Lecture 8:

Hearing II

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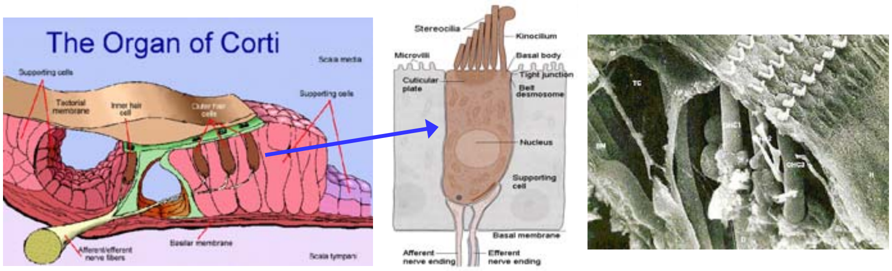
Topics:

- Active feedback in the cochlear: dancing hair cells
- Different aspects of information mediated by the auditory nerve
- How might the auditory system use this information to process complex sounds, such as speech?
- Where does it go from here? The central auditory system
- Spatial hearing

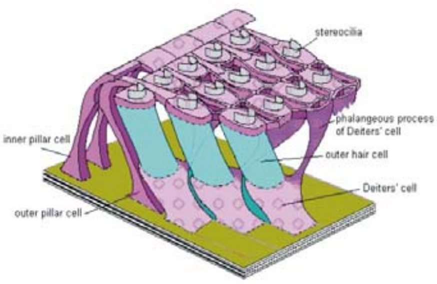
Rerun: Inner and outer hair cells

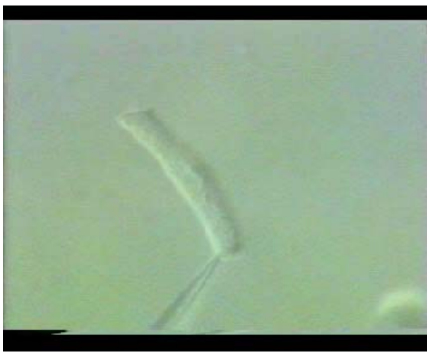
- Humans possess 1 row of ***inner hairs cells*** (***IHCs***) and 3 rows of ***outer hair cells*** (***OHCs***)
- Over 90% of the ***afferent*** auditory nerve fibers originate from the IHCs, which means that it is the IHCs that convey sound information to the brain



Active feedback

- The OHCs are depolarised in the same way as the IHCs
- When an OHC depolarises, the *entire cell contracts and shortens*, thereby literally pulling the basilar membrane towards the cell, because the OHCs are affixed to the basilar membrane through the supporting cells
- This phenomenon, which is known as ***electromotility***, causes the OHCs to *actively* feed *mechanical energy* back into the system!
- Electromotility it is powered by a specialized protein (prestin), lodged in the OHCs' membrane
- Movie of an OHCs, which has been isolated and whose membrane potential is being varied in the rhythm of a popular rock tune using the so-called patch clamp technique

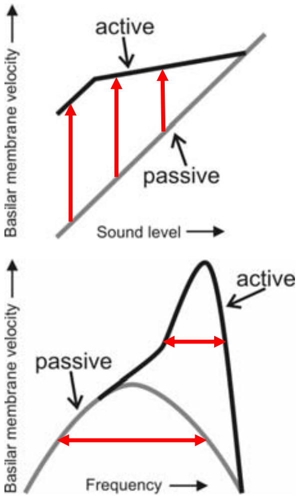


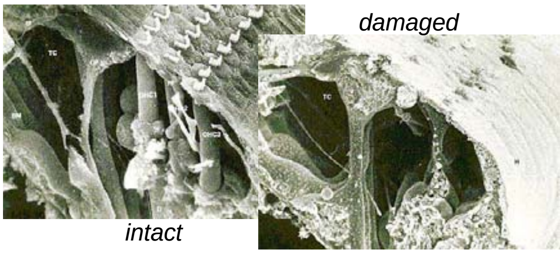


Active feedback

- While the exact mechanism of the active feedback is not yet understood, the feedback is known to have two important consequences on hearing:
- First: to amplify the movement of the basilar membrane at low sound levels
- Second: to increase the sharpness of the frequency tuning of the basilar membrane

➢ Thus, when the OHCs are damaged or missing, there is not only a loss in sensitivity (increase in hearing threshold), but also in frequency resolution, leading to particular difficulties in hearing in noisy environments





