Olfaction (Chap 14)

Lecture 20

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Sensation & Perception (NEU 325 / PSY 345)
Spring 2023
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?

our “machinery” is less sensitive than other animals (dogs, etc.)

• 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

Bloodhound tracking a pheasant through a field

Conventional wisdom is wrong!

Human tracking a scent trail through a field

Porter et al 2007
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

“nasal prism”

(24% slower w/ 1 nostril)
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
• **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

- Short life span: OSNs die and are regenerated every ~6 weeks
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

% pseudogenes

species (color-coded by family)

Old World Primates

New World Primates

tri-chromats

di-chromats

howler monkey

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.
The trigeminal nerve’s role in the perception of odors

(a) The trigeminal nerve (cranial nerve V) carries pain and temperature information from the mouth and nose.

(b) The diagram illustrates the distribution of sensory nerves:
- Ophthalmic nerve (nose)
- Ethmoid nerve (nose)
- Ciliary nerves (cornea)
- Maxillary nerve
- Lingual nerve (tongue)
- Inferior alveolar nerve (teeth)

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](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

![Molecular structures of $d$-carvone and $l$-carvone](image)

- **(a) $d$-carvone** smells of caraway
- **(b) $l$-carvone** smells of spearmint
OR receptor activation timing and order

- Different odorants activate the same receptors with different timing
- Explains how we can detect far more odorants than # of ORs
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?

**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.

un-obstructed nostril (relaxed turbinates)

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-frequency sine waves, 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

(a) Phenyl ethyl alcohol

(b) Trimethylamine

inverted U-shaped function

Linearly decreasing function
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