Lecture 21 -- The Auditory System -- Das

OUTLINE:

I will start with an introduction to the physics of sound and the most important features that define our perception of simple sounds. (pitch, loudness).

I will then describe the auditory system, with a primary focus on function, on showing how well the system has been "designed" as though to optimally pick out the perceptually salient features. In the process I will describe:
- Organizing principles that the auditory system shares with other sensory systems, i.e. receptive field, "place" maps, Weber-Fechner laws describing our ability to discriminate pitch or loudness.
- Organizing principles unique to the auditory system, i.e. coding based on timing, used to locate sources of sound or to differentiate between complex sounds.

I will finish by touching upon 2 new areas: the current understanding of language processing and plasticity in the auditory cortex.

1: The properties of sound and their match with the auditory system:

The auditory system is optimally designed to pick out the most salient features of sound.

Sound is a longitudinal pressure wave, causing tiny vibrations of local air pressure. The ear has to be sensitive enough to pick these up:
- barely audible sounds have an amplitude of $\sim 1/10^{10}$ of atmospheric pressure.
- even the loudest sounds, bordering on the painful, have an amplitude of $\sim 1/1000$ of atmospheric pressure.

Simple sounds can be described by pitch (frequency) and loudness.

Pitch:
- Pure tones (e.g. from a tuning fork) have a single frequency or pitch.
- Pitch perception follows Weber-Fechner laws, common to many sensory areas:
    o Octaves – equal steps in perceived pitch - are a logarithmic function of the physical frequency.
    o Two-tone discrimination is a function of the frequency. Analogous to two-point discrimination for touch.

In addition, most natural sounds – speech, animal calls, music – have complex mixtures of frequencies (think of a piano chord, hitting a number of keys simultaneously). The frequencies in natural sounds also constantly change (prosody in language; trills in bird song). Thus the auditory system must recognize these more complex patterns.

Loudness:

- Loudness also follows the Weber-Fechner law. Equal steps in perceived loudness correspond to geometric increases in physical sound intensity. Sound intensity is therefore expressed using a logarithmic scale, the decibel or dB (defined by Fechner, in the 1860's in honor of Alexander Graham Bell)

  Absolute intensity of a sound I, in dB = $10 \log_{10} (I / I_{th})$
  where I_{th} = intensity at the threshold of hearing (20 μPascals at 1 kHz).

- Huge working range of loudness: a factor of 5,000,000 in power – i.e. a factor of 10^{13} in pressure amplitude between the softest audible sounds and the loudest tolerable.

Timing:
Sounds also carry precise timing information. This, while not perceived directly, is used by our auditory systems to locate sound sources in space.

The auditory system is designed to extract and process all these salient features of sound – to encode pitch in octaves, loudness in decibels and timing to 10 μs accuracy. In higher auditory centers the auditory system also extracts progressively more complex features of sounds. The various auditory features are transformed, across a hierarchy of brain locations, into maps or "place" codes similar to maps in the sensory systems of vision and touch.

2: How the ear works, transducing (converting) sounds into nerve impulses:
The pathway external ear -> middle ear -> inner ear. Encoding frequency, loudness, timing.

Middle ear:
Matching sounds in air to the fluid in the inner ear.
Adapting to loud sounds
Conductive hearing loss: can easily be surgically corrected.

Inner ear
Cochlea -> organ of Corti -> basilar membrane + tectorial membrane + hair cells, inner & outer.

Basilar membrane
The basilar membrane as a set of piano strings, picking up vibrations at different frequencies.
Properties of the basilar membrane and:
- Place map of frequencies: tonotopy on a logarithmic scale.
- Receptive fields and two-tone discrimination:

Hair cells:
Inner hair cells: for transduction, sending afferent information.
Outer hair cells: getting efferent innnervation, for feedback.
How transduction happens: channels on inner hair cell hair bundle, opening under tension as the hair bundle moves; cation (mainly K^+) entry to depolarize cell.
Specializations:

- to sharpen frequency tuning: mechanical resonance of hair bundles; electrical resonance of cell membrane potential.
- for high temporal resolution: specializations at the synapse.
- to adapt to high intensity signals: adaptation to shift; also, outer hair cell stiffness

Sensorineural hearing loss: damage to hair cells. Cochlear prosthesis.

3: The central auditory pathway:

Auditory nerve:
Encoding frequency, loudness, timing:
- "Labeled Line" code carrying information about frequency from the "place" code on the cochlea. Maintaining Weber-Fechner two-tone discrimination.
- Loudness (in overall spike firing rate) and in recruitment of higher-threshold nerve fibers
- In addition to frequency (by labeled line), phase or timing information.

Cochlear nuclei: (dorsal / anteroventral / posteroventral)
First locus where "features" are processed in parallel, with different cell classes responding to different aspects of the sound. *Stellate* cells encode the sound frequency while *bushy* cells encode sound onset. (Unlike the auditory nerve where every nerve fiber does the same thing as every other fiber, just at different frequencies). From the cochlear nucleus, the stellate and bushy cells project to different relay nuclei.
Tonotopic maps: nerve fibers in the pathway maintain their geometric relations with each other in projecting to successive nuclei.

The path projecting onwards from the cochlear nuclei:
Extensive binaural interaction.
Tonotopic maps maintained at all points.
Progressively more complex features extracted from the sound.

I will then focus on just a few specific centers of complex auditory processing:

A: Locating sound sources, using timing and intensity between the two ears
The **Medial Superior Olive (MSO)** has a beautiful mechanism to detect interaural time differences. It combines the sound from the two ears; the ipsilateral inputs come in directly, while the contralateral inputs pass through a graded series of delays. For a sound source at a particular angle relative to the listener, only one particular delay will allow the ipsi and contra inputs to match. Thus a sound source location in space is "read in" as a phase (timing) signal, which is then converted into a place map in the MSO.
The **Lateral Superior Olive (LSO)** similarly encodes interaural intensity differences into a place map of sound source location. This works best at high frequencies where the head casts a clearer shadow in the soundscape.

B: Primary Auditory Cortex:
Tonotopic map along one axis
Along the orthogonal axis of the map: Excitatory/Excitatory or Excitatory/Inhibitory interactions between the two ears, rising or falling pitch, etc.

Intrinsic connectivity: long-range connections that link regions at octave intervals. Selective responses to complex sounds. E.g. selective to particular features of species-specific calls: will not respond if the elements of the call are played backwards.

C: Secondary Auditory Cortex: moving into "what" (e.g. anger/alert etc.) and "where" pathways.

D: The Language areas:
Classical division into "Broca's" & "Wernicke's" Areas
Current (fMRI) view of language as much more distributed: category-specific, e.g.
- Words for manipulable objects (tools) activate reaching/motor areas
- Words for movement activate next to visual motion areas
- Words for complex objects (faces) activate visual recognition areas

4: Plasticity:

- Damage to auditory nerves or to hair cells in the cochlea lead to complete remapping in auditory cortex.
- Expansion of specific cortical representations, not just with gross insults, but also with training (e.g. as a musician learns to discriminate tone frequencies).
- Training animals to discriminate between different tones (by associating a mild foot shock with one tone but not a nearby tone) leads to a change in the neural responses.
- Pairing a tone with simultaneous stimulation of the Nucleus Basalis (release of ACh, believed to mediate the plasticity in auditory response) leads to a complete remapping of auditory cortex.

Relevant reading: ch. 30 and 31 in "Principles"