Information in auditory nerve – (1) sound level

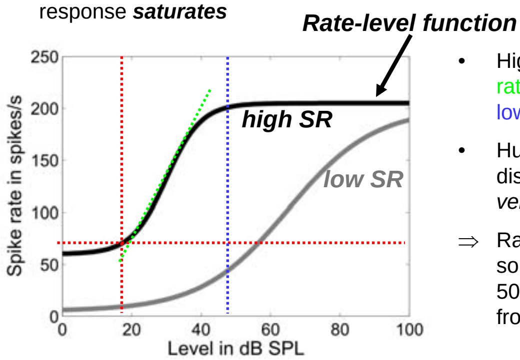
➢ A higher sound level ⇒ produces a larger movement of the basilar membrane ⇒ causes more tip-links to open ⇒ creating a larger receptor potential in the hair cells and thus more spikes in the respective auditory nerve fibers

➢ Each IHC is contacted by ~20 auditory nerve fibers

➢ Most (90%) of these fibers are very sensitive ⇒ so sensitive that they produce a substantial background level of spikes (~60 spikes per s) even in the absence of any sound [***spontaneous rate*** (***SR***); ***high-SR fibers***]

➢ The remaining fibers are less sensitive (spontaneous rate ≤ ~10 spikes per s; ***low-SR fibers***)

➢ Spike rate increases with increasing sound level up to a maximum rate at which the response ***saturates***

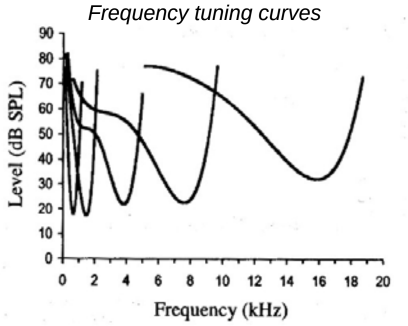


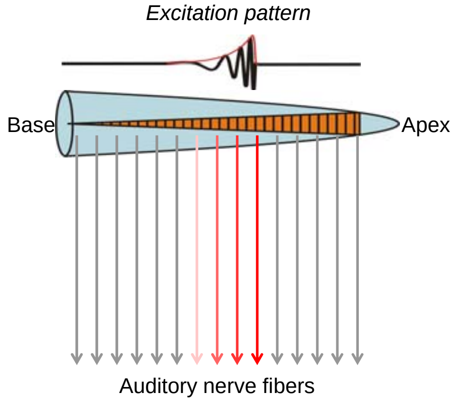
- High SR: lower threshold, steeper rate-level function and saturate at lower level than low SR
- Humans are very good at discriminating sound levels *even at very high levels*

⇒ Rate-level functions suggest that sound level discrimination above ~40-50 dB SPL must rely on the signal from the low-SR fibers!

Information in auditory nerve – (2) frequency

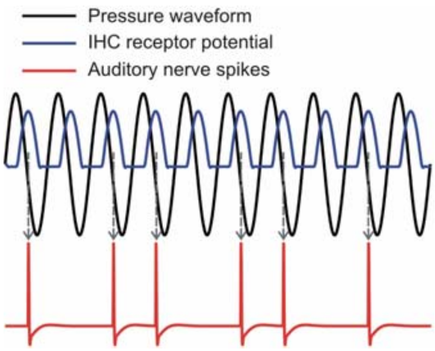
- As a consequence of the mechanical tuning for sound frequency of the basilar membrane, the auditory nerve fibers also exhibit tuning for frequency ⇒ each nerve fiber responds only to a limited range of sound frequencies
- ➢ Thus, the profile of activation strength across the auditory nerve (***excitation pattern***) reflects the place where the basilar membrane is stimulated, which, in turn, reflects the frequency/spectral composition of the sound





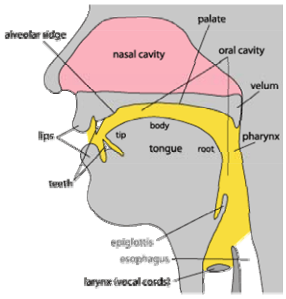
Information in auditory nerve – (3) timing

