Hearing: Auditory perception

Katrin Krumbholz

Contact: katrin@ihr.mrc.ac.uk, 922 3431

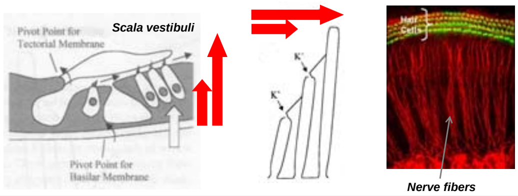
MRC Institute of Hearing Research (Science Road)

Topics:

- Different aspects of information conveyed by the auditory nerve (level, frequency and temporal)
- How might the auditory system use this information to create the perception of different sound attributes (loudness, pitch or spatial location)?

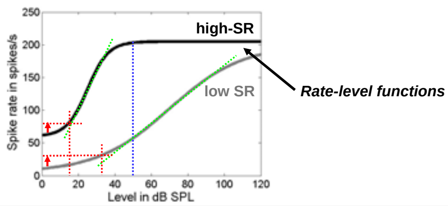
Sound level

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



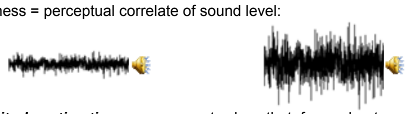
Sound level

- 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 saturate at about 50 dB SPL (no show any further increase in firing rate)
- Low-SR fibers don't saturate even up to the highest audible sound levels (100-120 dB SPL = pain threshold)
- Rate-level functions of low-SR fibers are much shallower than those of high-SR fibers
- Low-SR fibers might play crucial role in the perception of **loudness**

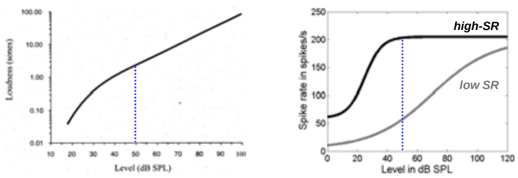


Loudness

- Loudness = perceptual correlate of sound level:

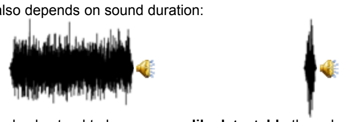


- ***Magnitude estimation*** measurements show that, for moderate and high sound levels, loudness grows at a remarkably steady rate
- 10-dB increase in level ⇒ doubling in loudness
- Suggests that loudness perception above 50 dB SPL is based on the signal from the low-SR fibers, even though their number is much lower (only 10%)

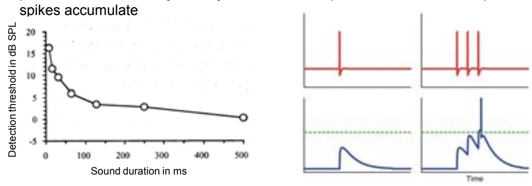


Temporal integration

- Loudness also depends on sound duration:



- Longer sounds also tend to be **more readily detectable** than shorter sounds
- Suggests that the sound level information conveyed by auditory nerve is **integrated over time** somewhere higher up in the auditory system
- ***Temporal integration*** could be implemented by neurons, the membrane potential of which decays slowly over time ⇒ responses to successive input spikes accumulate



Temporal resolution

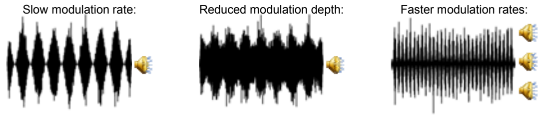
- Temporal integration is beneficial when trying to detect weak and/or noisy sensory stimuli
- Striking example of temporal integration: visual systems of nocturnal toads integrate incoming light for **record period of ~1.5 s** to increase sensitivity to very low light levels
- ➢ However: temporal integration can also be **detrimental** ⇒ makes the world look/sound temporally blurred ⇒ **limits ability to resolve fast changes in sensory input over time**
- Visual modality: images on computer screens appear static, when they actually flicker at a ~60-Hz rate

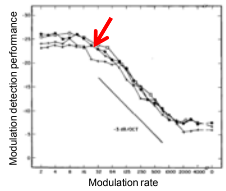
Nocturnal toad, *Bufo bufo*

Temporal resolution

- In auditory modality, limitations in temporal resolution can be measured using a technique adapted from visual psychophysics
- ➢ Involves measuring audibility of ***amplitude modulation*** in sound (≅ flicker in vision)

Slow modulation rate: Reduced modulation depth: Faster modulation rates:

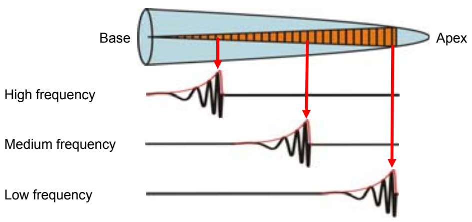




- ➢ Reflects the **limit of temporal resolution** in auditory processing
- ➢ ***Temporal modulation transfer function (TMTF):***
- These measurements suggests that **auditory processing is much faster than visual processing**

