Olfaction (Chap 14)

Lecture 20

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Sensation & Perception (PSY 345 / NEU 325)

Spring 2022

But first: somatosensory illusions

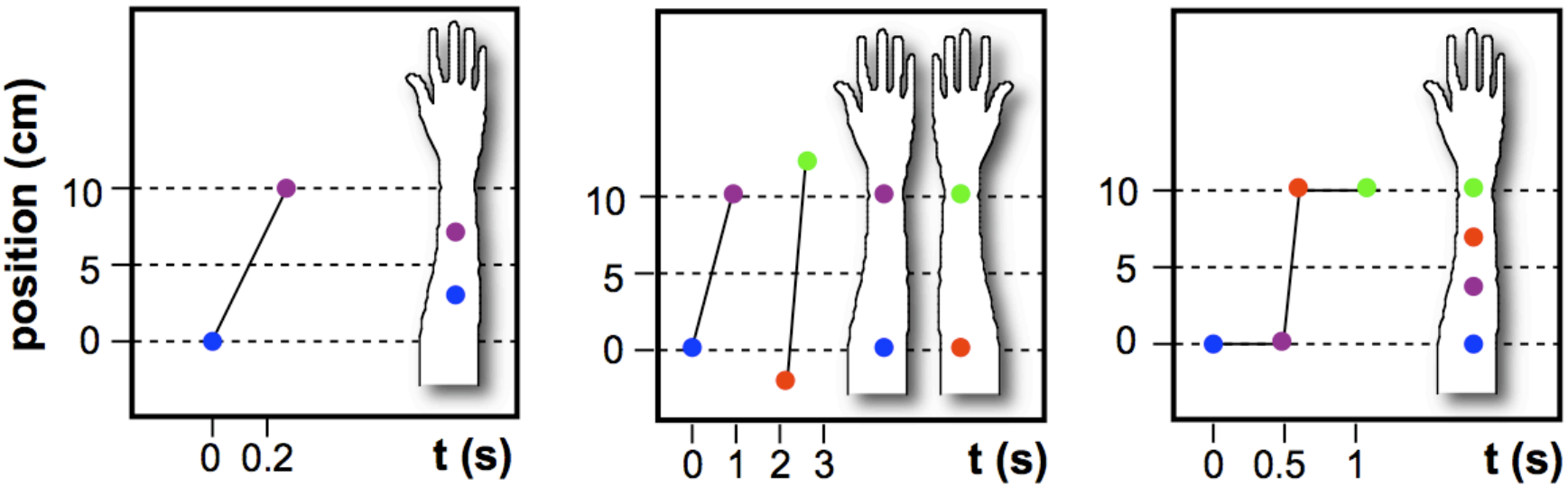
Aristotle Illusion

- brain fails to account for crossing of body parts

2. Close eyes, have a partner tap backs of hands in rapid succession

- easy if hands are uncrossed
- with crossed hands, significant error rate

Rabbit Illusion



- points appear closer together if presented rapidly in time
- like “rabbit hopping up the arm.” (Geldard & Sherrick, 1972)

The Chemical Senses

Olfaction: The sense of smell (today)

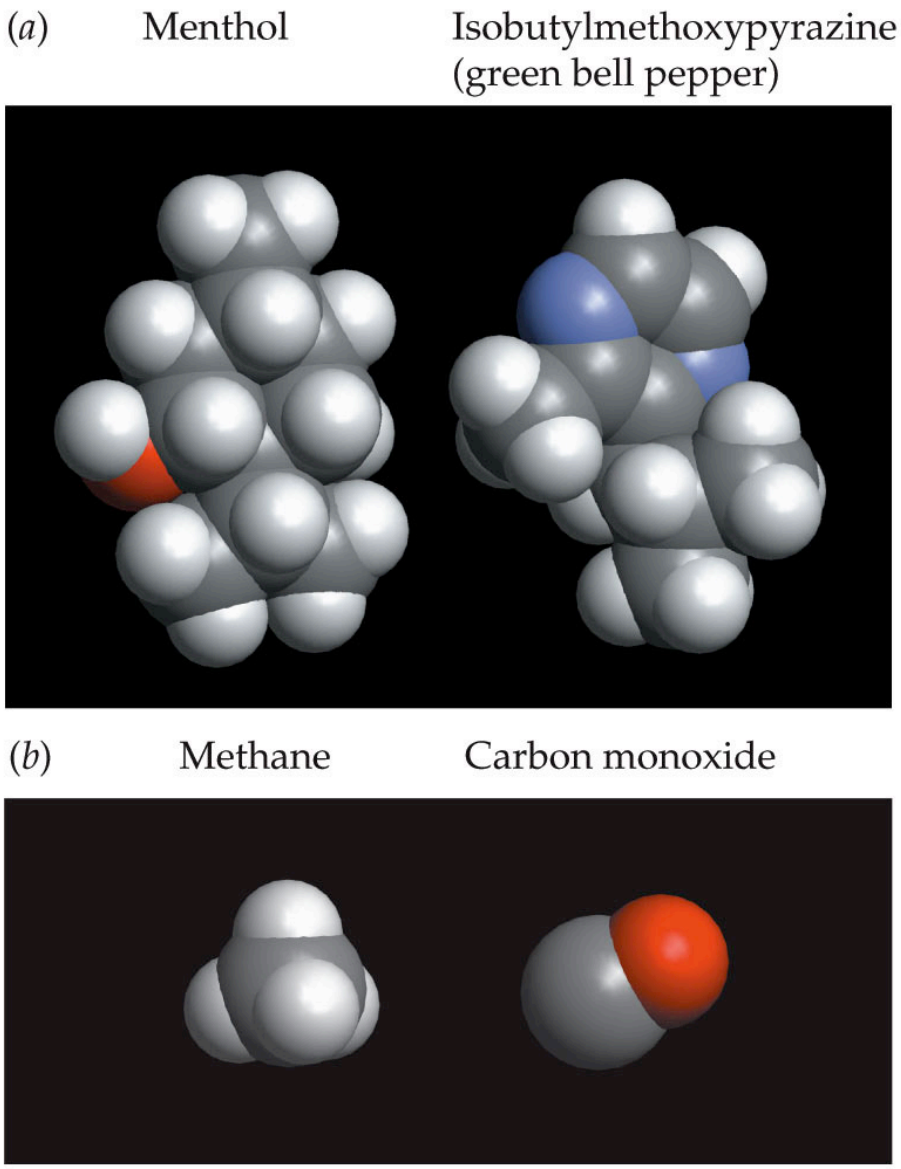
Gustation: The sense of taste

Odor:

A general smell sensation of a particular quality

Odorants:

- Chemical compounds
- But not every chemical is an odorant
- Most are small, volatile, and hydrophobic (don't diffuse in water)



Is smell even relevant to humans?

<u>our "machinery" is less sensitive than other animals (dogs, etc.)</u>

- dogs can detect odorant concentrations 100x lower than humans (dogs: can detect 1 part-per-million, humans: 100 parts-per-million)
- but, experiments show that *human receptors respond to single odorant molecules*
- the difference? Dogs have ~ 1 billion receptors, humans have ~ 10 million

Conventional wisdom: humans not very good at olfaction

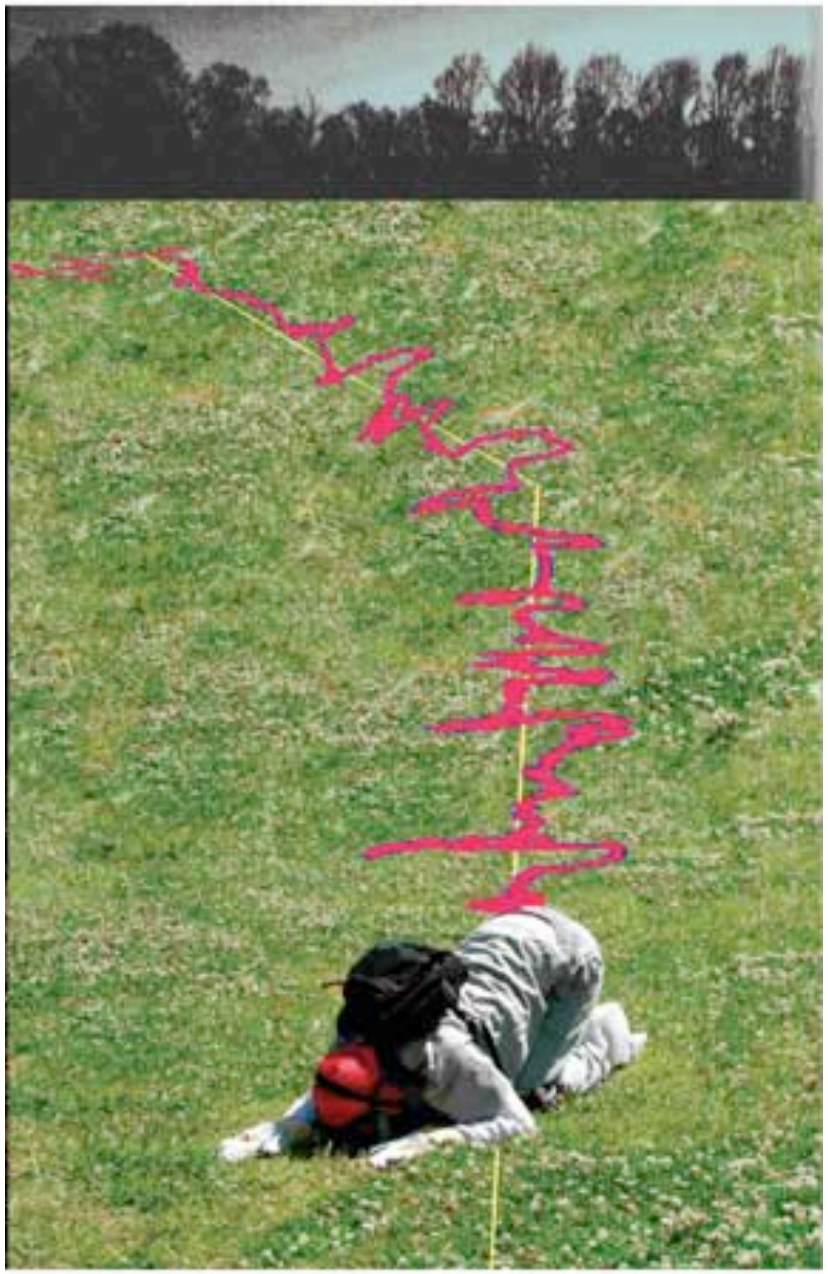
Gibbons, B. Nat. Geogr. Mag. 170, 324–361 (1986).

Bloodhound tracking a pheasant through a field

Conventional wisdom is wrong!

