COURSE NOTES FOR
SENSATION AND PERCEPTION II
3270

The web page for this course is: http://www.yorku.ca/harris/3270

Section 1  Principles of Neural Organization
Keywords
Notes on sensory coding
READINGS: Goldstein Chapter 2 pg 22-41

Section 2  Psychophysics
Keywords
READINGS: Goldstein Chapter 1 pg 11-18
Goldstein Appendix. pg 401-406

Section 3  Somatosensory System
Keywords
READINGS: Goldstein Chapter 14 pg 329-351
Vestibular keywords and notes

Section 4  Taste and smell
Keywords
READINGS: Goldstein Chapter 15 pg 355-377

Section 5  Time perception
Keywords
See web page http://www.yorku.ca/harris/ppt_files/

Section 6  Speech perception
Keywords
READINGS: Goldstein Chapter 13 pg 311-327
Section 1
Principles of Neural Organization

KEYWORDS

Electrode, Microelectrode, Micron (1/1000th mm) membrane, nucleus, cytoplasm, Neuron, axon, dendrite, Schwann cell/glial cell, myelin sheath, node of Ranvier, Synapse, synaptic cleft, vesicle, neurotransmitter, receptors, ions, permeability, voltage-dependent permeability, sodium channels, positive feedback, sodium (Na+), potassium (K+), pump, electrochemical potential, sodium-potassium pump, action potential (AP), equilibrium potentials, all-or-none, action potential (AP), sodium (Na+) +55mv, neuron threshold, potassium (K+) -75mv, -55mv, resting potential polarisation/polarization/depolarisation/depolarization/hyperpolarisation/hyperpolarization, Inhibitory post-synaptic potential (IPSP), Excitatory post-synaptic potential (EPSP), integration, axon hillock, saltatory propagation, AP propagation, refractory period, spontaneous firing rate, second messengers, ion channels, transduction, graded generator potential

AP's produced in response to:
- electrical stimulation (artificial depolarization of a neurone)
- spatial and temporal integration of EPSPs and IPSPs across the neurone's membrane resulting in the neuronal threshold being reached generator potential
- sensory stimulation (transduction);
- mechanical (deformation of cytoskeleton);
- chemical (receptors, second messengers);
- light (hyperpolarization)

codes:
— modality (Müller's doctrine of specific nerve energies 1826; labelled line)
— intensity (APs/sec; frequency coding; population coding; thresholds)
— duration (rapidly and slowly adapting neurones)
— location (absolute, two-point discrimination, topographical coding)
Pacinian corpuscle, adequate stimulus, receptive fields, thalamus, cortex, sulcus, gyrus, brainstem, topographic (maps) representation, superior colliculus, inferior colliculus, Brodmann, phrenology, homunculus, PET scans, functional MRI,

areas of cortex:
— primary sensory areas (chemical, somatosensory, visual, auditory),
— motor cortex, association cortices (parietal, inferotemporal, frontal)
Introduction to Sensory Coding

Brain researchers are concerned with the answering the question: how do nerve impulses represent characteristics of the environment? This question is the problem of sensory coding and research on this problem seeks to determine the sensory code, the characteristics of nerve impulses that represent various characteristics of the environment.

Types of coding

How might neural activity carry, represent or code sensory information? One proposal, called **across-fibre pattern theory**, is that different perceptions are signalled by the pattern of activity in a population of neurones. According to this idea, the sensory code for blue might be the pattern of neural activity shown on the left of Fig. A and the sensory code for red might be the pattern of neural activity shown on the right of Fig. A. A variant of this method of coding is known as **population coding** in which a peak of activity can be detected by comparing all the cells’ activity levels (Fig. B). Another proposal is that different perceptions are signalled by activity in specific neurones. According to **specificity coding**, shown in Fig. C, when a given neurone fires, we perceive blue and when a different neurone fires we perceive something else, e.g. red. A variant of this is called **channel coding** (Fig. D) in which the relative firing of specific neurones carries the information. Since a ratio can vary continuously, a complete range of values of an attribute (e.g. colour) can be coding by a small number of neurones. All of these coding systems require that the firing of one cell means something different from the firing of another. They therefore require the cells to be **labelled** in some way.
Section 2

Psychophysics

Fechner, Weber, Stevens

Threshold, Suprathreshold

Method of limits,
  staircase,
Method of constant stimuli,
Method of adjustment,

two alternative forced choice,

Signal detection theory,
  sensitivity versus response bias,
  criterion,
  outcome matrix,
  hit/miss/false alarm/false positives/correct rejection,
  Receiver-operating characteristic curves (ROC curves),
  sensitivity,
  d-prime (d')

just noticeable difference,
Weber fraction/law/constant,
Fechner's law,
Stevens' power law,
  magnitude estimation,
  standard stimulus,
  response compression
Section 3

