Lecture Notes on Chris Brown's Section: Audition

Okay, here goes nothing. The lecture notes were a little hard to digest and organize, but the notes here proceed mostly as follows:

1. Nature of sound and auditory stimuli
2. Peripheral anatomy and function
3. Brainstem anatomy and function
4. Sound localization and echolocation
5. Auditory cortex
6. Speech
7. Descending pathways

This is somewhat different from the way the lecture notes proceed, but it seems like a more natural grouping to me. Also, there are some figures from the notes which would probably be useful, but which I'm too low-tech to include. You'll want to study a lot of the response histograms as well.

Abbreviation guide:

AI	primary auditory cortex
AC	auditory cortex
CF	characteristic frequency/constant frequency
CN	cochelar nucleus/nuclei
FM	frequency modulation
IC	inferior colliculus
ICX	exterior nucleus of the IC
ILD	interaural level difference
ITD	interaural time difference
IHC	inner hair cell
LSO	lateral superior olive
MG	medial geniculate (nucleus)
MSO	medial superior olive
OAE	otoacoustic emission
OHC	outer hair cell
PST	peri-stimulus time (histograms)
SC	superior colliculus
SG	spiral ganglion
SOC	superior olivary complex
SPL	sound pressure level

- Sound is mechanical, radiated energy transmitted by longitudinal vibrations in a medium
  - amplitude is defined in terms of **sound pressure level** (SPL) and is

measured in **decibels**
  - the formula for SPL is SPL = 20 * log [pressure / reference pressure]
  - where the reference pressure is 20 $\mu N/m^2$, which is approximately the human **hearing threshold** at 1 kHz
  - human hearing extends from about 10 Hz to 20 kHz, and relevant sound levels are from 0 dB to about 120 dB
  - 1 dB is also approximately the **minimum discernible difference** for humans

o Common auditory stimuli for experiments include **pure tones**, **tone bursts**, **clicks**, and various kinds of **random noise**
  - each of these stimulus types produces a different response in receptors and auditory neurons

o The complex sounds produced by e.g. instruments are composed of a primary pitch, and also additional higher harmonics which together determine the overall sound (referred to as the **timbre**)

o The auditory cortex combines multiple pitches to perceive them as a single sound, but this effect can be broken if one of the frequency components is removed and then replaced (remember the demo?)

o Now for the anatomy of the auditory periphery
  - the **external ear** is the **pinna** (i.e., your ear) and the external auditory canal
  - the **middle ear** is the **tympanic membrane** (eardrum), and the three little bones: the **malleus**, **incus**, and **stapes**
  - the inner ear is the **cochlea**, where sound vibrations are separated by frequency along the **basilar membrane**, which is lined with **hair cells**
    - Low freqs are detected at the apex, high freqs at the base
  - the auditory nerve transmits signals from the hair cells along the **VIIIth** cranial nerve; this nerve also carries efferent signals back to the receptor cells

o The function of the middle ear is to amplify the pressure transmitted to the inner ear
  - **otosclerosis** is a form of hearing loss in which the stapes (the stirrup bone) is fused with bony growths; it can be fixed by replacing the stapes with an artificial one

o Hair cells are the receptor cells in the cochlea
  - they have stereocilia, which are the little hairs that deform due to waves in the fluid in the cochlea
  - the afferent neurotransmiter is unknown but excitatory (how do they not know this?)
  - the efferent neurotransmitter is ACh, and is detected by nicotinic receptors
  - the transducers are at the tips of the stereocilia, probably one per

cilion
- **inner hair cells** (IHCs) connect to 95% of afferents, but receive few efferent connections
    - these form a single row on the cochlea
    - they are surrounded on all sides by supporting cells
    - Type I nerve fibers (45,000 total): myelinated, 3-5μm diam.
- **outer hair cells** (OHCs) connect to the remainder of the afferents, but receive many efferents
    - form three lines, with the cilia looking like a "V" from the top
    - secured only at the upper and lower surfaces
    - OHCs are motile, and can create a cochlear amplifier by changing their shape (through the protein prestin)
    - loss of OHCs decreases sensitivity and broadens frequency tuing curves; complete loss increases threshold about 60 dB
    - Type II nerve fibers (5,000 total): unmyelinated, .3-.5μm diam.
- the **organ of corti** is the name for the receptor complex (IHC and OHCs) at a given point on the cochlea