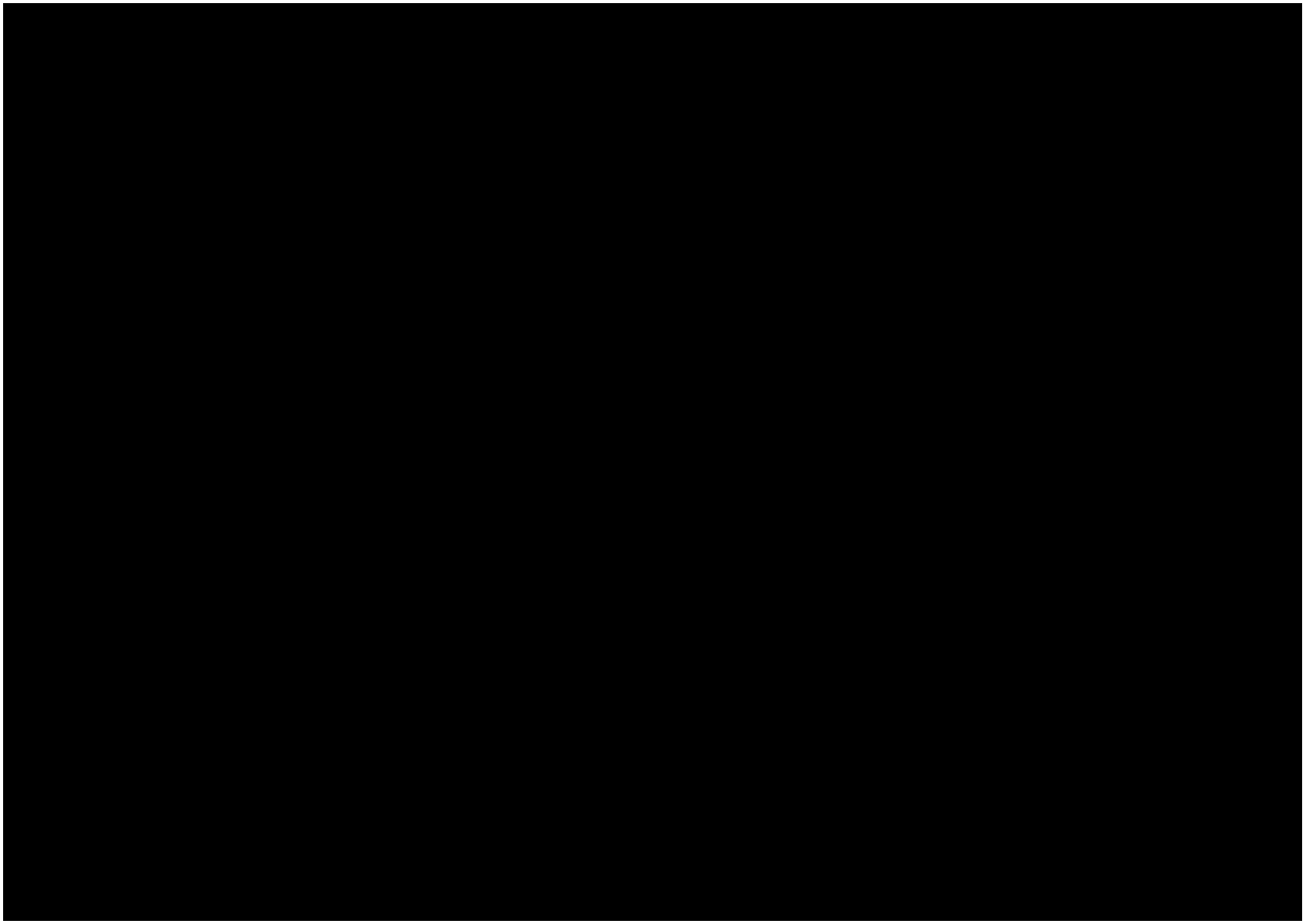
Porter et al 2007

Human tracking a scent trail through a field

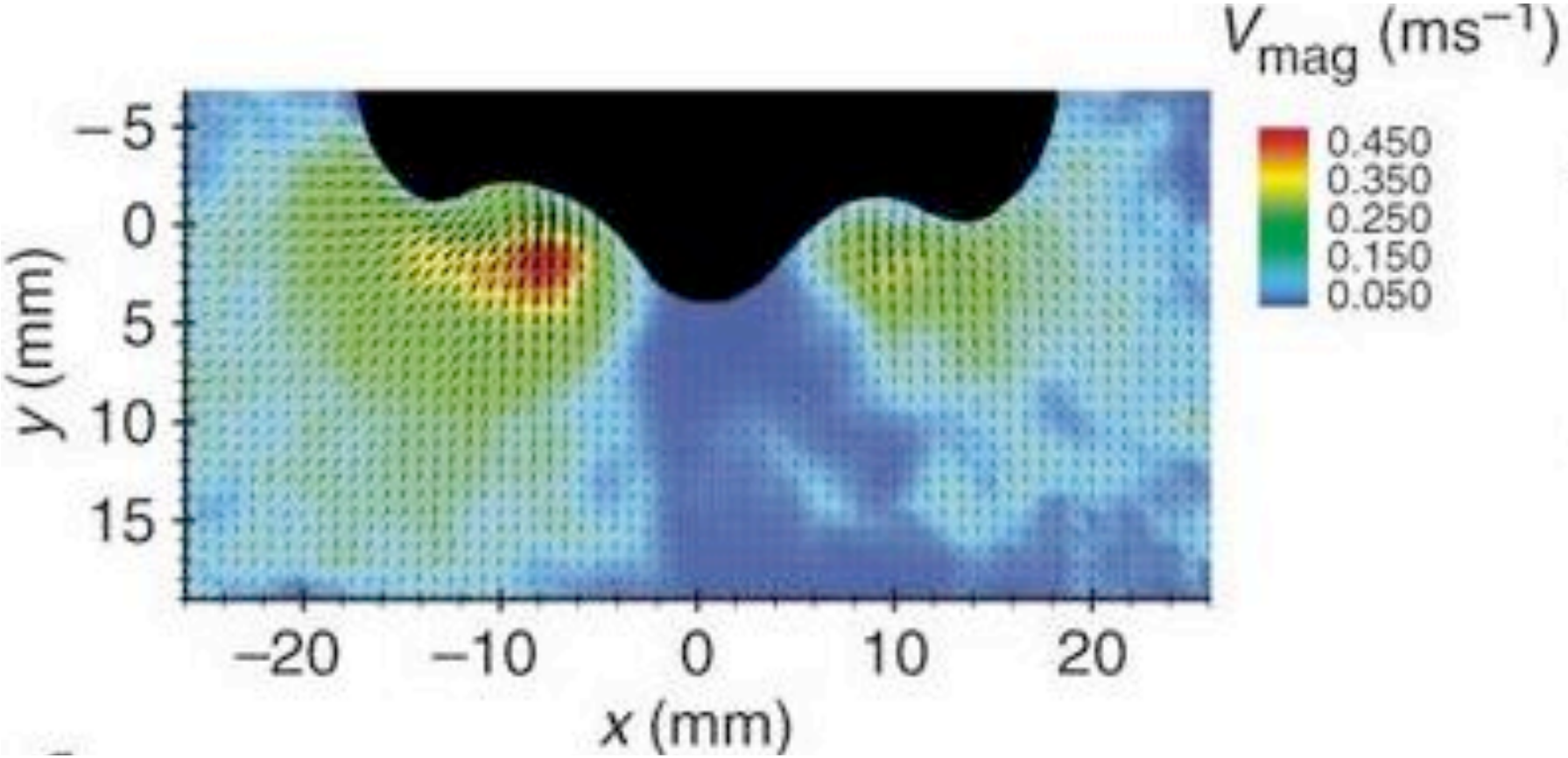


Human scent-tracking

Porter et al 2007

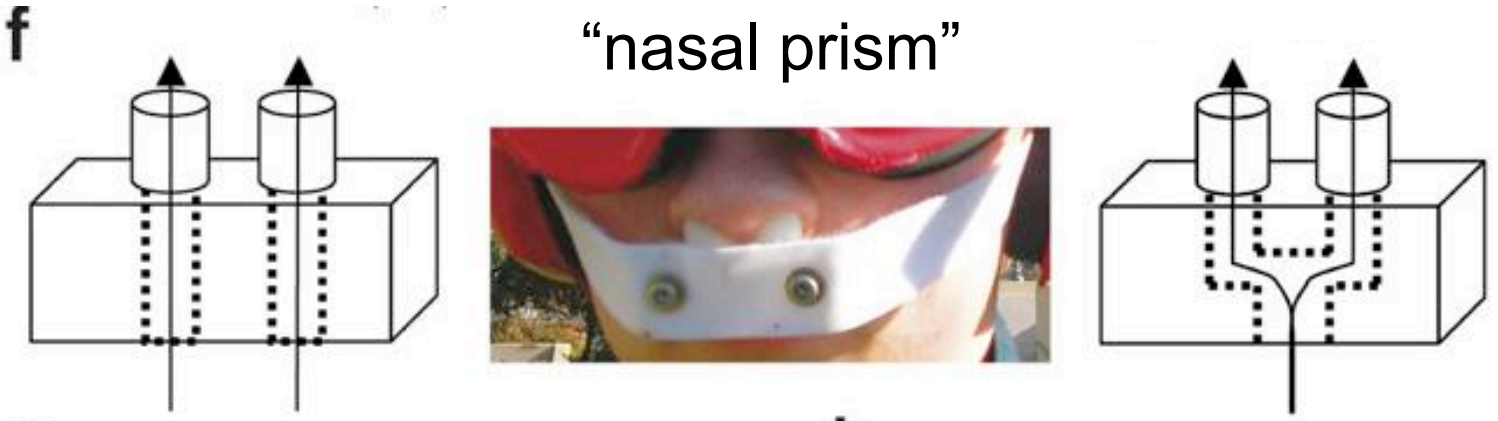


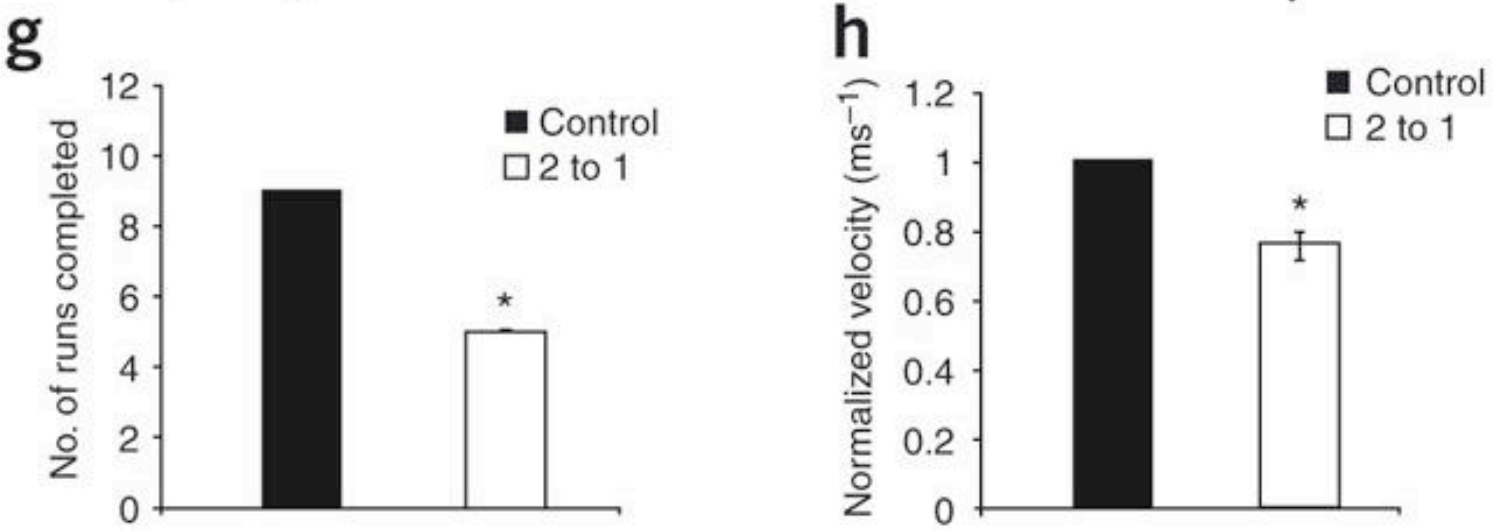
Two nostrils sample different regions of space



single- vs. dual-nostril sniffing

- humans use info from both nostrils for scent tracking





(24% slower w/ 1 nostril)

From the book:

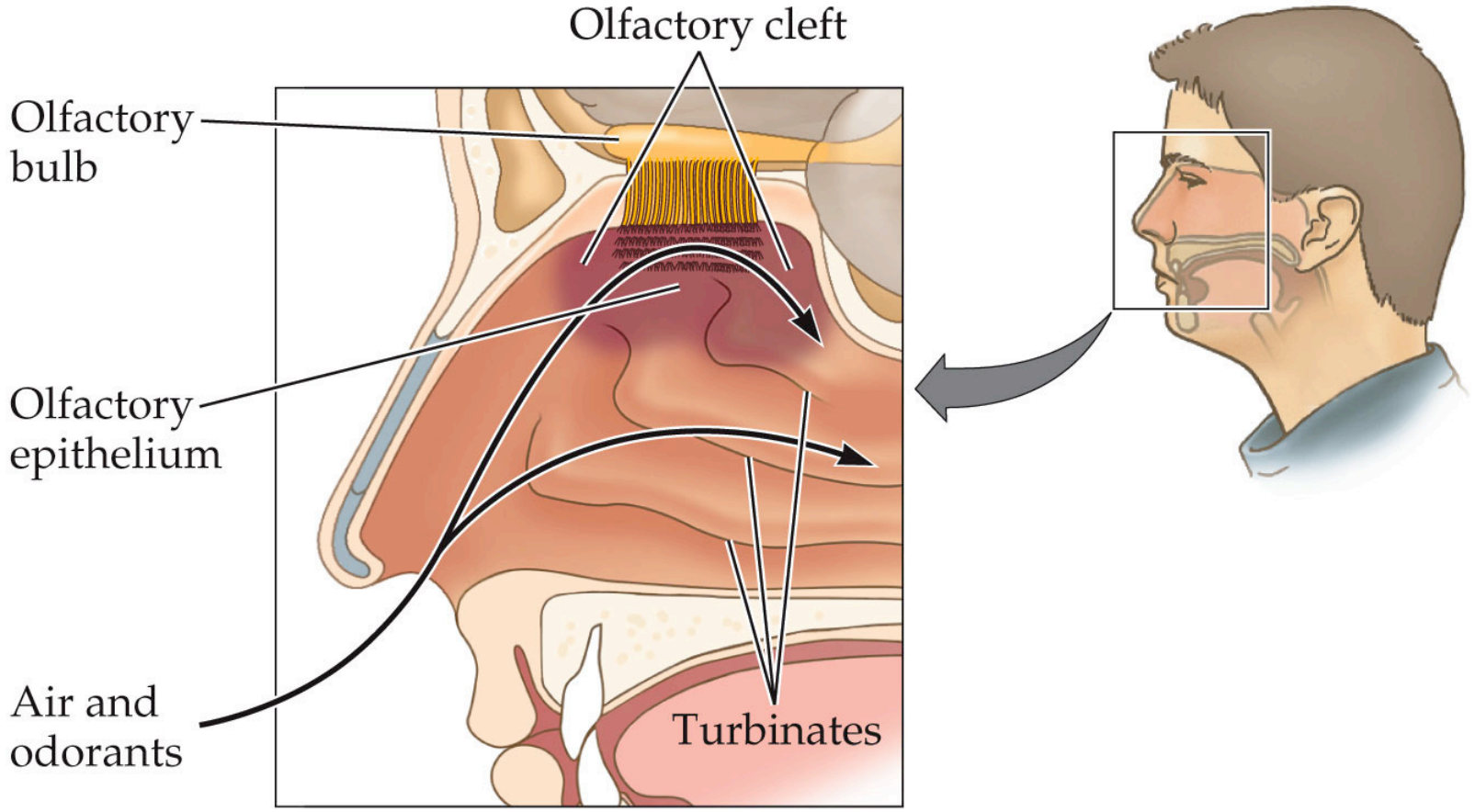
How good is our sense of smell?

- Latest findings suggest we can detect over one trillion smells!
- We can only detect about 7.5 million colors.

(Oh really!)