Somatosensory System

dorsal columns, dorsal column nuclei, lateral inhibition, inhibitory interneurones, divergences, convergence, sharpening of receptive fields, cortex, Brodmann areas 3a, 3b, 1, 2, stereognosis, muscle spindles, joint receptors, multiple representations

dorsal root, lateral inhibition, inhibitory interneurones, divergences, convergence, sharpening of receptive fields, cortex, Brodmann areas 3a, 3b, 1, 2, stereognosis, muscle spindles, joint receptors, multiple representations

dorsal root, lateral inhibition, inhibitory interneurones, divergences, convergence, sharpening of receptive fields, cortex, Brodmann areas 3a, 3b, 1, 2, stereognosis, muscle spindles, joint receptors, multiple representations

end organs, hairy/glabrous skin, rapidly/slowly adapting (RA/SA), transduction, Meissner's corpuscles (RA), Merkel's discs (SA), Nerve ending around hair (RA), Pacinian corpuscle (RA), Ruffini Ending (SA), free nerve endings, receptive fields dorsal root, lateral inhibition in dorsal column nuclei, inhibitory interneurones, receptive fields temperature, free nerve endings, paradoxical cold, adaptation: physiological neutral zone, menthol/capsaicin somatosensory psychophysics, detection thresholds, point threshold, two-point discrimination (larger than point thresholds because of need for unstimulated receptive field in between stimuli), von Frey hairs, variations over body surface

1 detection
2 identify (modality)
3 identify (properties, spatial form)
4 magnitude
5 location
6 movement

which fibre?, mapping of location, identifying modality/ sub-modality

what pattern?
frequency coding of magnitude

Braille,
Active touch,
Aristotle's illusion
Pain (perception), anterolateral tract, crossed at level of spinal cord, nociception (information),nociceptors, non-specific thalamic nuclei, referred pain, gate theory, transmission cell, inhibitory interneurones, endorphins, natural opiates, naloxone (antagonist), acupuncture plasticity, increase of cortical area with training, combination of areas if movement restricted
The Vestibular System

*is part of the Somatosensory System.*

*It is a proprioceptor that reports about the motion and orientation of the head.*

- rotation: semicircular canals, cupula, hair cells, angular acceleration, firing in nerve proportional to velocity (temporal code), also depends on orientation of canal, need to compare 3 canals to decide on what the axis of rotation is (pattern code)
- translation: otoliths (ear stones), calcium carbonate, mucus, hair cells, linear acceleration, gravity, hair cells arranged with their preferred directions to cover all possibilities within the plane of that otolith, utricle (horizontal plane), saccule (vertical plane), despite careful arrangement of otolith hair cells most movement activates many cells (because of each one responding to such a broad range), most active cell found by comparing cell activity, population code
- hair cells: kinocilium, stereocilia, depolarization, broadly tuned to direction (+/- 90 degs), preferred direction
- systems transduce force (mass x acceleration), angular (semicircular canals) or linear (otoliths) acceleration
- three outputs: perception, eye movements (vestibulo-ocular reflex: VOR), postural reflexes (vestibulo-spinal reflexes)
- perception, subtle sense, easily confused (because of responding to acceleration), need to construct overall movement from its parts, pathway: hair cell > vestibular afferent nerve (VIII) > vestibular nucleus > vestibular thalamus > vestibular cortex (near to somatosensory cortex)
- eye movements (rotation), equal and opposite to head movement, three pairs of eye muscles whose direction of pull roughly corresponding to planes of the canals, mathematical integration required to change acceleration signal into a position signal (must be done by the brain)
- eye movements (translation), depend on (i) head movement (ii) direction of target (eg. left or right) and (iii) distance of target, geometry shown to be taken into account by system
- eye movements (neural pathway), hair cells > afferent nerve (VIII) > vestibular nucleus > oculomotor nuclei > oculomotor nerves (III, IV and VI) > eye muscles
- vestibulo-spinal reflexes, primitive (evolutionarily), but capable of remarkable complexity (organized response with many muscles)
- multi-modal cues to self motion: vision and vestibular normally active together, vestibular nucleus responds to EITHER vision OR vestibular (or both), if visual motion provided without actual motion (eg. in a lab by moving an artificial room or in a car when the one next to you moves) it produces a convincing sensation of motion calledvection (linear or circular depending on the type of motion), this is because the vestibular nucleus (and therefore the rest of the brain from there on up) cannot tell the difference between activity arising from vision or from vestibular stimulation.
- alcohol creates illusions of self motion because of passing into the canals and cause fluid motion within fluid up > so head feels moving down (pitch nose down) > creates upward VOR > eyes moving up in front of stationary visual world > retinal motion down > sensation of head moving up > incompatible with original sensation > inter-sensory conflict > interpreted as poison > vomit out poison
- other examples of motion sickness due to sensory conflict: reading in vehicle, head movements in space, being below deck in a ship
Vestibular Processing

vestibular apparatus
semicircular canals
utricle/saccule
otolite
hair cells
cupula
VIII nerve
transduce FORCE
force=mass × acceleration