o The signals of the auditory nerve fibers are **phase-locked** to the stimulus frequency
- spikes occur at the same time in the sound waveform
- each fiber may not carry spikes for each cycle, especially at high frequencies where this would require spikes biologically impossible rates
- phase locking may be used by central systems to determine sound frequency

o Otoacoustic emissions are sounds generated by the ear
- infants are tested for OAEs soon after birth; no OAEs indicates deafness
- distortion-product OAEs are used in experiments and use a two-tone stimulus

o Auditory brainstem
- contains many more nuclei than the analogous areas for other sensory systems
- ascending from the auditory nerve, the main areas are
    1. spiral ganglia (SG): end of auditory nerve
    2. cochlear nucleus (CN)
        --- (trapezoid body) ---
    3. superior olivary complex (SOC)
    4. inferior colliculus (IC)
    5. medial geniculate (MG): thalamic, midbrain
    6. auditory cortex (AC): forebrain
- the primary function of these nuclei is probably to process information regarding the source of a sound (i.e., sound localization)

    - the cochlear nuclei
        - each auditory nerve fiber branches to form many synapses in the CN
        - there are many types of synapses from the auditory nerve, and many different CN cell types
        - the different cell types each project from the CN to higher centers by way of a certain output pathway (i.e., parallel pathways with separate functions)
        - **large endbulbs** completely envelop **spherical bushy cells**; these are very good at preserving timing information and are almost certainly involved in ITDs
        - CN units can be classified by their response to short tone burst
            - primary-like: same profile as auditory nerve fiber; initial high onset response followed by sustained but attenuated activity
            - chopper: phasic
            - pauser: brief onset response, pause, then ongoing attenuated response
            - onset: brief onset response only
    - the superior olivary complex
        - the medial SO processes interaural *time* differences (see below)
        - the lateral SO processes interaural *level* differences
        - the first binaural processing occurs here, since it receives input via the trapezoid body

o Auditory neurons are sharply tuned for a certain frequency
- the tuning curve broadens as SPL is increased, and conversely
- the **best frequency** is the frequency which requires the lowest amplitude to generate a response
- there is a background firing rate, but this is increased during response to favored stimuli
- using this tuning, humans are very good at distinguishing between two frequencies (e.g., 1000 Hz vs 1002 Hz)

o **Sound localization** (SL)
- the pinna provides some cues: different frequencies are differentially amplified, and the gain for a given frequency depends on azimuthal position (elevation)
    - this is the main cue for sound source elevation
- interaural time differences (**ITDs**) occur because sounds reach each ear at different times
    - this means that sounds will be out of phase at the two ears
    - for humans, the maximum lag is about 0.6 ms
- interaural level differences (**ILDs**) happen because the head casts a

sound shadow, so one ear will hear with less intensity than the other
    - the ILD will depend greatly on the frequency, with high frequencies having much greater ILD (up to 20 dB for 6 kHz) compared to low frequencies (0 dB at 200 Hz)
- sound localization is accurate at low frequencies (ITDs dominate) and high frequencies (ILDs dominate), and not so good for middle frequencies (where both ITDs and ILDs suck)
    - under ideal conditions, source movements as small as one degree can be detected (corresponds to an ITD of 10 μs, or an ILD of 1 dB)
- effect of lesions on sound localization:
    - lesions above the SOC (e.g., in the Lateral lemniscus or inferior colliculus) affect SL on the opposite side, but SL on the ipsi side remains largely unaffected
- **Jeffress' model** of ITD posited delay lines (remember the animation?); the relative timing could then be determined by which pair of lines lit up at the same time (by **coincidence detector** neurons)
    - while there is a circuit like this in the MSO (using the spherical bushy cells), it only appears to contain delay lines for the contra side
- MSO neurons do, however, respond best to binaural stimuli, and the response depends greatly on the ITD
    - MSO neurons respond best to ipsilateral delays, meaning sounds located in the contra field
- LSO neurons respond to ILDs by receiving excitatory ipsi input and inhibitory contra input
    - this leads to high activation for ipsi sound sources and low activation for contra sound sources
- both MSO and LSO are tonotopically organized, with more space devoted to those frequencies which provide the best SL cues (which are?)
    - also, both LSO and MSO project to IC so as to excite IC in response to sound sources from the contralateral side
- unlike mammals, **barn owls** have a map of auditory space in the MLD nucleus (which corresponds to the ICX of mammals)
    - both avians and mammals have these maps in the SC
    - this is thought to be relevant to owls' ability to accurately locate prey sounds in space

