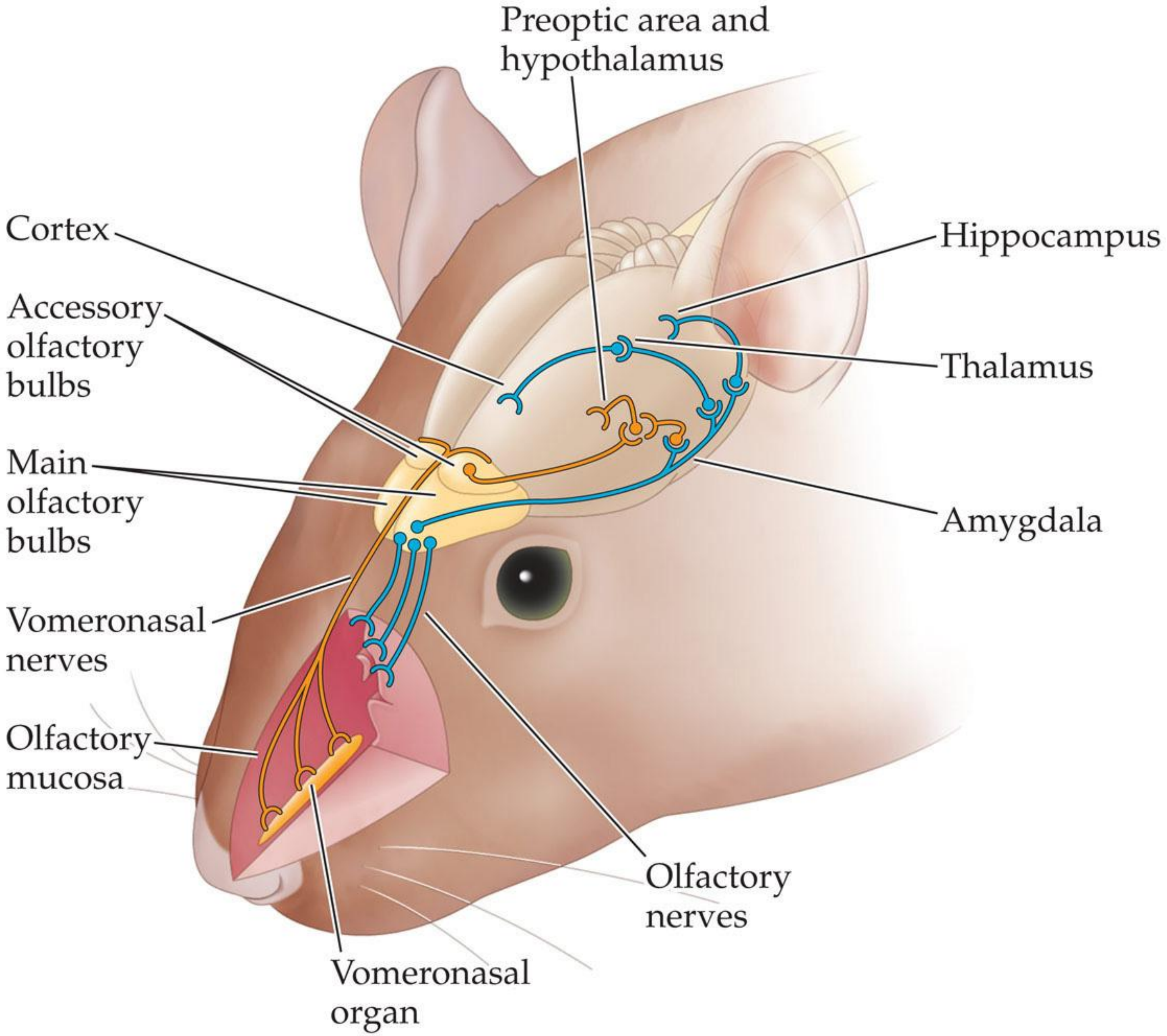
- Evolved to detect chemicals that cannot be processed by the olfactory epithelium, such as large and/or aqueous molecules—the types of molecules that constitute pheromones

Associative Learning and Emotion: Neuroanatomical and Evolutionary Considerations

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.

Figure 14.19 The olfactory system of a hamster, showing the location of the vomeronasal organ and accessory olfactory bulbs



SENSATION & PERCEPTION 4e, Figure 14.19

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

Associative Learning and Emotion: Neuroanatomical and Evolutionary Considerations

- 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.

Releaser pheromone: Triggers an immediate behavioral response among conspecifics.

Primer pheromone: Triggers a physiological (often hormonal) change among conspecifics.

- This effect usually involves prolonged pheromone exposure.

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.

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.

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.

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.

Do humans respond to chemosignals? (*continued)*

- Androstadienone is a hormone derived from testosterone that is in higher concentration in male body fluids (e.g., sweat) than females.
- Androstadienone improves women's mood, self-rated sexual arousal, and cortisol, but only in the presence of men.
  - Same effects not observed with female experimenters

Do humans respond to chemosignals? (*continued*)

- 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.

Odor-evoked memory and the truth behind aromatherapy

- Memories evoked by odors are more intensely emotional than memories evoked by other senses. However, they are not more accurate.
- 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.

Odor-evoked memory and the truth behind aromatherapy (*continued*)

- Effects of aromatherapy can be explained by memory associations, not pharmacological effects of the odors themselves.