Physiology of the Olfactory System

The nose



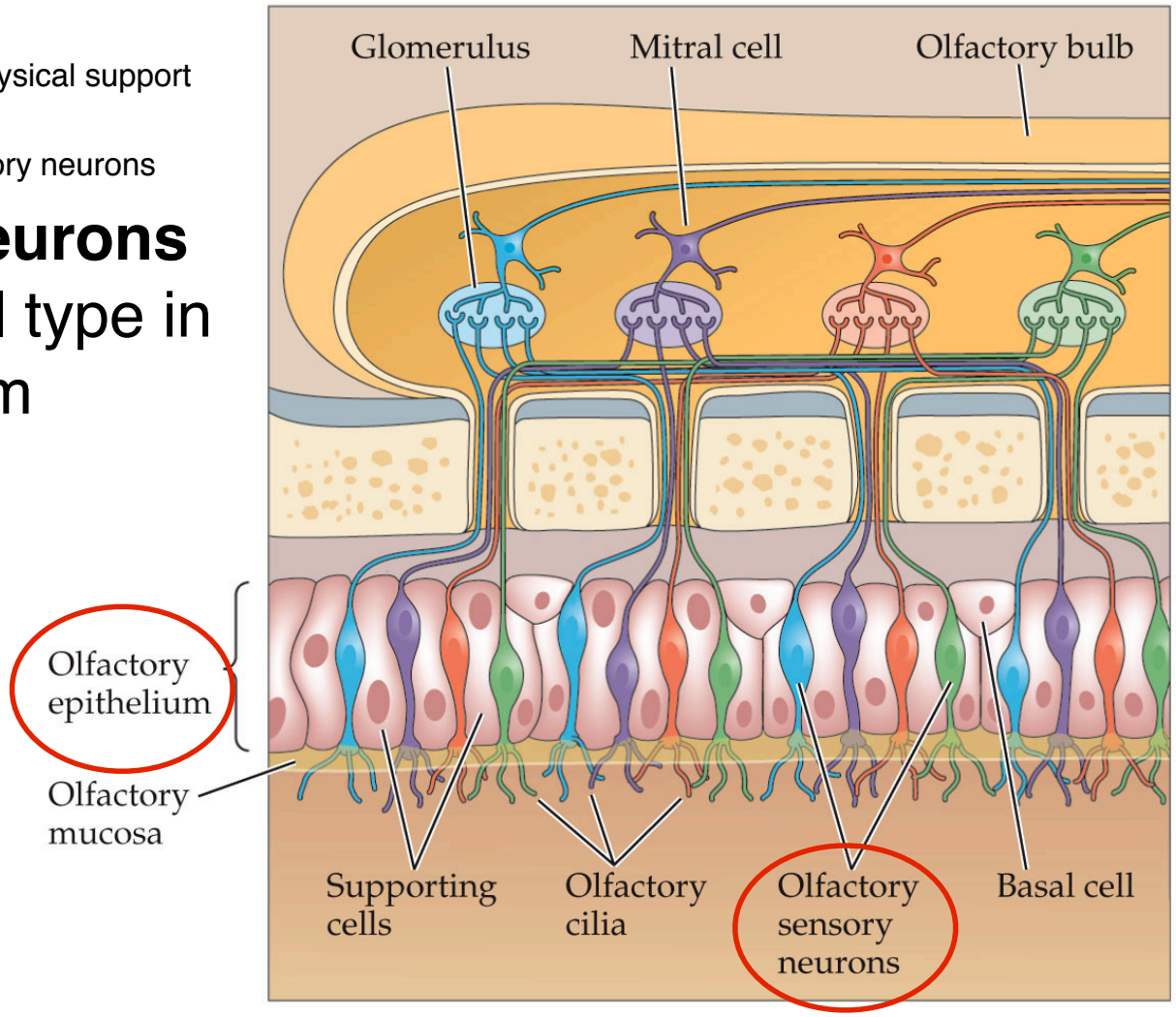
- **Olfactory cleft**: space at the back of the nose into which air flows, where the main olfactory epithelium is located
- **Olfactory epithelium**: secretory mucosa whose primary function is to detect odorants

Olfactory epithelium: the "retina of the nose"

Three cell types

- **Supporting cells**: Provides 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

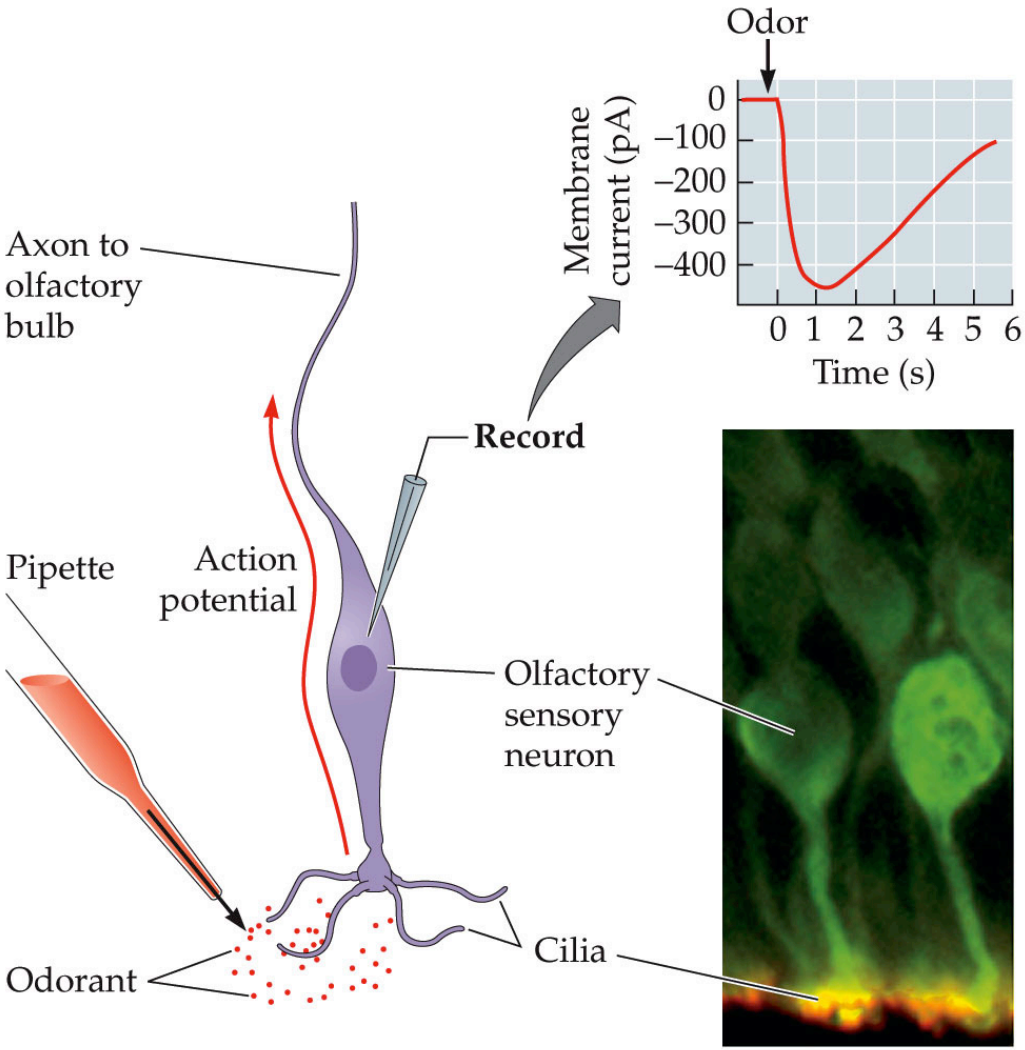
• OSNs make direct contact with physical stimulus
(i.e., unlike in retina, cochlea, or skin)



Olfactory sensory neuron

- Responses are slow!

- OSN axons among the thinnest and slowest in the body

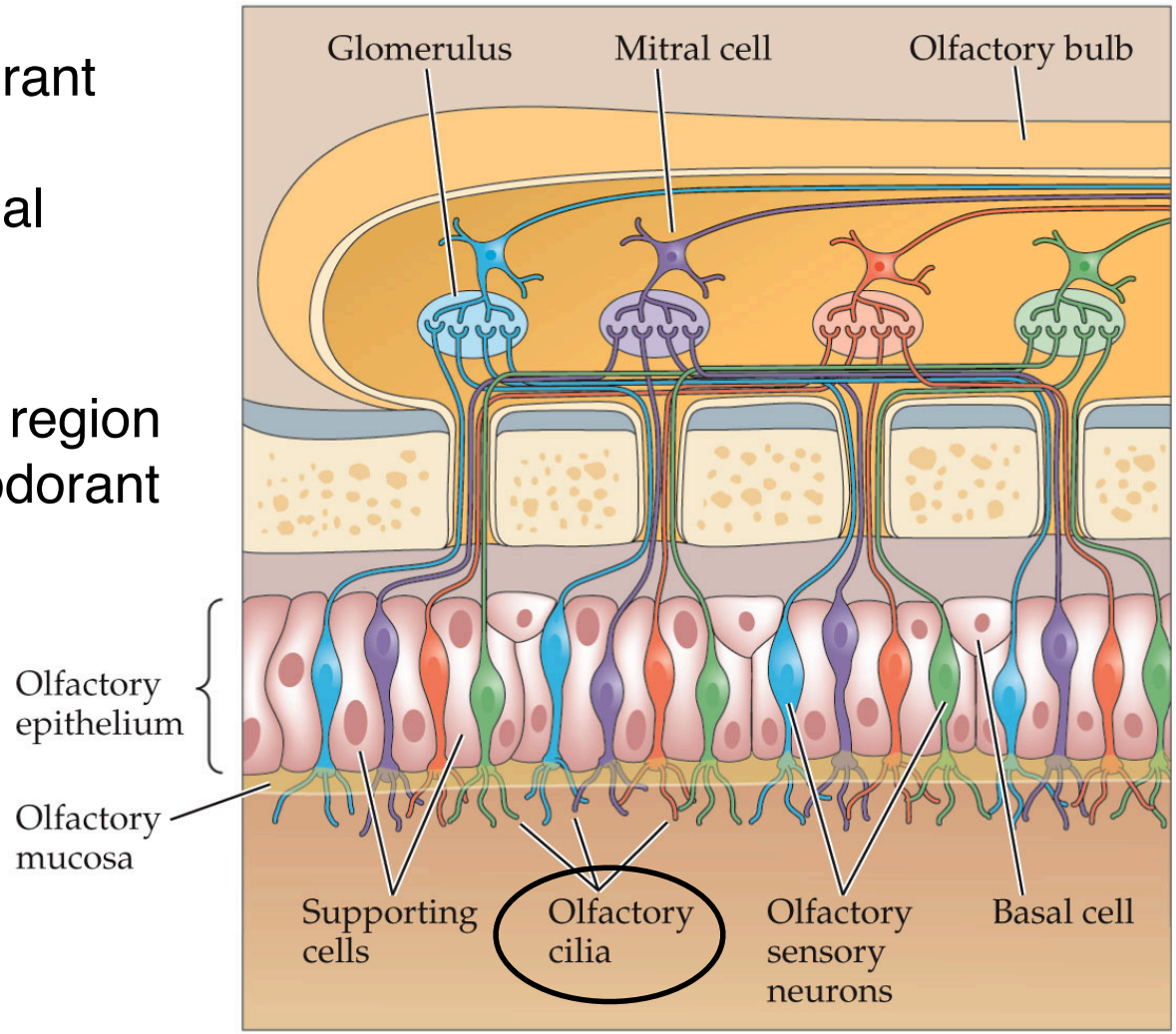


Olfactory epithelium: the "retina of the nose"

Cilia: Hairlike protrusions on OSN dendrites
- Have receptor sites for odorant molecules.
- structures for olfactory signal transduction

Olfactory receptor (OR): The region on the cilia of OSNs where odorant molecules bind

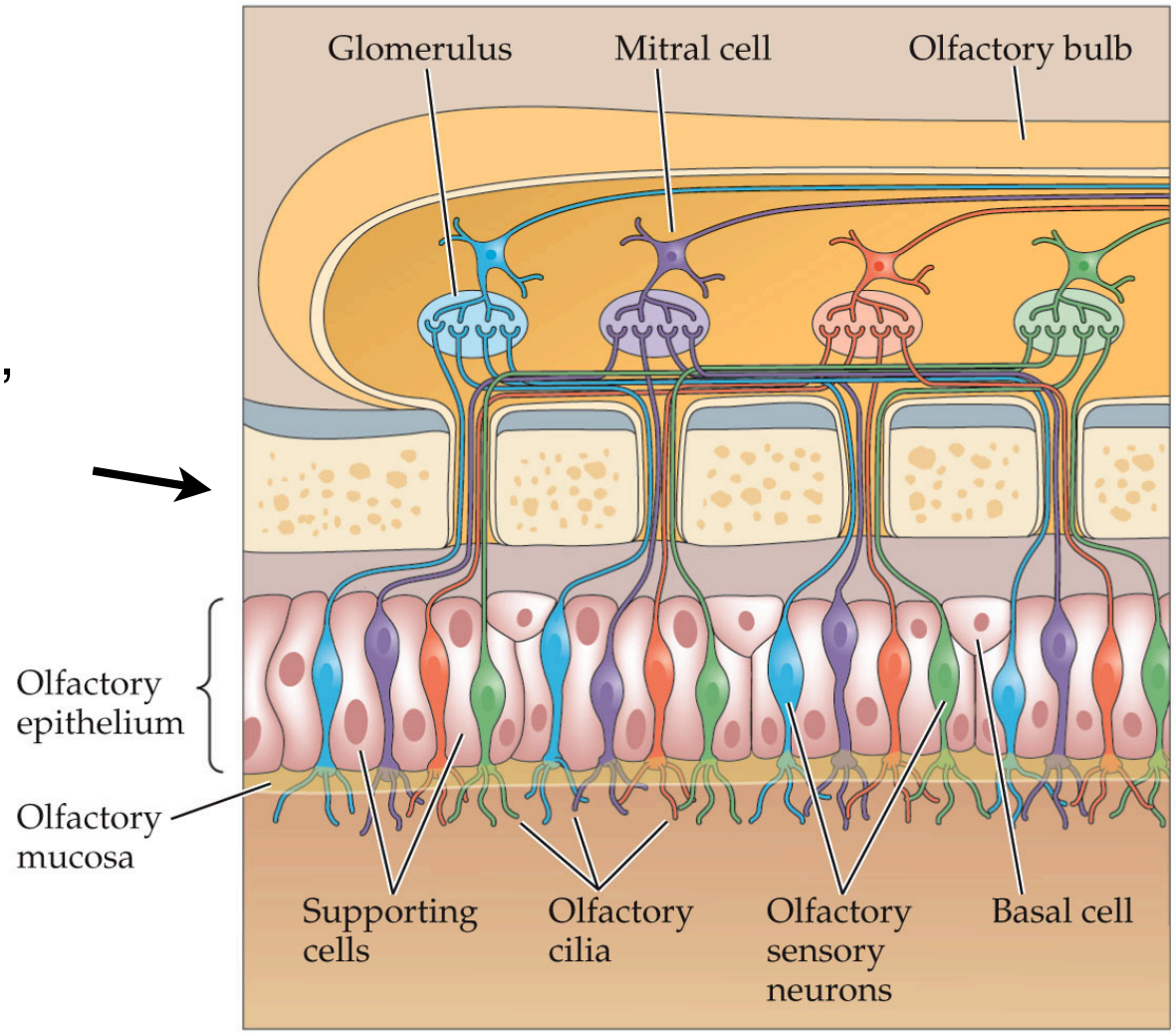
- Takes seven or eight odor molecules binding to a receptor to initiate an action potential