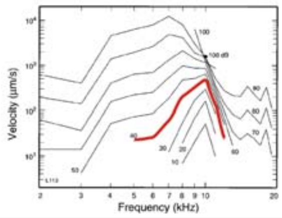
Frequency selectivity

- The basilar membrane (BM) exhibits mechanical tuning for sound frequency ⇒ different places along the membrane respond maximally to different frequencies



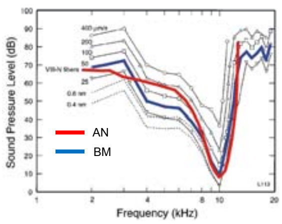
Frequency selectivity

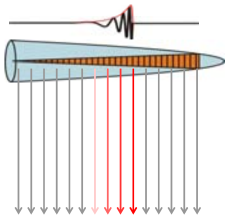
- As a result of this mechanical tuning, each point along the BM is ***selective for frequency*** (only responds to a limited range of frequencies)
- ➢ Each point on the BM acts like a ***bandpass filter***, which passes through frequencies within a certain frequency band, but attenuates all other frequencies
- ➢ Common to refer to different points along the BM as "***auditory/cochlear filters***" (analogous to tinted glasses in vision)
- Frequency that produces largest response is referred to as the ***characteristic frequency (CF)***



Frequency selectivity

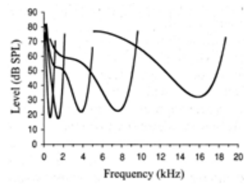
- ➢ Each ascending AN fiber **only innervates a single hair cell** ⇒ AN fibers are also tuned for frequency, with very similar tuning properties as the BM
- ➢ Thus, the distribution of activity across the AN (***excitation pattern***) mirrors the profile of response along the BM, which, in turn, reflects the frequency/spectral composition of the incoming sound

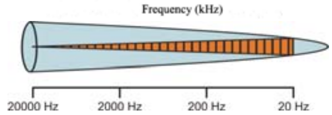




Frequency selectivity

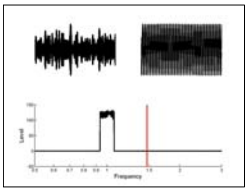
- As a result of the gradient in the mechanical properties of the BM, the CF of the cochlear filters changes along the length of the membrane ⇒ AN fibers attached to different places along the membrane also have different CF
- ➢ Tuning curves become broader towards higher CFs
- ➢ The cochlear frequency map becomes progressively compressed towards higher frequencies (like retinotopic map moving away from the fovea)





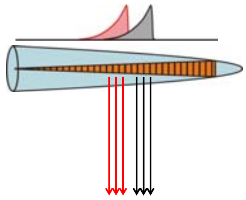
Masking

- One of the most important consequences of cochlear frequency selectivity is to minimise ***masking***
  - Masking refers to the fact that sounds can be rendered inaudible by the presence of other sounds
- Measure audibility of target sound (“signal”) in the presence of interfering sound (“masker”)



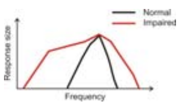
Masking

- A masker only “masks” a signal, when the masker and signal are close to each other in frequency
  - When the masker and signal frequencies are sufficiently separated, masking is avoided ⇒ the overlap between basilar membrane responses is minimal ⇒ stimulate different sets of AN fibers
  - Avoidance of masking through cochlear frequency selectivity = important prerequisite for being able to communicate in noisy environments
- In contrast to normal-hearing people, people with hearing impairment often find this task very difficult/impossible, even when using a hearing aid

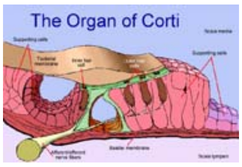


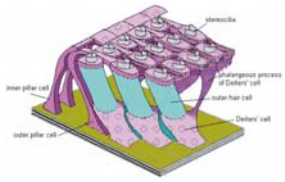
Hearing impairment

- One of main causes for this deficit**: the cochlear filters in hearing-impaired people are much wider than in normal-hearing people**
  - Each point on the BM of a damaged cochlea responds to a much wider range of frequencies than in a normal cochlea



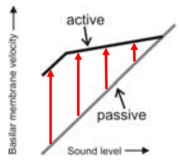
- In the majority of cases: Hearing impairment = consequence of **damage to, or death of, outer hair cells (OHCs)**, because most delicate cells
- The OHCs elongate and contract when stimulated ⇒ push and pull the BM in its direction of motion ⇒ **create active amplification** of its response

