Amplitude specified in terms of SPL

$$SPL = 20\log\frac{P}{P_{ref}}$$ where P_{ref} is 20 μPa

Frequencies important in human hearing: 10 Hz to 20 kHz
SPLs important in human hearing: 0 dB to 120 dB SPL

Common auditory stimuli: pure tone (sinusoid), square wave, tone burst, click, noise
A above middle C = 440 Hz
Tone color of a particular instrument depends on higher harmonics above the fundamental.

External ear: pinna, external auditory meatus
Middle ear: tympanic membrane, ossicles
Inner ear: cochlea, basilar membrane

Pinna introduces "notches" in the sound which are the main cue for sound-source elevation, also helps somewhat in azimuthal location

Cochlea has three turns: apical, middle, basal
A single point on the basilar membrane responds to a broad array of frequencies
Cochlea maps frequencies

Parameter	**IHC**	**OHC**
Stereocilia	40	140
Humans have	3500	13000
Support	all sides	top/bottom
Innervated by	Type I	Type II
Innervation %	~95	~5
Single neuron	single cell	many cells
Proportion	25%	75%
Descending input	lateral OC	medial OC

OHCs are probably physical basis of "cochlear amplifier": more sensitivity, sharper tuning than if no OHCs

Fibers can be "high CF" or "low CF" – low CF fibers have a U-shaped response profile, not much of a tail (or tip)

Almost a linear relationship between point of innervation in the cochlea and CF – high frequency at base and low frequency at apex
We are very good at distinguishing frequency. Can tell 1000 Hz from 1002 Hz – equivalent to changing vibration peak from one IHC to its nearest neighbor.
Tone suppression produced by mechanics of basilar membrane – type of masking
Phase locking – neuron fires at a consistent point in the stimulus waveform

Path:
Cochlea – Auditory nerve – cochlear nucleus (brainstem) – superior olivary complex (brainstem) – inferior colliculus (midbrain) – medial geniculate nucleus (thalamus) – auditory cortex
Strange because most sensory paths go straight to the thalamus without so many brainstem nuclei

Cochlear Nucleus
Low CFs project ventrally, high CFs dorsally
Lots of different cell types classified by their appearance under Nissl/Golgi stains: spherical, multipolar, globular, small, octopus, pyramidal
Spherical/bushy cells are targets of endbulbs (largest terminals in the brain)
Different cell types also classified by their PST (peristimulus time) graphs: primarylike, chopper, pauser, onset
Probable associations: bushy – primarylike, multipolar – chopper, octopus – onset, pyramidal – pauser
Lots of bushy in anterior, lots of multipolar in posterior
Each cell type has a characteristic place of projection: superior olivary complex, lateral lemniscus nuclei, inferior colliculus

Descending Systems
More neurons project from the cortex to the thalamus than from the thalamus to the cortex, but we don't always know why
Medial olivary complex → OHCs, lateral olivary complex → auditory nerve fibers below IHCs. Easier to record from MOC.
Electrical stimulation of MOCs shifts dynamic range of auditory nerve fibers to higher levels, enabling animal to hear louder sounds
Noise masks ANF response due to two-tone suppression and adaptation, but stimulation of MOCs helps alleviate this effect
Each nerve fiber may innervate 100 or so OHCs (in a tonotopic fashion)
The MOC reflex protects the cochlea from damage due to acoustic overstimulation by contracting middle ear muscles (which act as mufflers)

Binaural Cues for Sound Localization
Can detect changes of 20° in elevation and 1° in azimuth
Interaural time difference is a useful cue below 1.5 kHz
600 μs is the maximal ITD for human head
ILDs pick up slack from ITDs at high frequency -- ~20 dB difference
1° angle = 10 μs ITD. Amazing given that action potential encoding this info take 1 ms
Duplex theory: ITD low frequency, ILD high frequency
There is a Jeffress-like circuit in the MSO, but only delay line for contralateral input
MSO neurons: respond best to binaural stimuli, response depends on ITD

Superior Olivary Complex
Inputs to LSO are sensitive to ITD, with excitatory input from ipsilateral CN and inhibitory from contralateral trapezoid body (glycine)

LSO projections are excitatory to contra and inhibitory to ipsi
As a result of both LSO and MSO projections, sounds on one side will tend to excite IC neurons on the *opposite side*
MSO has an over-representation of low CFs, LSO and MNTB have over-representation of high CFs
Above SOC, lesions of auditory pathway affect sound localization on contralateral side, but animal still has some crude sound localization capacity

Ascending Sytstems from Midbrain to Cortex
Tonotopic: ICC → tonotopically organized regions of thalamus
Diffuse: ICD → dorsal region of medial geniculate body (no tonotopy)
Multisensory: ICX → medial region of medial geniculate body (lots of sensory modalities)
Inferior colliculus is a sorting station

In auditory cortex, tonotopic mapping is logarithmic. More cortial area devoted to higher frequencies.
Several tonotopic mappings, reverse at boundaries.

	Tonotopic system	**Diffuse system**
Fields	AI, AAF, PAF, VPAF	AII, DP, V, T
Tuning curves	sharp	broad
Tonotopy	yes	not as obvious
Latency	often short	longer
Response	brisk, robust	poor, high threshold

Multiple tonotopic areas in humans in the region of Heschl's gyrus: possibly seven
Tonotopic mapping has plasticity – if lesioned, surrounding frequencies will spread into lesioned region
Presbycusis – age-related peripheral hearing loss, starts at high frequencies

Cortical units have best frequency and best intensity (sometimes)
Closed curves when plotting these against each other only found in higher processing areas

AI is necessary and sufficient for sound localization (although it probably does other stuff too)
Units in a cortical column have similar azimuth-level response areas (response as a function of azimuth and sound level). Shows that cortical neurons have preferred spatial response areas, although not necessarily a mapping

Bats
Two types of bats: CF-FM and FM
A CF-FM bat (mustached bat) emits a constant CF (w/ 4 different harmonics), then a downward-sliding FM region
An FM bat (little brown bat) emits a downward-sliding FM region only

For a CF-FM bat, 60 kHz is overrepresented in cortex (most prominent harmonic)
Different fields specialized to respond to components and delays of pulse/echo
Some feature extraction arises at lower levels (MGB, IC) and is reflected in cortex

Language
Each voiced speech sound has a different pattern of formants (always 3)
Passed through the "filter function" of the vocal tract
Consonant sounds briefer than vowels

Speech is like echolocation, but flipped. FM region, then CF region.
Whether FM region is swept up or down makes a difference in the final sound
Duplex theory: percept is a speech sound when components presented together, not when presented separately

Perisylvian cortical areas are associated with language
Sylvian fissure = lateral sulcus

Broca's aphasia: have difficulty articulating words
Wernicke's aphasia: lots of words, no sense; also disturbance in comprehension
Anomic aphasia: disturbance in producing single words (ex common nouns)

Language processing is lateralized and there are hemispheric differences in anatomy
Most people have language processing in the left hemisphere