Olfactory epithelium: the "retina of the nose"

Cribriform plate: bony structure with tiny holes (even with the eyebrows), separating the nose from the brain

- Axons from OSNs pass through the tiny holes to enter the brain

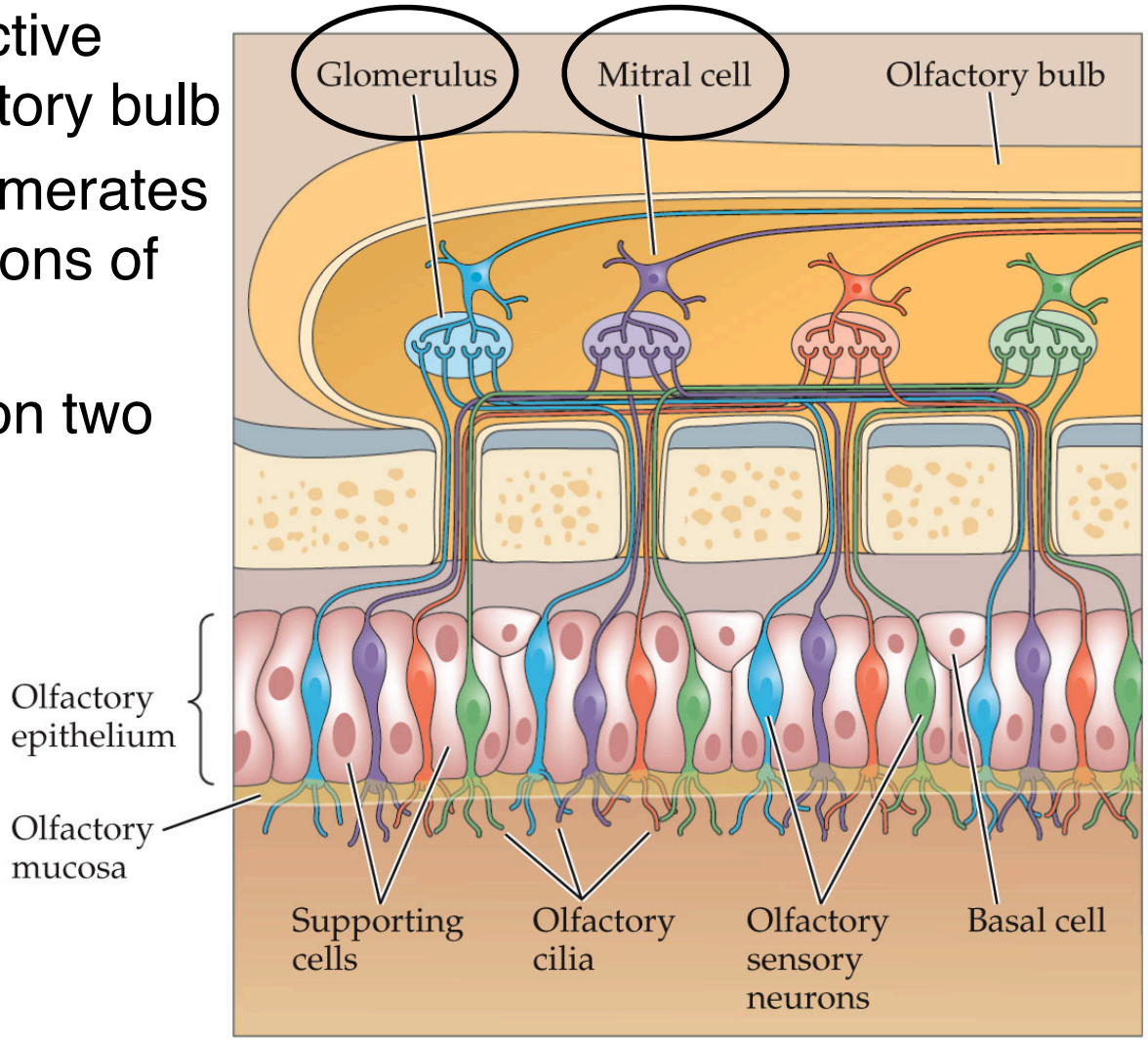


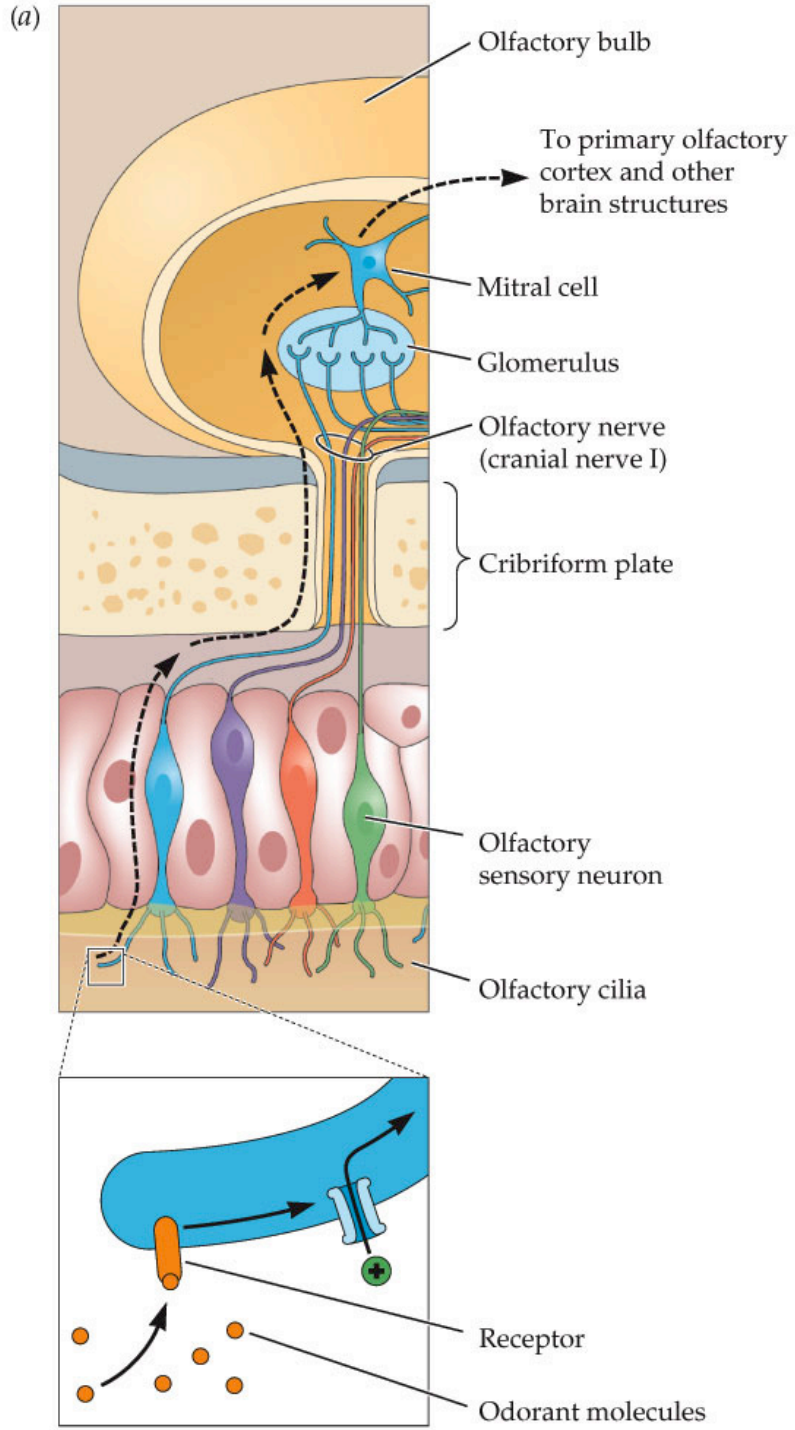
Olfactory epithelium: the "retina of the nose"

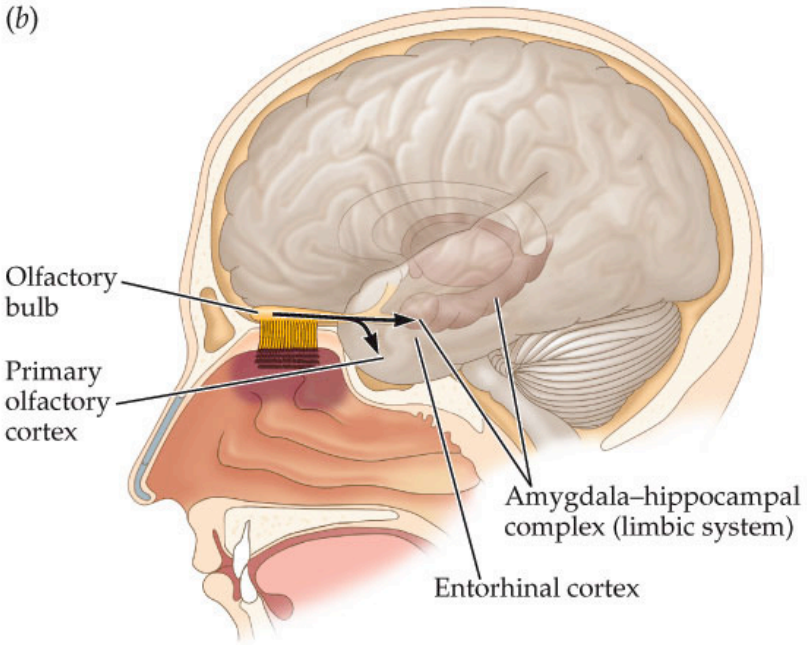
Mitral cells: The main projective output neurons in the olfactory bulb

Glomeruli: Spherical conglomerates containing the incoming axons of the OSNs

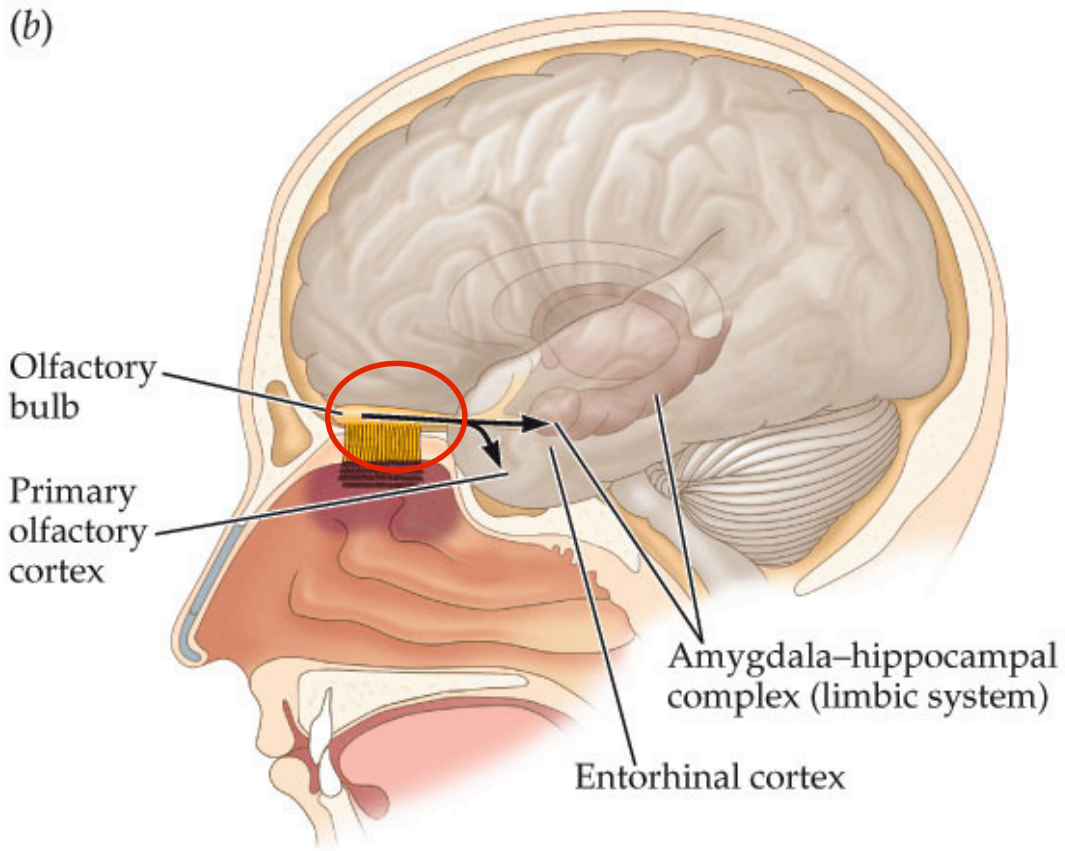
- Each OSN converges on two glomeruli





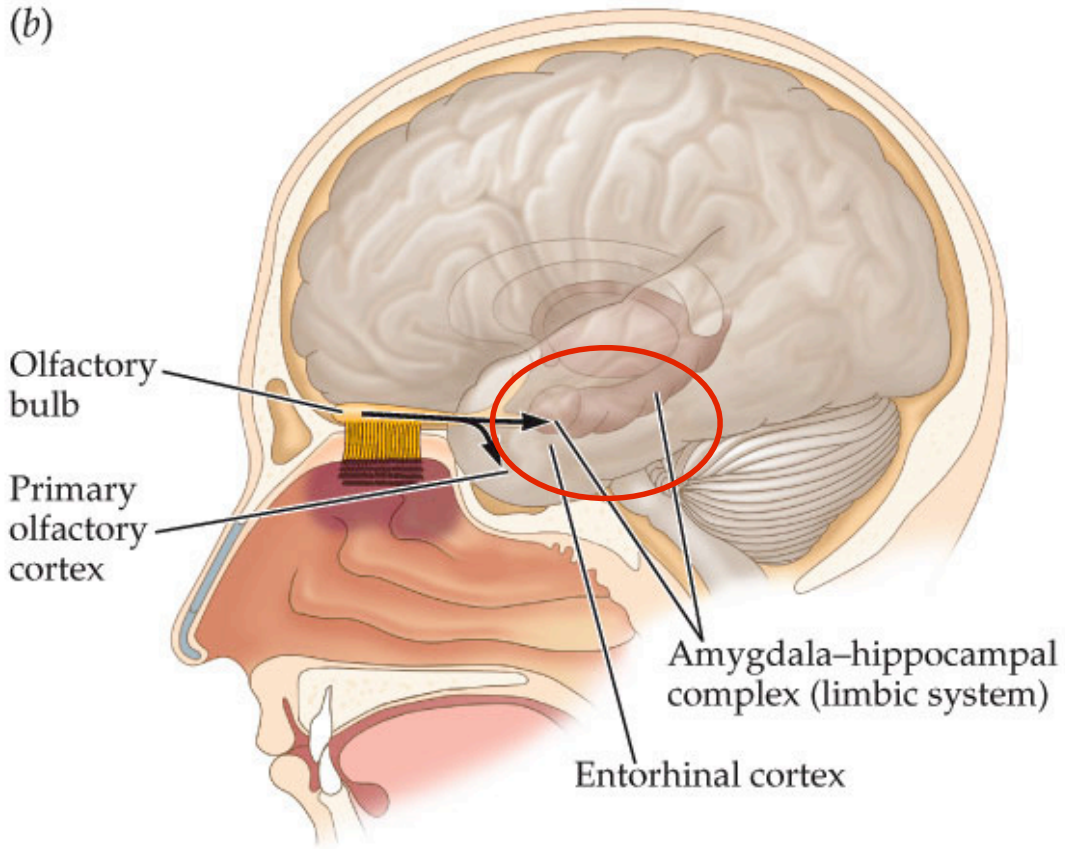


Sensory pathway for olfactory system



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.