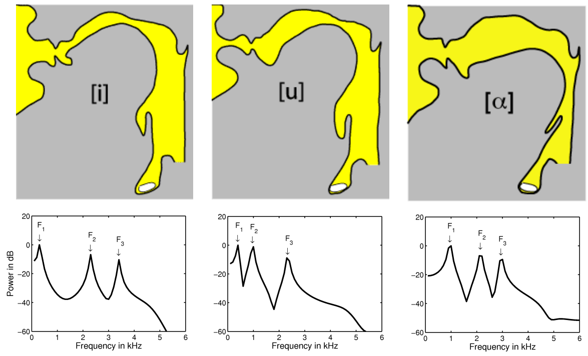
- Only one phase of the motion of the basilar membrane (the motion towards the scala vestibuli) is effective in eliciting a receptor potential in the hair cells
- Therefore, the receptor potential resembles a ***halfwave-rectified*** and slightly delayed version of the original pressure waveform of the sound
- This means that the spikes in the auditory nerve are *time-locked* to a particular *phase* in the waveform of the sound
- ➢ The temporal pattern of the auditory nerve spike trains reflects the temporal structure of the sound ⇒ ***phase locking***



Processing of complex sounds

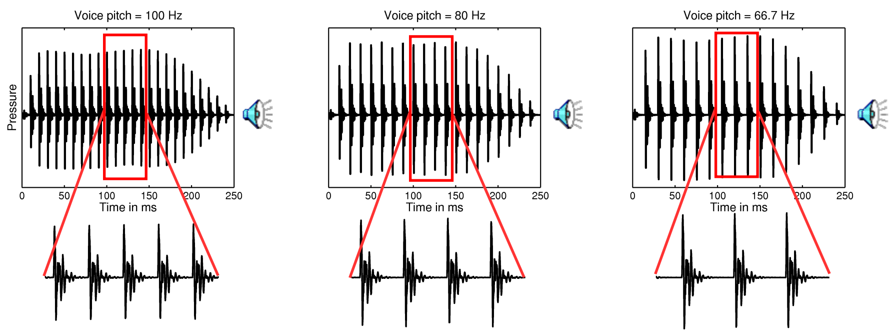
- When we speak, the opening of the vocal folds releases puffs of air into the oral cavity, thereby producing a sound (***glottal pulse***)
- The quality of the resulting sound depends on the shape of the oral cavity
- Different vowels contain different frequencies
- The frequency spectra of vowels are characterised by three prominent frequencies, the ***formants*** $\Rightarrow$ different vowels have different formants
- ➢ This is why the spectral information conveyed by the auditory nerve may be expected to play an essential role in the identification of speech sounds





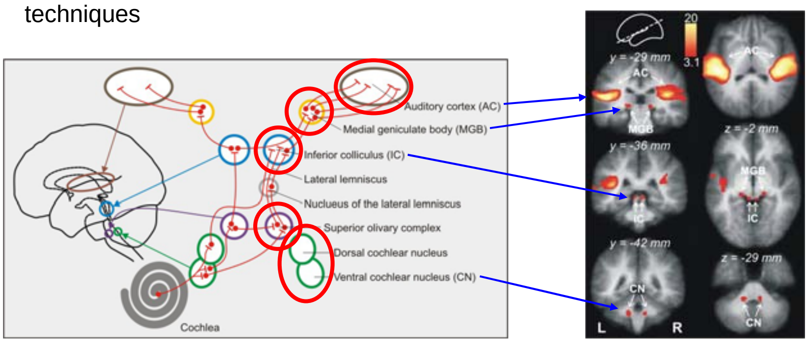
Processing of complex sounds

- In contrast, the perception of pitch/melody in speech and music may be based on the temporal (phase-locking) information conveyed by the auditory nerve
- The pitch of the voice conveys information both about speaker identity (male/female) and about meaning (e.g., “Peter fed the dog?” versus “Peter fed the dog.”)
- The pitch of the voice is determined by the rate at which the vocal folds open and close $\Rightarrow$ the *faster* the rate of the ***glottal pulses***, the *higher* the pitch
- The glottal-pulse rate is reflected in the timing of the auditory action potentials $\Rightarrow$ the auditory system might use this timing information to derive pitch



