Hearing II

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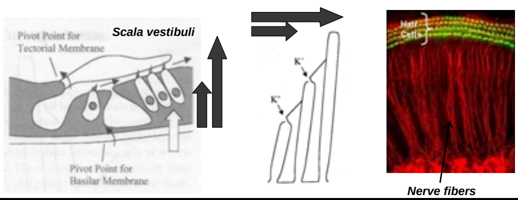
Topics:

- Different aspects of information mediated by the auditory nerve (level, frequency and timing)
- 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

Information in auditory nerve – (1) sound level

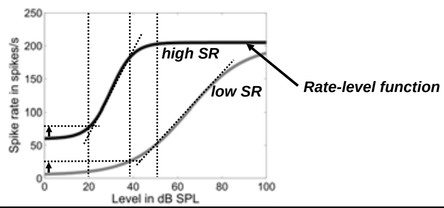
- Movement of the basilar membrane towards the scala vestibuli opens K^+ ion channels in the hair bundles of the IHCs via the tip-links ⇒ ***receptor potential*** ⇒ ***action potentials*** in attached auditory nerve fibers
  - A higher sound level ⇒ produces a larger movement of the basilar membrane ⇒ causes tip-links to open more ion channels ⇒ creating a larger receptor potential in the hair cells and thus more spikes in the auditory nerve fibers
- Each IHC is contacted by ~20-30 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***)



Information in auditory nerve – (1) sound level

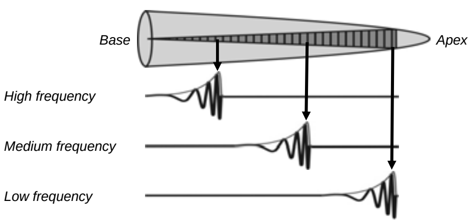
- ***Rate-level functions***: Spike rate increases with increasing sound level up to a maximum rate at which the response ***saturates***
  - High-SR fibers have lower firing thresholds than low-SR fibers (firing threshold = sound level that produces significant increase of firing rate above the spontaneous rate)
  - High-SR fibers also have steeper rate-level functions (unit increase in level produces larger increase in firing rate in the high- than in the low-SR fibers)
  - High-SR fibers saturate at higher sound levels (above about 50 dB SPL; increases in level above the saturation level does not produce any further increases in firing rate)
- Perception: Humans are very good at discriminating sound levels *even at very high levels*

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



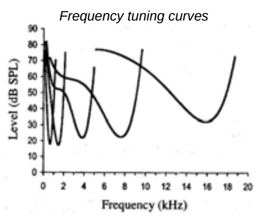
Information in auditory nerve – (2) frequency

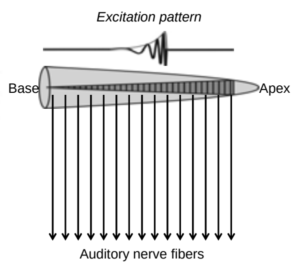
- The basilar membrane exhibits mechanical tuning for sound frequency ⇒ different places along the length of the membrane respond maximally to different frequencies



Information in auditory nerve – (2) frequency

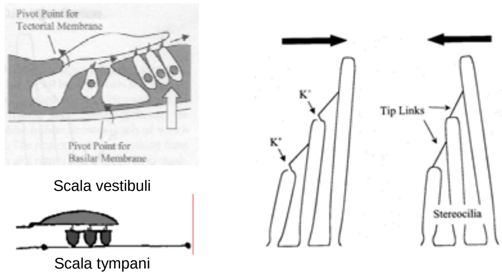
- As a consequence of this mechanical frequency tuning of the basilar membrane, the auditory nerve fibers also exhibit tuning for frequency ⇒ each nerve fiber responds only to a limited range of sound frequencies
  - Thus, the profile of activation strength across the auditory nerve (***excitation pattern***)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





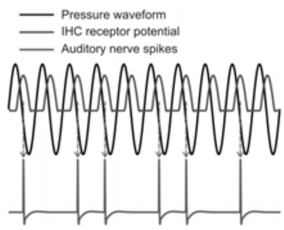
Information in auditory nerve – (3) timing

- Movement of the basilar membrane creates a shearing force, which deflects the hair bundles on the hair cells
- 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