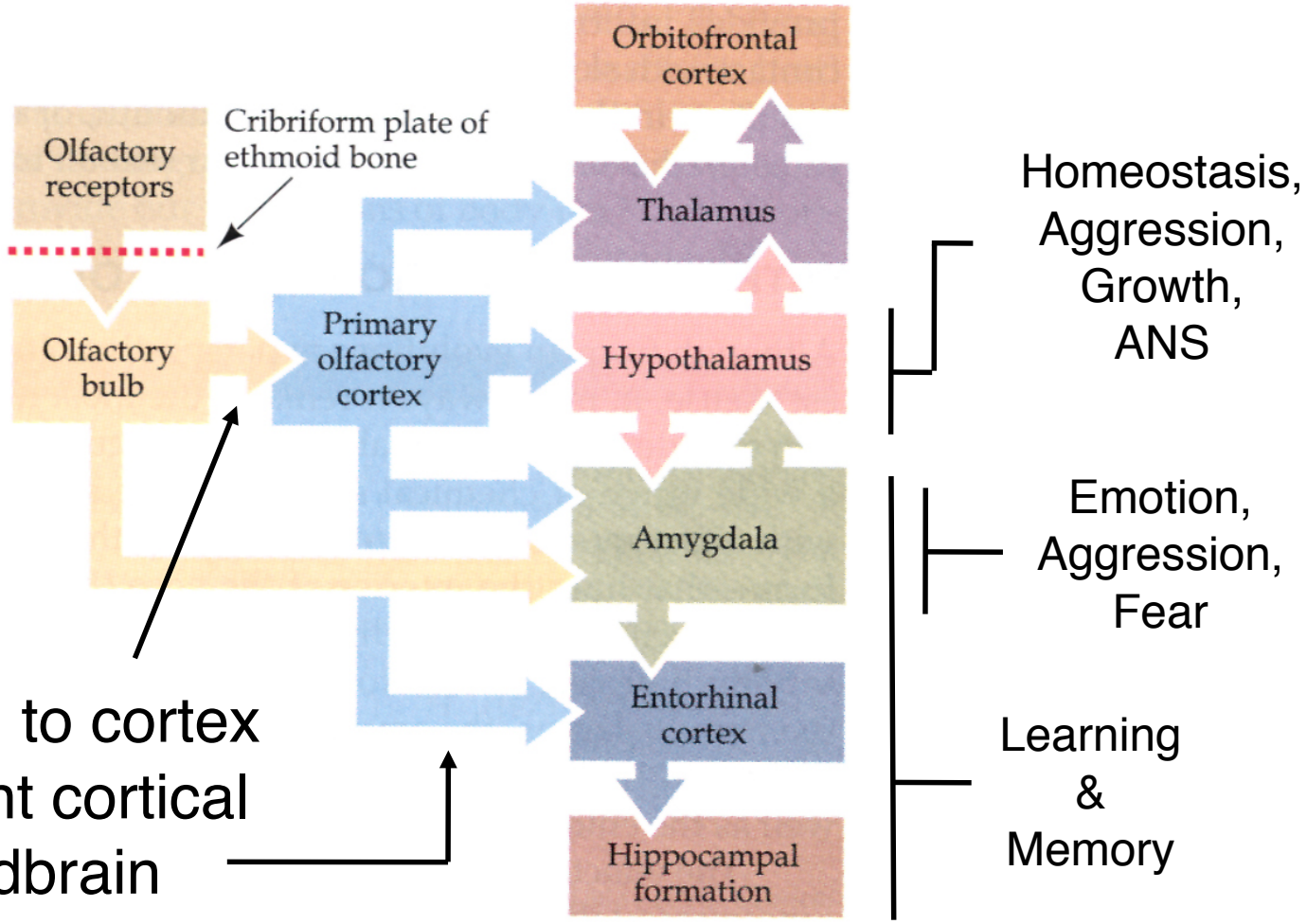


Primary olfactory cortex: cortical area where olfactory information is first processed.

Limbic system:

- Involved in many aspects of emotion and memory
- Olfaction is unique for its direct connection to limbic system

Why Olfaction is Weird



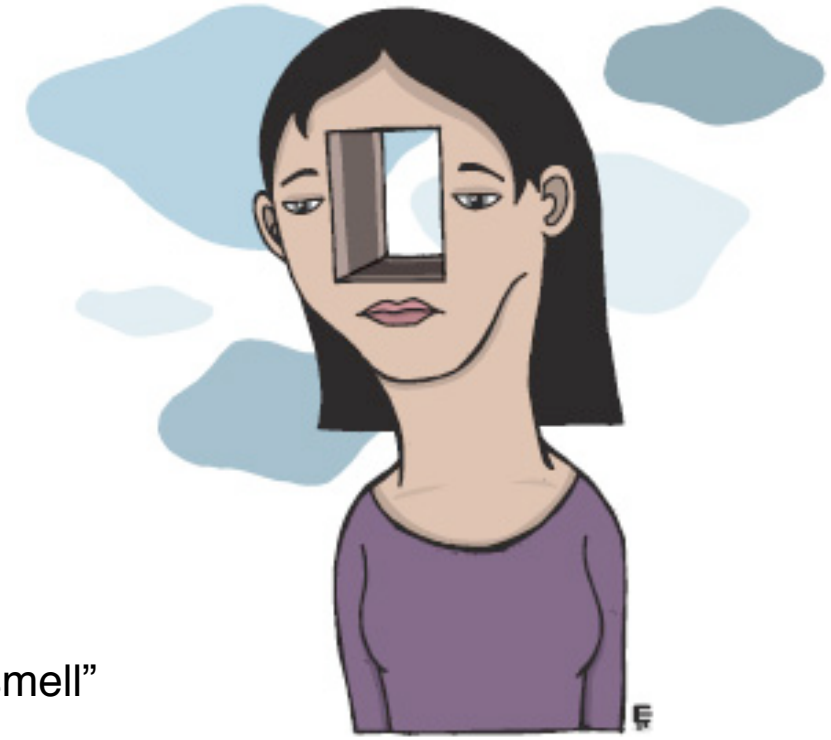
- *direct* connection to cortex
- many subsequent cortical connections to midbrain

- also, no "smell-o-topic" maps: no topography (that we know of)

Olfactory Physiology

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



Essay: "The Miseries of losing one's sense of smell"
http://www.slate.com/id/2195018/

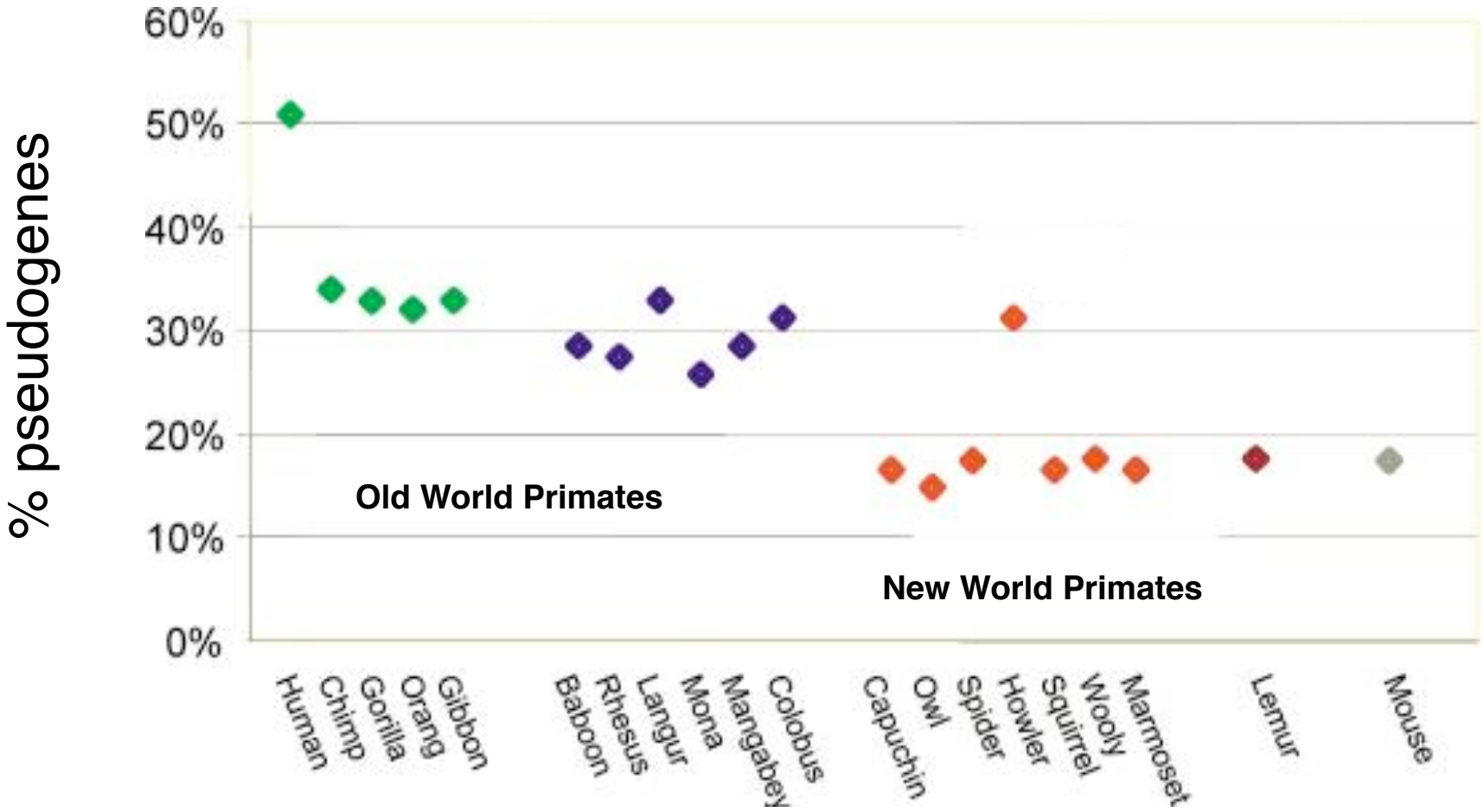
Genetic basis of olfactory receptors:

- Buck and Axel (1991) showed that genome contains about 1000 different olfactory receptor genes; each codes for a single type of OR

  - All mammals have pretty much the same 1000 genes.
  - However, some genes are non-functional **"pseudogenes"**
    - Dogs and mice: About 20% are pseudogenes
    - Humans: Between 60% and 70% are pseudogenes

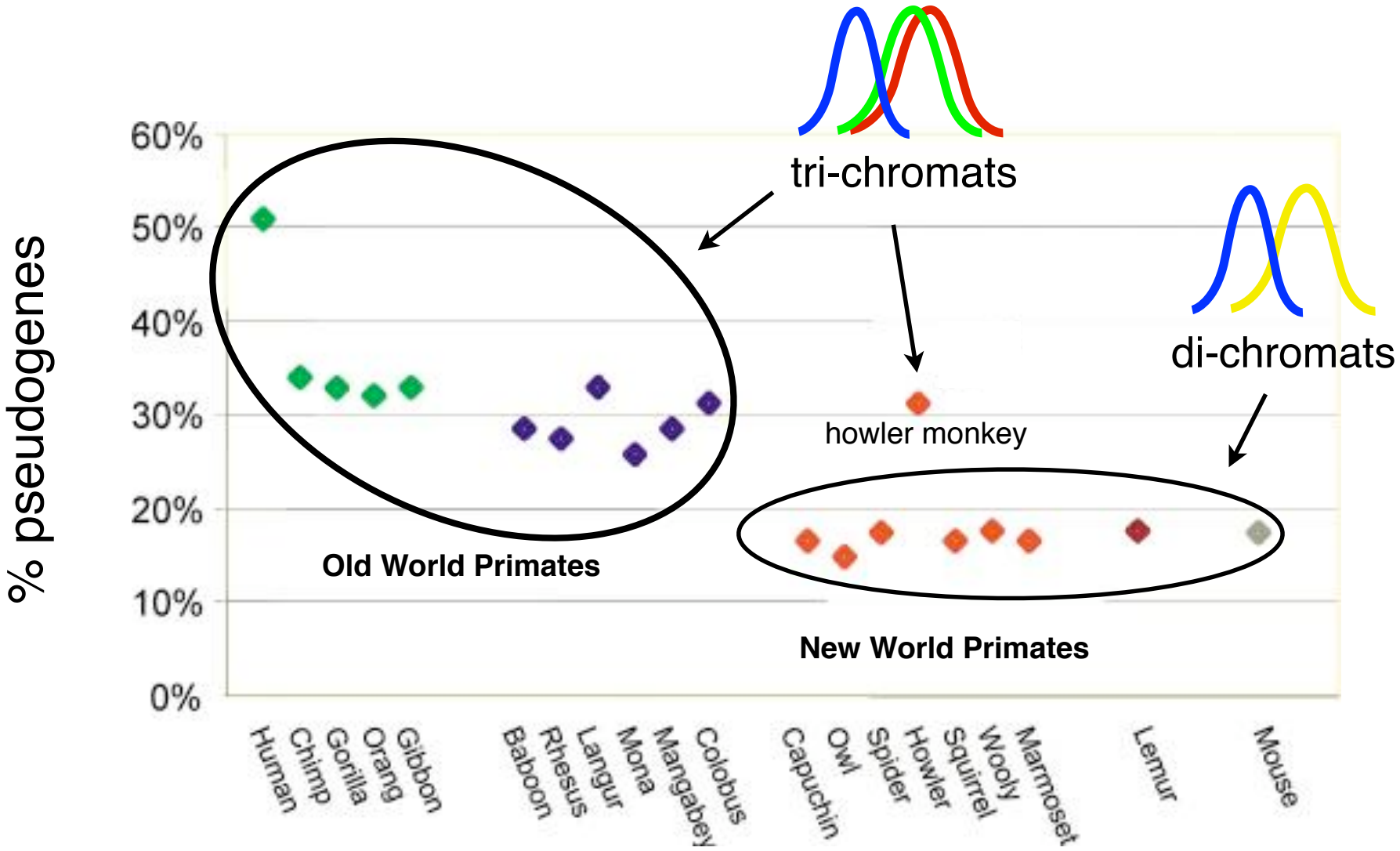
Each person has a different number of pseudogenes, resulting in individual differences in sensitivity to smells