*hair cells:
stereocilia
kinocilium
directional (bending towards kinocilium causes depolarization)

**Kinocilium**  →  Depolarization

**Afferent fibre**

### Semicircular Canal Division of VIII Nerve
firing frequency depends on orientation of axis of rotation compared to the plane of the canals

<table>
<thead>
<tr>
<th>Optima response</th>
<th>In between response</th>
<th>No response</th>
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### Otolith Division of VIII Nerve:
linear acceleration made up of movement of organism and gravity

- **Direction of otolith motion** (hair bending) due to person's movement
- **Direction of otolith motion** (hair bending) due to gravity

rotation velocity coded in temporal activity
rotation axis coded in which nerves active
goes to specific parts of the vestibular nucleus
Firing frequency depends on orientation of linear acceleration compared to the excitatory direction of each hair cell. Excitatory direction of hair cells varies in a regular way across each otolith membrane.

Firing frequency depends on amount of linear acceleration, which goes to specific parts of the vestibular nucleus.

Three outputs: vestibulo-ocular reflex, vestibulo-spinal reflexes, and perception.

Vestibulo-ocular reflex: helps keep retinal image stable. Nystagmus.

Three pairs of eye muscles.
Three pairs of canals approximately lined up.
Canals → hair cell → VIII nerve → vestibular nucleus → oculomotor nerves → eye muscles.

Each canal/eye muscle unit can work independently of the others.

Canals transduce angular acceleration: muscles need a position signal integration required. Eye movements to compensate for linear movements more complicated.

Perception: need to construct movement from its parts.

Vestibular thalamus

Vestibular cortex (its own area)

Vestibular information also contributes to somatosensory cortex. Comes in near representation of elbow on somatosensory map.

Visual and vestibular information found throughout pathway (right from vestibular nucleus).

Visual movement evokesvection (sense of actual physical movement).

Linearvection

Circularvection
TASTE

- Taste Primaries: sweet, sour, salty, bitter,
- papilla (nipple) types: fungiform (fungus-like), foliate (leaf-like), circumvallate (around the ramparts)
- Taste buds (found on papilla), respond to more than one ‘primary’
- taste cells (found within taste buds), no axons, connect/synapse with afferent fibres
- coding of quality, activity across a population, pattern of firing of nerves related to perceptual abilities in rats (responses to different salts,
- ammonium, potassium and sodium chloride), most fibres respond to more than one primary, spatial separation of receptor subtypes on tongue and in thalamus and cortex
- taste thresholds depend on: temperature (different primaries alter differently), tongue region, genetics (phenylthiocarbamide: to 2/3rds of white
- western folk tastes bitter; 1/3rd no taste), concentration (eg. saccharin low sweet; high bitter), age
- taste preferences, Humans: sweet (+); bitter (-), mostly in place at birth; Cats and chickens: indifferent to sweet; rat/cat/rabbit/sheep: salt (+); hamster: salt (-)
- taste cravings, salt, calcium, potassium, etc.. specific changes in threshold when deprived (eg. for salt)
- cultural influences, conditioned taste aversion
- neural pathway: uncrossed, taste cells, VII cranial nerves (chorda tympani division of facial nerve), IX cranial nerve (glossopharyngeal), solitary nucleus, ventral posterior medial nucleus of thalamus, taste cortex (near mouth representation of somatosensory cortex), brain stem, vomit centres
SMELL