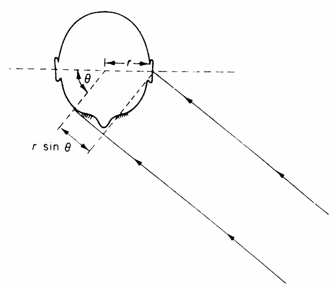
Central auditory system

- The auditory system is exceptional in the sense that many of the auditory structures are located in the brainstem rather than the cortex as, for instance, in the visual system
- Most important auditory structures: (i) ***cochlear nucleus*** (first processing stage), (ii) ***superior olivary complex*** (consists of several nuclei; this is the stage where information from the two ears is combined for the first time), (iii) ***inferior colliculus*** (relays practically all of the ascending auditory projections), (iv) ***medial geniculate body*** (auditory part of the thalamus), (v) ***auditory cortex***
- Most of these structures can now be investigated using brain imaging techniques



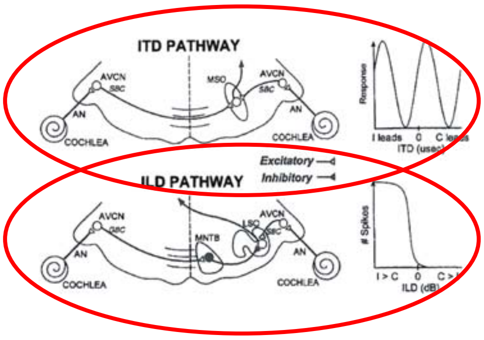
Spatial hearing

- It is generally assumed that one of the main functions of the sub-cortical part of the auditory system is to analyse the acoustical cues for sound location
- In humans, sound localisation mainly relies on the analysis of differences in sound level and sound arrival time at the two ears [referred to as ***interaural level*** and ***interaural time differences*** (***ILDs***, ***ITDs***)]
- In a sound originating from a lateralised source, ILDs are produced by the head casting a shadow on the farther ear ⇒ ILDs more prominent in high-frequency sounds, because low-frequency sounds can “bend around” the head (***diffraction***)
- ITDs are produced by the path length differences between the sound source and the two ears ⇒ ITDs are of the order of a few tens to a few hundreds of *microseconds* (a thousands of a thousands of a second) ⇒ thus, neural processing of ITDs requires a phenomenal temporal accuracy! ⇒ ITDs are more important at low frequencies, because temporal processing (phase locking) breaks down at high frequencies



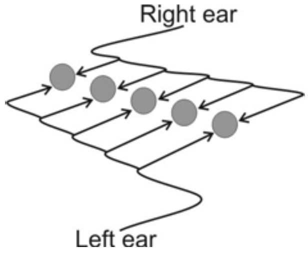
Spatial hearing

- The initial processing of ILDs and ITDs starts in the ***superior olivary complex*** (***SOC***) in the brainstem
- Generally assumed that ILDs and ITDs are processed by different types of neurons, located in different nuclei of the SOC
- The lateral superior olive (LSO) contains neurons that receive excitatory (activating) input from one ear and inhibitory (suppressing) input from the other ear ⇒ these neurons effectively compute the difference between the signals from the two ears, which makes them sensitive to ILDs
- Medial superior olive (MSO) contains neurons that receive excitatory input from both ears ⇒ sensitive to ITDs



Spatial hearing

- ➢ MSO neurons might be converting ITDs to a topographic (spatial) representation similar to the tonotopic representation of sound frequency
- Idea that ITDs might be converted to spatial code, which was first proposed by ***Jeffress*** in 1949, is still basis of most current models of spatial hearing
- ITDs are processed by a set of coincidence neurons receiving excitatory input from both ears and being activated only by simultaneous/coincident input
- Input to the coincidence neurons provided by axons whose length varies systematically across the set
- The longer the axon the longer it takes the spikes to travel to the neurons
- Difference in the time taken for the signal from each ear to reach the coincidence neurons varies systematically across the set
- A given ITD is represented by that neuron where the *axonal* time difference between the signals from the two ears compensates the *external/acoustical* time difference (ITD)



Spatial hearing

- While the Jeffress model appeals with its simplicity and physiological plausibility, newer physiological data seem to call the model into question $\Rightarrow$ whether or not the model is an appropriate description of the actual physiological processes is currently very much an area of active research and debate. But even if some aspects of the model turn out to be wrong, its basic ideas will undoubtedly still remain valid.

→ Further reading (books):

1. C. J. Pack, The Sense of Hearing
2. B. C. J. Moore, An Introduction to the Psychology of Hearing
3. W. A. Yost, A. N. Popper and R. R. Fay, Human Psychophysics
4. J. O. Pickles, An Introduction to the Physiology of Hearing
5. P. Dallos, A. N. Popper and R. R. Fay, The Cochlea