Evolutionary trade-off between vision and olfaction

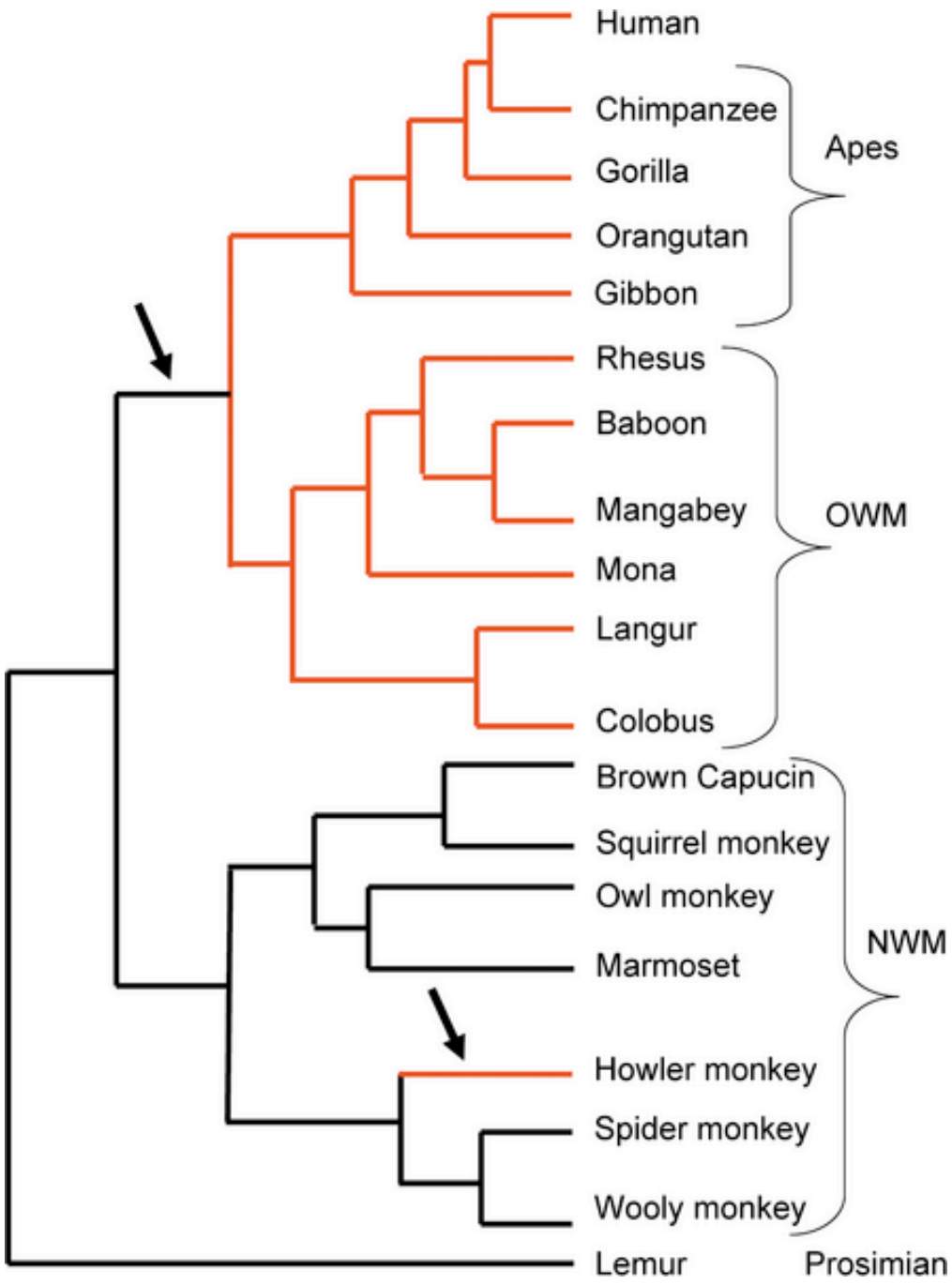


Gilad et al, PLoS 2004

Evolutionary trade-off between vision and olfaction



Gilad et al 2004

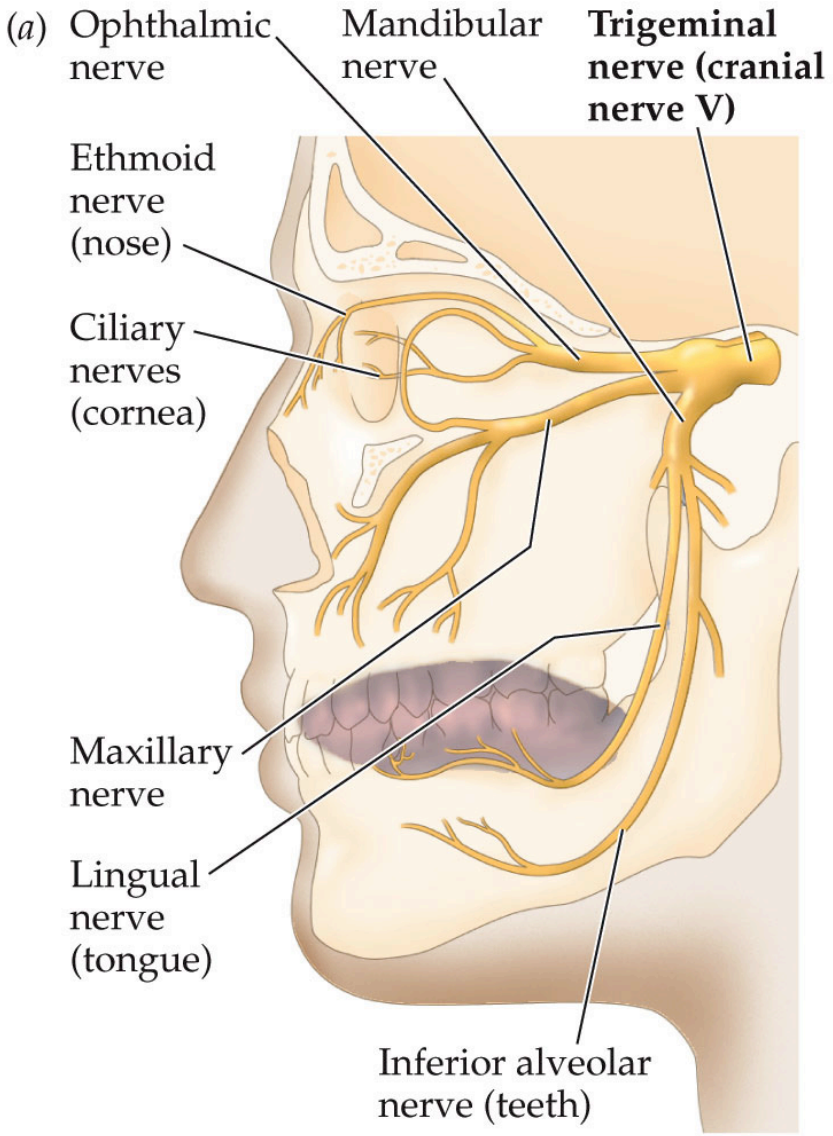


Black arrows indicate on which lineages the acquisition of full trichromatic color vision occurred.

Red lines show lineages with a high proportion of OR pseudogenes

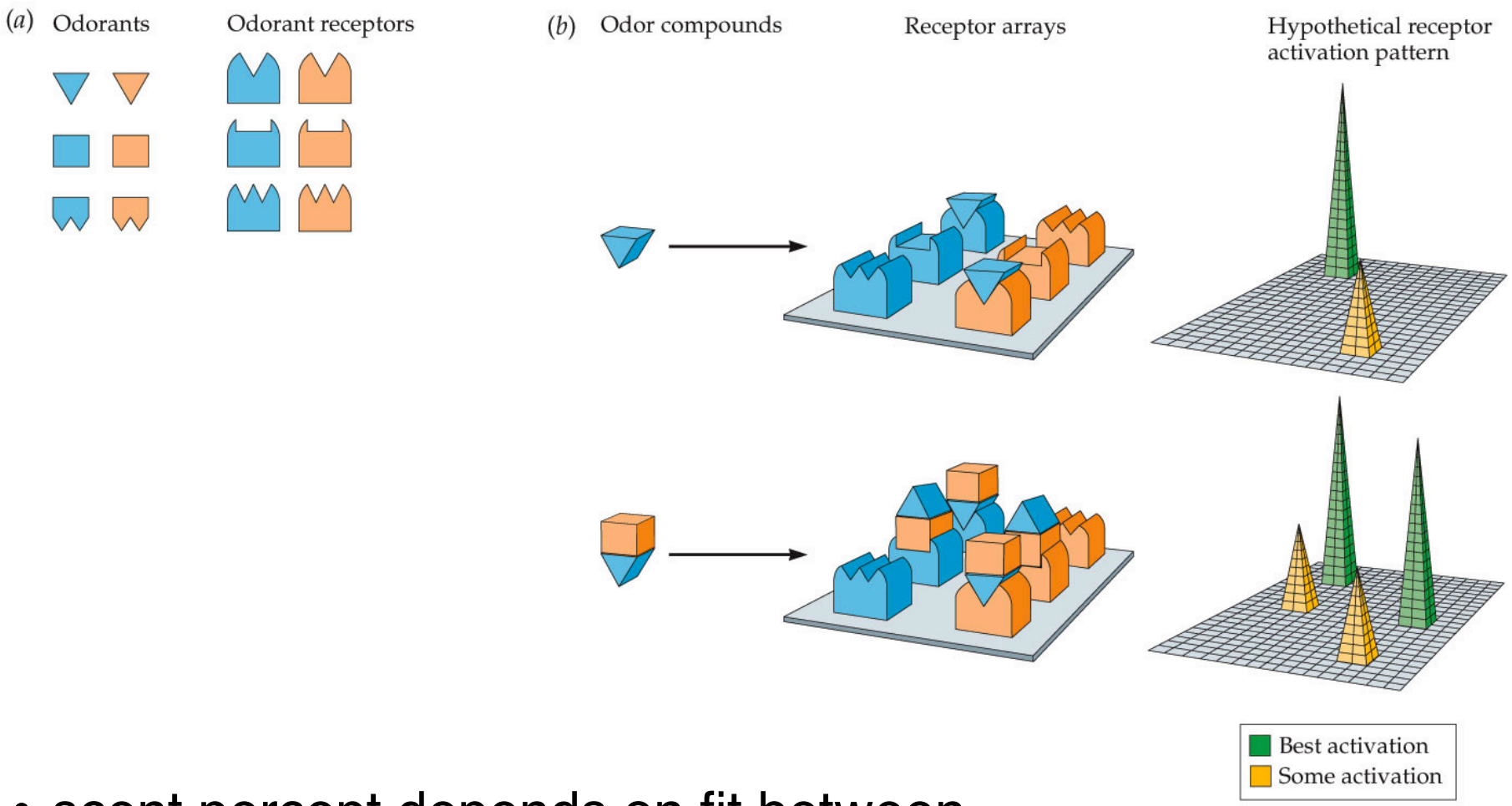
Gilad et al 2004

The trigeminal nerve's role in the perception of odors



Carries pain and temperature information from mouth and nose

shape-pattern theory of olfactory perception



- scent percept depends on fit between OR shape and odorant shape

Theories of olfactory perception:

- **Shape-pattern theory**: The current dominant theory.

  - The binding pattern of odorants in the olfactory epithelium produces specific firing patterns of neurons in the olfactory bulb, which then determine the particular scent we perceive

- **Vibration theory**: now defunct.