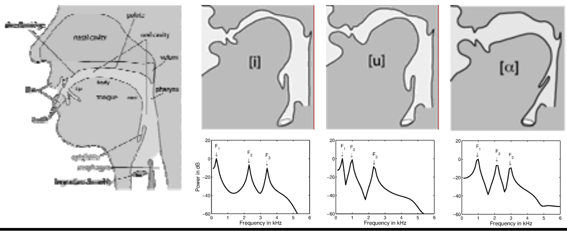
Information in auditory nerve – (3) timing

- Therefore, the receptor potential resembles a ***halfwave-rectified*** 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***



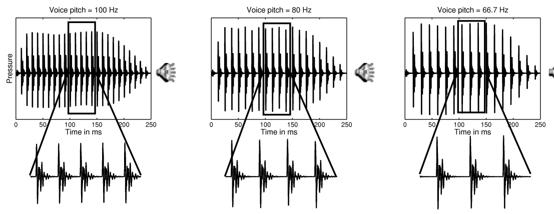
Processing of complex sounds

- When we speak, the opening of the vocal folds releases puffs of air into the oral cavity, thereby producing sound (***glottal pulse***)
- The quality of the resulting sound depends on the shape of the oral cavity (e.g., different vowels)
- Different vowels contain different frequencies
- The frequency spectra of vowels are characterised by three prominent frequencies, the ***formants*** ⇒ 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



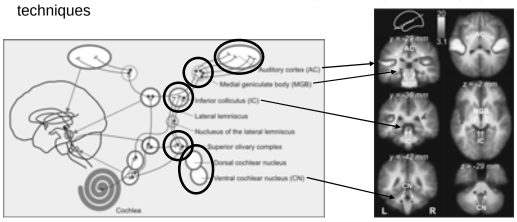
Processing of complex sounds

- 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 ⇒ 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 ⇒ the auditory system might use this timing information to derive pitch



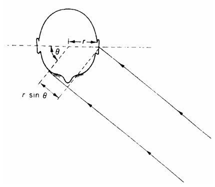
Central auditory system

- 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



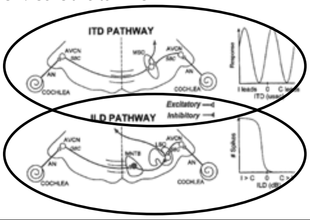
Spatial hearing

- 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



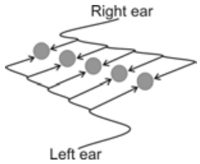
Spatial hearing

- 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



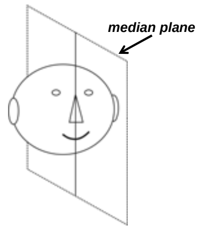
Spatial hearing

- 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
  - Jeffress proposed that 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 difference in the *axonal conduction delay* from the two ears compensates the *external/acoustical* time difference (ITD)



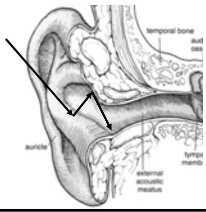
Spatial hearing

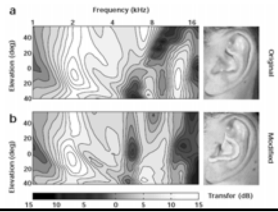
- In the ***median plane*** ⇒ sounds elicit neither ITDs nor ILDs
- Nevertheless, humans can localise the elevation of sound sources with reasonable accuracy



Spatial hearing

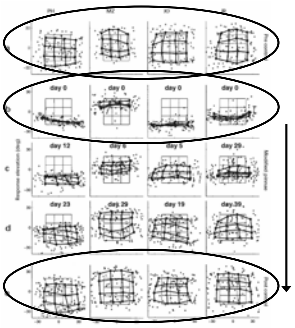
- In the median plane, sound location is conveyed by spectral cues
- Reflections from and deflections around surfaces enhance some frequencies and attenuate others
- Journey towards ear drum imparts spectral "profile" to the incoming sound ⇒ the shape of the profile depends on the sound source location
- Location-dependent spectral profiles are dependent on shape of outer ear ⇒ highly individual
- Being able to use spectral profiles for sound localisation means having learned the frequency transfer characteristics of one's own ears (Hofman et al., 1998. Nat. Neurosci. 1, 417-421)





Spatial hearing

- Ability to localise sound elevation was dramatically degraded immediately after the modification
- Over weeks of wearing the molds, subjects progressively reacquired their sound localisation ability



→ 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