- olfactory binding protein, olfactory receptors cells continuously regenerate (about every 60 days), cilia (on olfactory receptor cells),
- glomerulus (contact zones between receptor cells and mitral cells: plural glomeruli), convergence (1,000:1), mitral cell, olfactory tubercle of
- entorhinal cortex (part of paleocortex), medial dorsal nucleus of thalamus, olfactory neocortex
- paleocortex associated with limbic system, limbic system associated with emotions (electrical stimulation causes sham rage), limbic system
- associated with memories (H.M. had lesions here and lost the ability to memorize things), no topographic mapping in olfactory cortex (unusual),
- some hot spots in olfactory tubercle and on olfactory mucosa
- odour quality, no primaries identified in olfactory system, poor tuning of receptors (to chemicals or chemical types) (sharpened by lateral inhibition, inhibitory interneurones, granule cells)
- Henning smell prism, stereochemical theories based on lock and key partially successful, BUT no receptor sites identified, similar shaped
- molecules can be associated with different smell perceptions, cells broadly tuned (responding to many different chemicals associated with many different smells)
- coding, intensity = firing rate/recruitment, quality = distributed pattern code, problems in identifying many smells at once, binding problem
- odour thresholds, olfactorium; unique technical problems!, humans very sensitive (eg. mercaton can be detected at 1 part per 50,000,000,000), affected by gender; can be affected by menstrual cycle, affected by age
- adaptation, thresholds raised (by exposure), masking (by other chemicals), some cross effects: eg. adapting to orange affects smell of lemons
- identification, can identify gender from shirt, prefer own odours, odour memories long lasting; associated with emotions (via limbic system)
- "designed not to forget"
- pheromones, releasers (immediate effect), eg. bitch on heat, territorial markers, humans?, McClintock effect (synchronized menstrual cycles), primers (longer term) eg. mice need males around for proper oestrus cycles
- PATHWAYS olfactory receptor cells to mitral cells in olfactory bulb to olfactory tubercle in paleocortex THEN
  1 to medial dorsal thalamus to olfactory cortex (ORBITOFRONTAL CORTEX)
  2 to limbic system
  3 brain stem pathways associated with pheromones
- ALSO inhibitory pathway (via inhibitory interneurone: granule cells) from one olfactory bulb to the other to do with detecting the direction from which a smell originates
Section 5

Time perception

Time as relative (Einstein)

Events as the units of perception
  Change needed
  Micro saccades
  Stabilized images disappear

Percepts emerge over time (we live in the past)
  Visible persistence
  Flash-lag
  Cortex primes its own input
  Temporal integration
  Backward masking

Spatial analysis requires time

Temporal resolution
  Neural synchrony (Singer)
  Visible persistence
  Perceptual stability

Perception of the passage of time
  Duration estimation
  Biological clocks
  Circadian rhythms
  Suprachiasmatic nucleus
  Melatonin
  Biological pacemaker
  Cognitive clocks
  Filled duration illusions (perceived as longer)
  Restricted environment stimulation (perceived as shorter)
  Processing effort (harder takes longer)
Section 6

Speech perception

**Physical Stimulus**
1) Phonemes:
"sounds that create meaning" 48 in English; different in different languages

2) Phonetic features:
   Voiceing (2):
   - voiced/unvoiced
   Place of articulation (7):
   - alveolar ridge
   - labiodental
   - etc....
   Manner of articulation: (6)
   - stop
   - fricative
   - nasal
   - etc...

3) Acoustic signal:
   Sound spectrogram
   Formants (characteristic of vowel sounds)

4) Variability problem
   context creates variable acoustic cues eg. formant transitions because of coarticulation; its solution is an example of perceptual constancy

5) Segmentation problem
   “In mud eels are, in clay none are.”

**Is speech special or just performed by a general auditory analysis method?**

Motor theory of speech perception (yes, it is special)
 sound > brain > phonetic analysis > recreate activity in vocal tracts > phoneme identification

1) Categorical Perception
   - voice onset time (VOT)
   - phonetic boundary
   - BUT also for non-speech sounds
   - also for other species eg. monkeys, chinchillas, quail

2) McGurk Effect
   - vision affects hearing
   - /ga/ (lips) + /ba/ (sound) = /da/ (perception)
   - links production to hearing
   - BUT works with plucked/bowed cello note too

3) Are there INVARIANTS for phonemes? Something that stays the same despite different contexts, different coarticulations etc... Some hints...
   **TOP DOWN influences**

[Image of spectrogram and voice onset time (VOT)]
1) Segmentation
   influenced by meaning
   "Anna Mary Candy lights since imp pulp lay things"
   "I scream, you scream, we all scream for ice cream"

2) Semantics (meaning) and syntax (grammatical word order) both contribute to your ability to shadow (repeat what you have heard) a text.

3) Phonemic restoration
   "...time to meet with their respective legi * lat..."
   = cough and is moved to end of word
   "... time to ave..." which phoneme slotted in depends on FOLLOWING words.

**PHYSIOLOGY of speech perception**

1) Selective adaptation
   after adapting to /ba/ a voiced syllable, phonetic boundary shifts (towards the voiced side of a boundary), suggesting a "voiced" phonetic detector
   how does /be/(sound) + /ge/(lips) = /de/ (perception) (McGurk) affect the phonetic boundary between /de/ and /be/? Does it move towards /be/ or /de/? In other words does the perception or the acoustic cue do the adapting? ans: towards /be/, it is the acoustic cue.

2) Neural responses
   nerve show phoneme information carried in a population of fibres
cortex cells with special requirements eg. frequency sweeps compatible with the idea of phoneme cells...

3) Lateralization of cortical function
   auditory pathways crossed
   for most people there is a right ear advantage for speech
   Broca's area underlies TALKING
   Wernicke's area underlies UNDERSTANDING