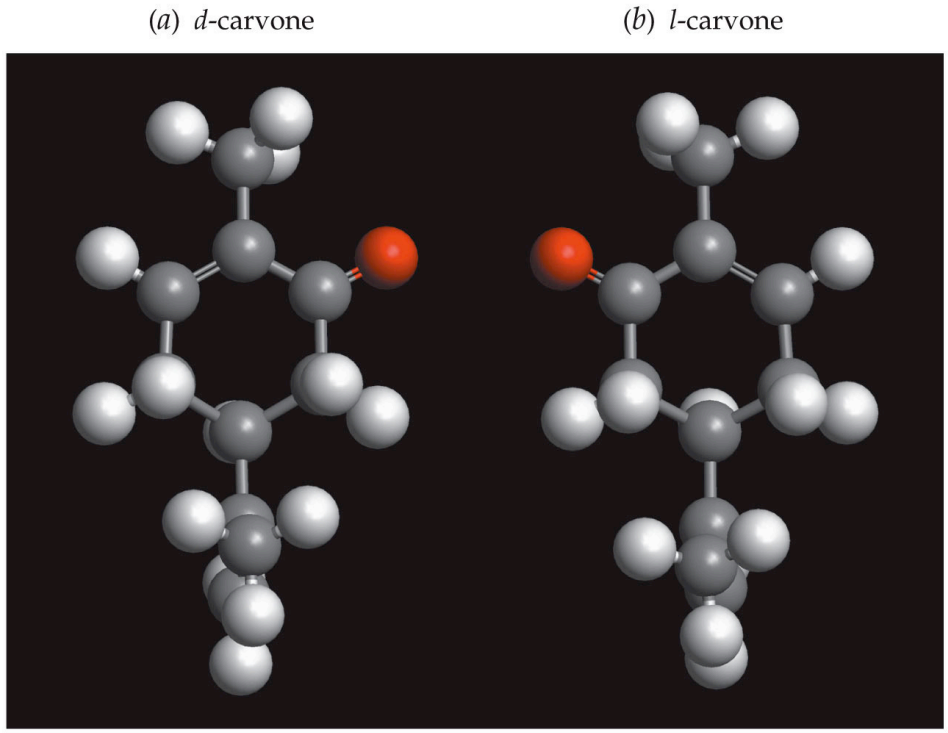
  - Proposes that every perceived smell has a different vibrational frequency, and that molecules that produce the same vibrational frequencies will smell the same

(or is it? See this bizarre TED talk: https://www.ted.com/talks/luca_turin_on_the_science_of_scent)

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 cannot explain this phenomenon

Theory that molecules with similar vibration frequencies should smell similarly



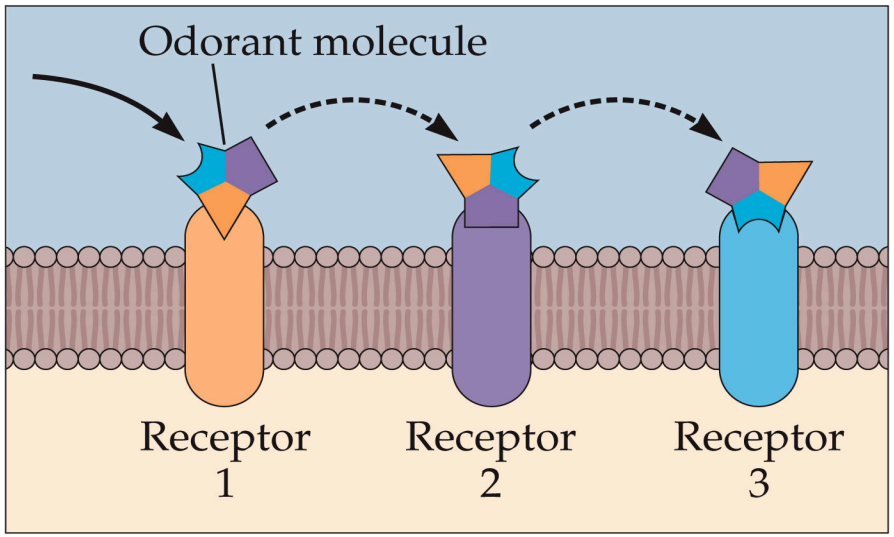
smells of caraway

smells of spearmint

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 pattern of activity across many receptor types
- Intensity of odorant changes which receptors are activated (Weak concentrations of an odorant may not smell the same as strong concentrations of it!)
- Specific time-order of activation of OR receptors is important



Bi-nostral smelling: why have two nostrils?

"The world smells different to each nostril"

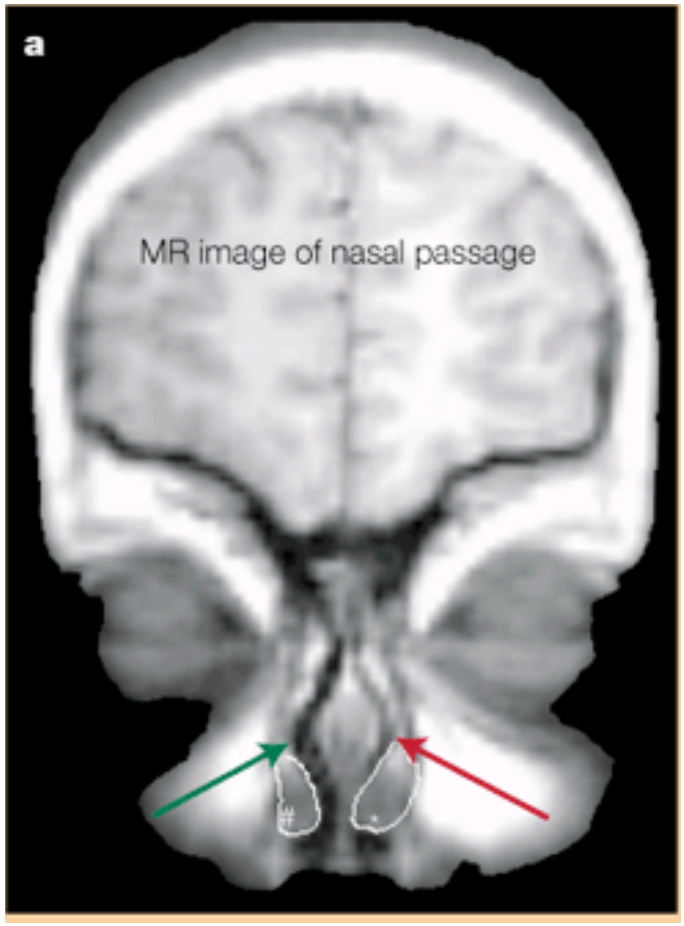
Sobel et al, Nature 2000

Background

1. Airflow is greater into one nostril than the other, due to slight swelling that obstructs airflow.
2. Switches nostrils several times per hour.

Q: What are the consequences for olfaction?

Bi-nostral smelling: why have two nostrils?



un-obstructed nostril
(relaxed turbinates)

Background

1. Airflow is greater into one nostril than the other, due to slight swelling that obstructs airflow.
2. Switches nostrils several times per hour.

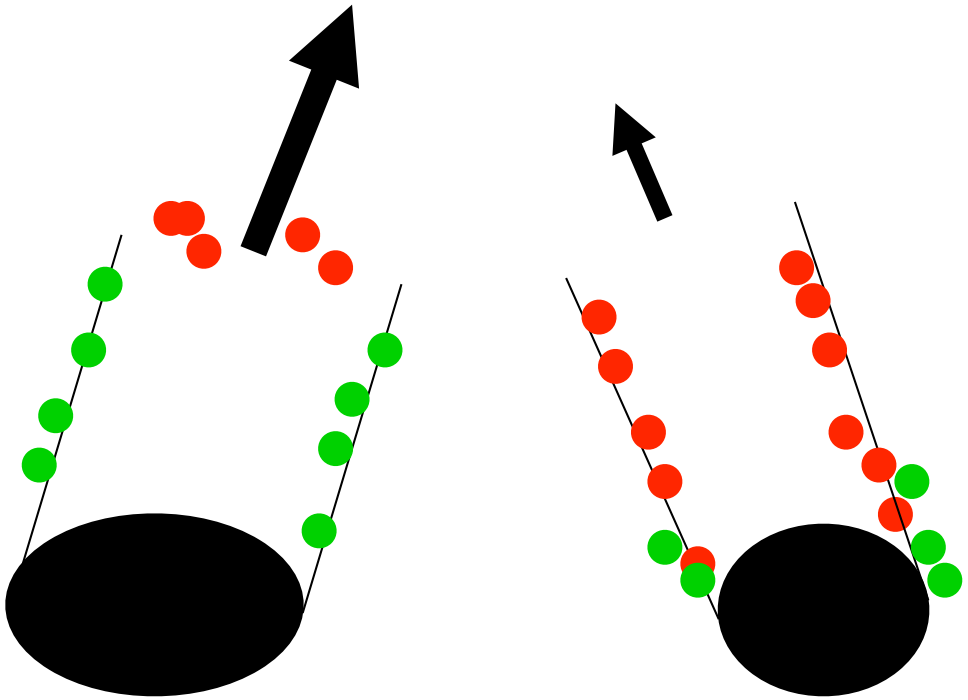
Obstructed nostril
(swollen turbinates)

- Odorants sorb across nasal mucosa at different rates

- “high-sorption” odorant – induces small response when airflow is low, and large one when airflow is high

- “low-sorption” odorant – large response when airflow is low; small

Finding: odorants do indeed smell different in nostrils, depending on the air flow and sorption of the odorant!



Olfactory Psychophysics

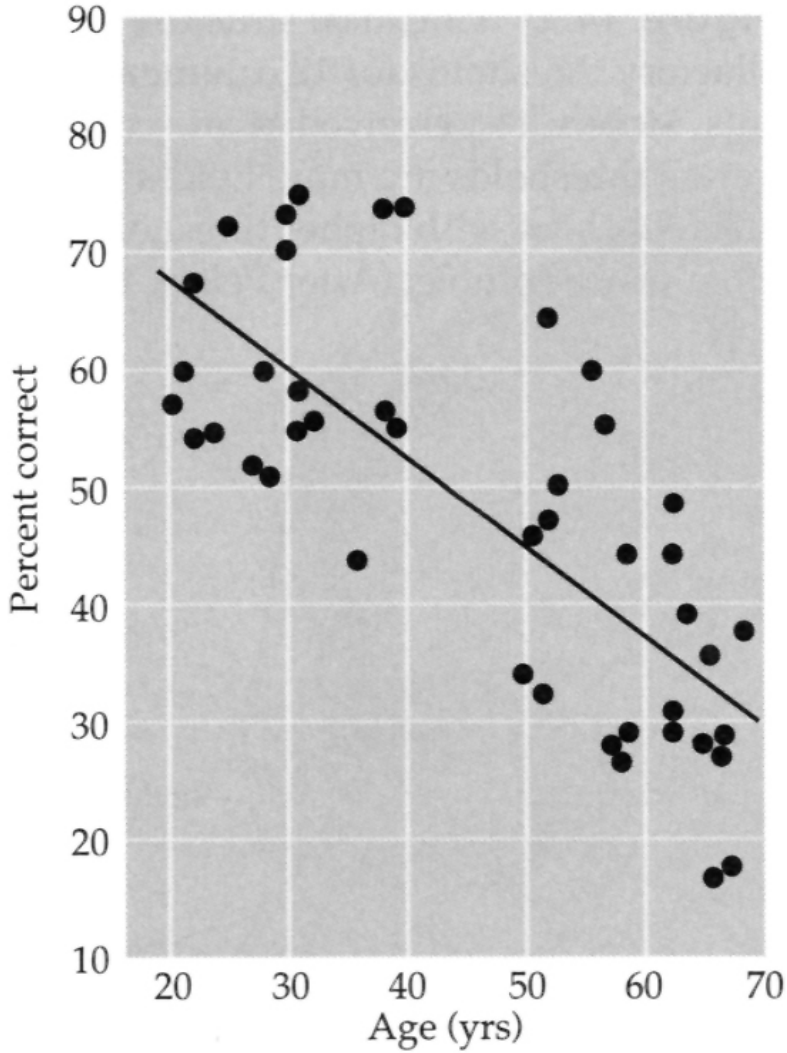
- How much stimulation is required before we perceive something to be there?

- 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

And also:

- Age: By 85, 50% of population is effectively anosmic

(like those high-pitched noises, enjoy smelling while you still can!)



Olfactory Hedonics

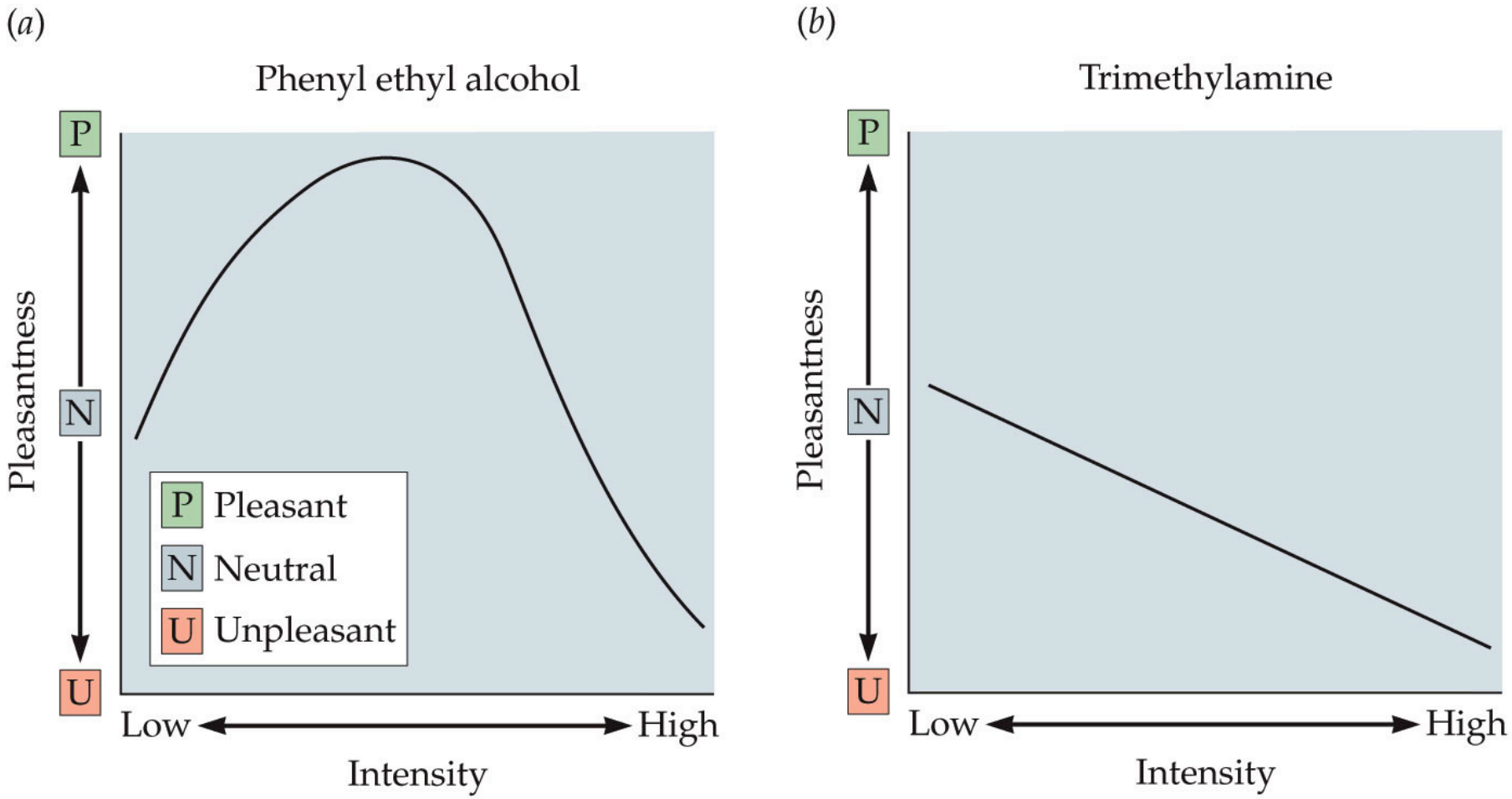
Odor hedonics: the “liking” dimension of odor perception

- measured with scales of *pleasantness*, *familiarity*, and *intensity*

Familiarity and intensity:

- Pleasantness: obvious
- Familiarity: tend to like odors we’ve smelled before
- Intensity: more complicated relationship with odor liking

Odorants: Pleasantness vs. intensity



inverted U-shaped function

Linearly decreasing function

Olfactory Hedonics

Nature or nurture?