o **Echolocation** in bats
- the basic idea is that moving targets (i.e., lunch) will produce a different **doppler shift** than stationary ones
- two basic types of bats
    - **CF-FM** bats first emit a constant-frequency sound followed by a frequency-modulated sound
        - they hunt mostly in vegetation

      - cortical fields overrepresent 60 kHz, since this is the most prominent freqency in echolocation chirps
    - **FM** bats emit only frequency-modulated sounds
      - they hunt mostly in the open air
  - as a bat nears its prey, the chirp rate goes up and the chirps become shorter
  - many neurons in bat auditory cortex are **tuned for specific delays** between the chirp emission and the echo; these are used to determine the distance to the target
    - these delay-tuned neurons can be tuned to specific components of the chirp and echo, such as the higher harmonics

o **Cat** auditory cortex
  - Two general systems
    - **Tonotopic** system (AI, AAF, PAF, VPAF): sharp tuning curves, tonotopically organized
    - **Diffuse** system (AII, DP, VT): broad tuning curves, no obvious tonotopic organization
  - lesions of AI affect SL in contra hemifield, but not in ipsi field or at midline
  - lesions of other cortical fields do not affect SL

o **Primate** auditory cortex
  - located on the superior surface of the temporal lobe, in particular the superior temporal gyrus (STG) and the lateral sulcus (LS)
  - **core fields** (AI, R, RT) are tonotopically organized
  - surrounding **belt fields** (CM, CL, ML, AL) respond maximally to spectrally complex stimuli
  - the **parabelt fields** have not been explored much

o Speech
  - most speech areas are located in the **peri-Sylvian region**, and lesions to these areas result in specific speech deficits
    - Areas include **Broca's area**, **Wernicke's area**, and other more basic auditory cortical regions (e.g., AI)
      - Broca's area is activated in both speech comprehension and production
    - **Broca's aphasia:** deficit in speech production; sparse, halting speech, missing function words and parts of words
    - **Wernicke's aphasia:** deficit in auditory comprehension; fluent speech with problems in word sound and structure
  - language processing is almost always lateralized (right-handed: 98% have speech in left hemi; left-handed: 60% right hemi, 40% left hemi or both hemis)

    - this is confirmed by anatomical asymmetry in the peri-Sylvian region, such as the fact that the planum temporale is usually larger in the left hemi

- o Descending Pathways
  - **olivocochlear neurons** (medial and lateral) project from the SOC to the cochlea
    - OC neurons are thought to **shift the dynamic range** of auditory nerve fibers, allowing a wide range of stimuli to be discriminated without saturation
    - **LOC efferents** project to the ipsilateral side, have thin and unmyelinated axons, and terminate near inner hair cells
      - send collaterals to vestibular nuclei and the LSO
    - **MOC efferents** project bilaterally, are thick and myelinated, and terminate on outer hair cells
      - send collaterals to vestibular nuclei, cochlear nucleus
      - MOC activity shifts range of nerve fibers to higher levels
      - MOC activity also reduces the masking effect of noise (from two-tone suppression
      - project tonotopically to OHCs, more heavily at middle and basal cochlear areas (middle and high fequencies)
  - **middle-ear muscles** contract to reduce air flow through middle ear and therefore tune dynamic range
    - **stapedial motoneurons** in the motor nucleus of the facial nerve
      - protect from damage due to high sound
      - helps speech understaning at high background sound levels (filters low frequency)
      - contracts during vocalization to prevent speech sounds from interfering too much
    - **tensor tympani** motoneurons project through trigeminal nerve
    - both neuron types are ipsilateral to innervation
  - other mechanisms also modify the dynamic range, including two-tone suppresssion, and recruitment of high-threshold nerve fibers

- o Loud sounds damage hair cells, either patchily or entirely
- o **Cochlear implants** can reverse hearing loss by directly stimulating individual areas of the cochlea