- Long-standing debate: innate vs. learned
- **verdict**: almost completely "nurture"
- infants: not put off by sweat or feces; don't discriminate banana from smell of rancid food
- Cross-cultural data support associative learning

- Wintergreen study (Moncrief, 1966)
  - Americans like it.
  - English rated it the most unpleasant of many odors (used in medicine)

- US Army: tried to develop stink bomb for crowd dispersal: couldn't find a smell that was universally disgusting (including "US Army Issue Latrine Scent")

Japanese and American people have very different tastes in food

Cheese

• disgusting to most Japanese

Natto

• fermented soybeans; Japanese breakfast food

Olfactory Hedonics

- Evolutionary argument: *generalists* (like us, and roaches) don't need innate smell aversions to predators

- **learned taste aversion**: Avoidance of a flavor after it has been paired with gastric illness.
  - finding: from the smell, not the taste (Bartoshuk 1990)

Two caveats for theory that odor hedonics are mostly learned:

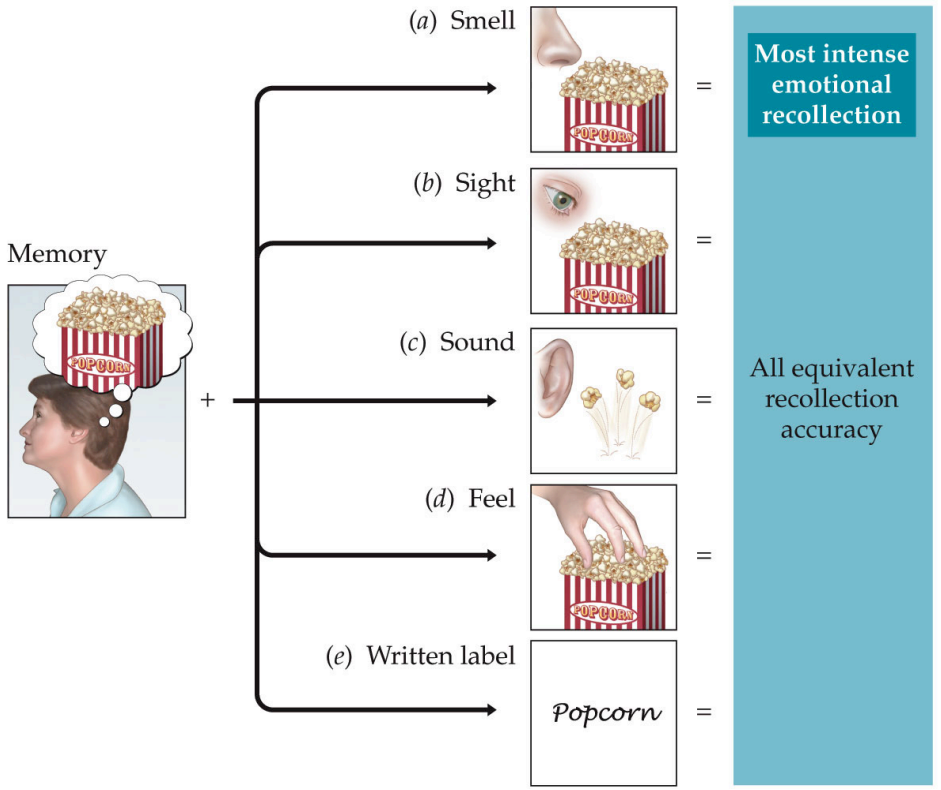
- (Trigeminally) irritating odors may elicit pain responses, which all humans have an innate drive to avoid.
- Potential variability in receptor genes and pseudogenes that are expressed across individuals.

Olfaction and memory

Q: are odors really the best cues to memories?

- Memories triggered by odor cues are distinctive in their emotionality
- But *not* (it turns out) more accurate

The smell, sight, sound, feel, and verbal label of popcorn elicit memories equivalent in terms of accuracy but not emotion



Olfaction summary

- odors, odorants
- scent tracking, binostril smelling (2 reasons)
- olfactory cleft, olfactory epithelium
- Olfactory Receptors (ORs), located on cilia
- Olfactory Sensory Neurons (ORNs)
- cribiform plate, glomeruli, mitral cells, olfactory bulb, primary olfactory cortex, limbic system
- anosmia
- pseudogenes and trichromatic color vision
- shape-pattern theory
- olfactory hedonics, learned taste aversion
- olfaction and memory
- pheromones / chemosignals & VNO (in book)

Extra slides
(not discussed in lecture):

Pheromones and the
Vomeronasal Organ (VNO)

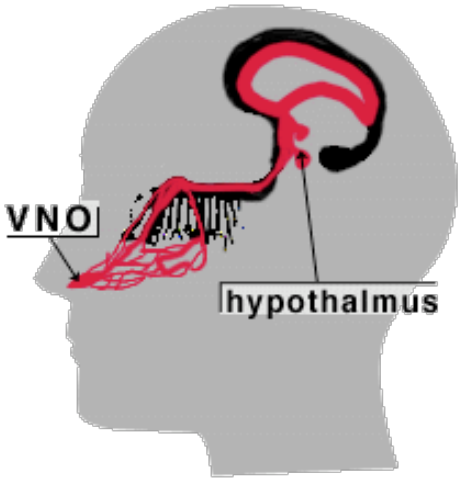
Pheromones and the vomeronasal organ

Pheromone: chemical (bigger than odorants!) emitted by one member of a species that triggers a response in *another member of the same species*

- for communication; need not have any smell

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 (e.g., pheromones)

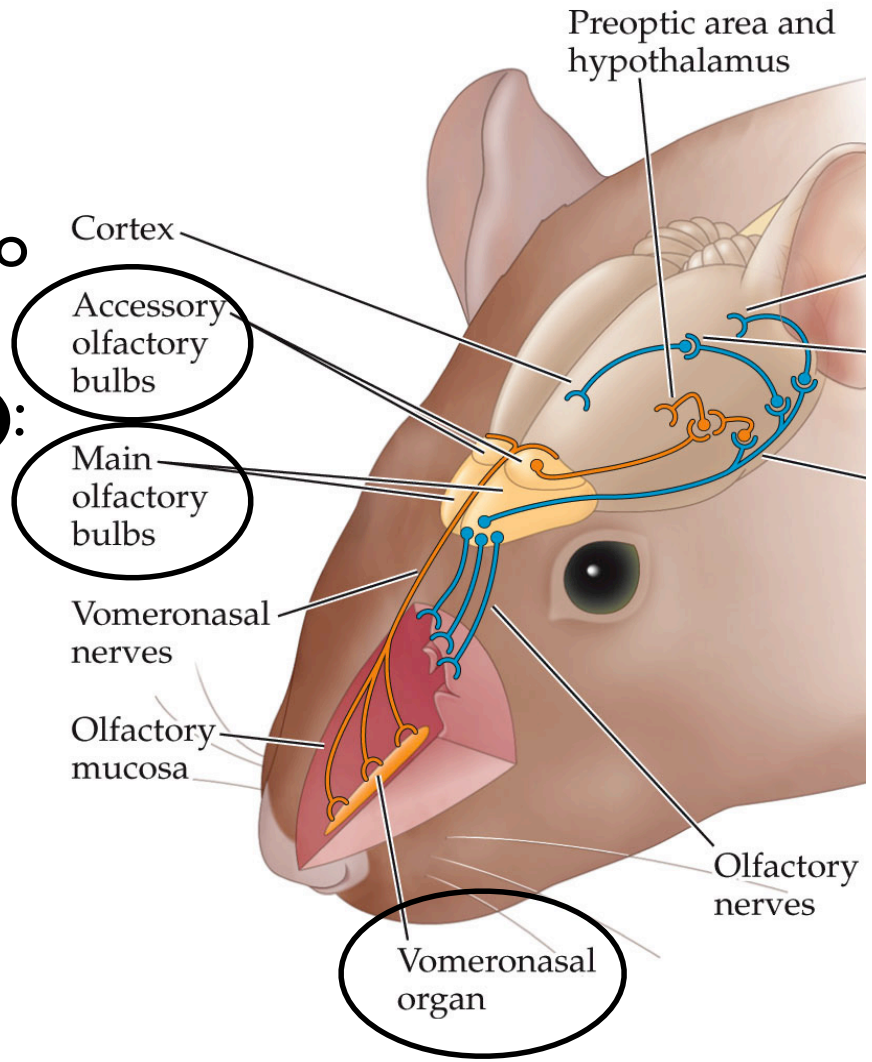


• Snakes collect pheromones on tongue.
• VNO on roof of mouth

The olfactory system of a hamster

In 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"
- **Accessory olfactory bulb (AOB)**: A smaller neural structure located behind the MOB that receives input from the vomeronasal organ



Pheromones

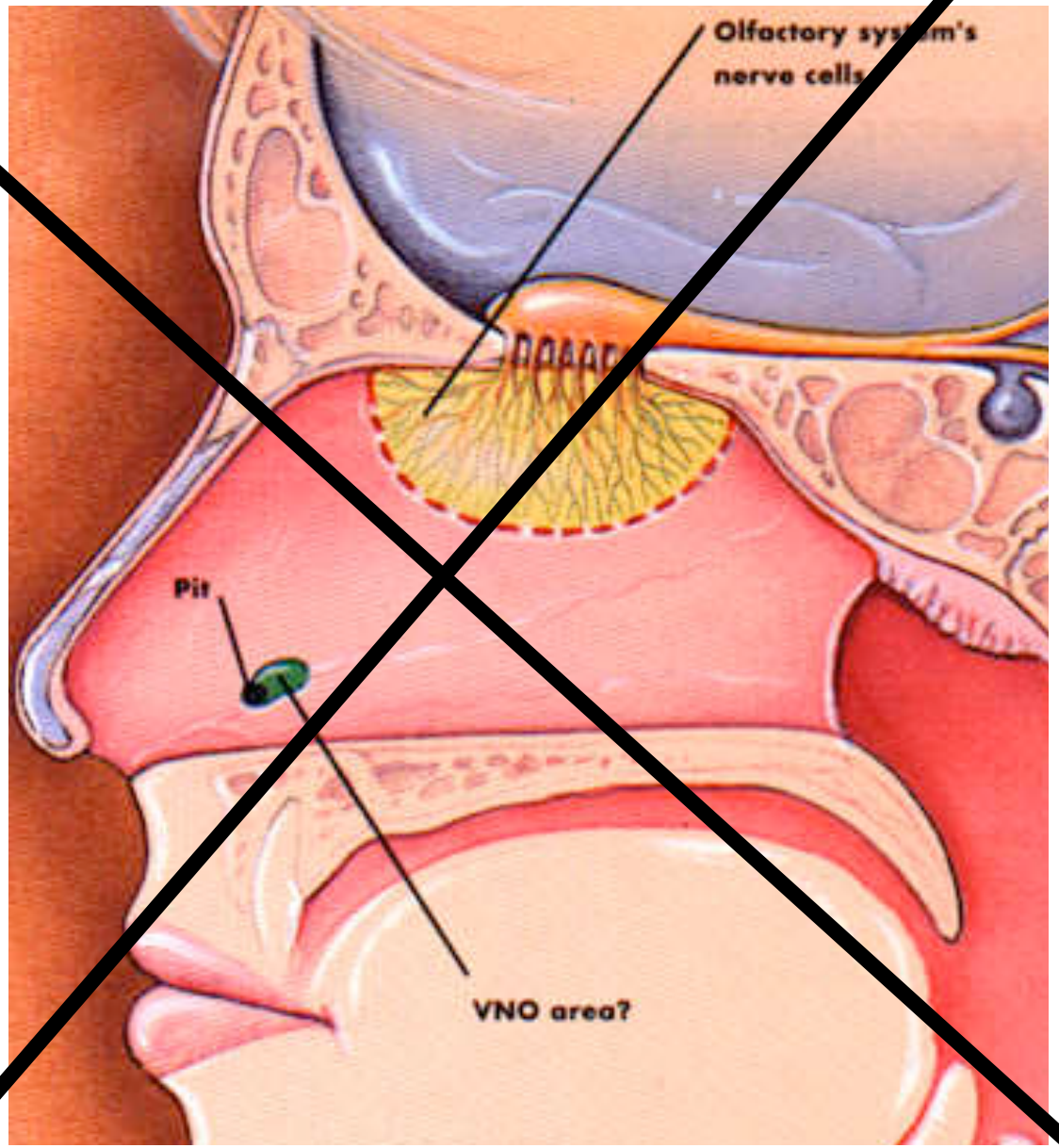
- most important for communication in the social insects
    - e.g., tell other bees when to sting us

- also convey important information for many non-insect species, including primates

- Often provide signals about when a female is fertile, signaling 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

VNO in humans?

- tiny pit located on the divider between the nostrils
- highly controversial!



No functioning VNO or AOB in adults

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

- Controversial - some have argued it's a statistical artifact.
- Unknown mechanism

Do humans respond to pheromones?

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 neutral word than "pheromone" should be used when discussing humans.

e.g. **"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 pheromones?

- 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

(take with giant grain of salt!)

Miller et al 2007