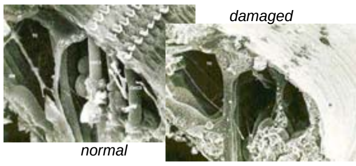


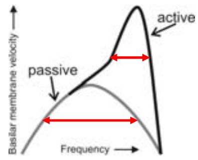


Hearing impairment

- While the exact mechanisms of this active amplification process are not yet fully understood, the process is known to have two important properties:
- First: amount of amplification is large at low sound levels and **decreases towards higher levels**
- Second: the **amplification is highly frequency-selective** and thus **increases the sharpness of the BM frequency tuning**
  - Without active amplification, BM response is not only smaller than with amplification, but is also much less selective for frequency

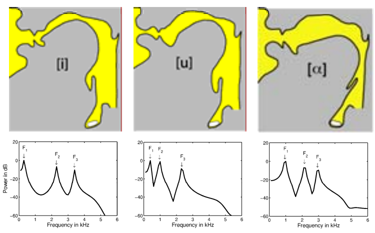






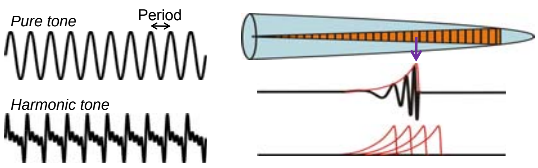
Pitch perception

- Next to avoidance of masking, the frequency selectivity of the cochlear response also enables us to form a representation of the spectral composition of the incoming sound
  - Spectral information = one of most of important determinants of “timbre” (sound quality)
- Frequency spectra of vowels contain series of prominent peaks (formants); different vowels are characterised by different patterns of formant peaks



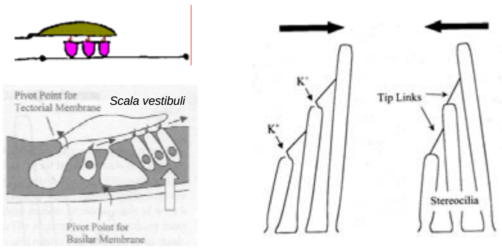
Pitch perception

- The frequency information conveyed by the AN may also be important for **pitch perception**
- Pitch is usually associated with sounds that have **temporally period waveforms** (e.g., pure tones and harmonic tones)
- **Perceived pitch value = reciprocal of repetition period = repetition rate**
- Pure tones: repetition rate corresponds to the pure-tone frequency ⇒ determines the **place of maximum response along the BM**
  - Thus, **different frequencies (pitch values) are associated with different places of peak response**
  - The auditory system could use this **“place” information** to create the sensation of pitch
- Similar general principles also apply to harmonic tones



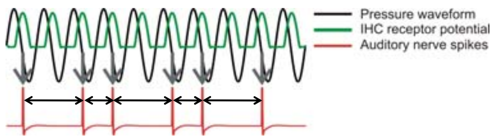
Pitch perception

- Another aspect of information thought to be important for pitch perception = fine-grain temporal information
- Movement of the BM creates a shearing force, which deflects the hair bundles on the hair cells
- Only one phase of the BM motion (the motion towards the scala vestibuli) is effective in eliciting a receptor potential in the hair cells



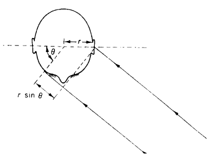
Pitch perception

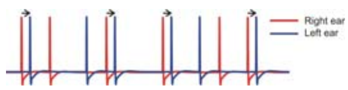
- ➢ Receptor potential only reflects one half-cycle of BM motion
- This means that the spikes in the AN are *time-locked* to a particular *phase* in the waveform of the stimulating sound
- ➢ ***Phase locking*** ⇒ the temporal pattern of the AN spike trains reflects the temporal structure of the sound
- Pure tones: Time intervals between the spikes are close to integer multiples of the waveform repetition period ⇒ related to pitch value
- ➢ Rather than using the "place" information, the auditory system could also use the temporal information to create sensation of pitch (measure time intervals between spikes in AN responses)
- Similar principles also apply to harmonic tones
- Whether pitch perception involves processing of "place" or temporal information is still a matter of debate



Spatial hearing

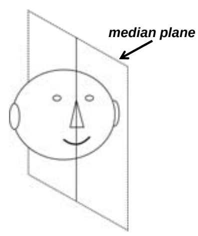
- In humans, sound localisation mainly relies on the analysis of differences in sound level and sound arrival time at the two ears [referred to as ***interaural level*** and ***interaural time differences*** (***ILDs***, ***ITDs***)]
- In a sound originating from a lateralised source, ILDs are produced 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 only few tens to a few hundreds of *microseconds*
- Analysis of ITDs requires comparison of spikes trains across the left and right ears
- ITDs are more important at low frequencies (≤ 2 kHz), because phase locking breaks down at high frequencies ⇐ physiological processes involved (creation of receptor potential and elicitation of spikes) are too slow to follow high frequencies

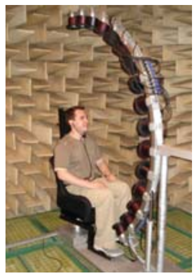




Spatial hearing

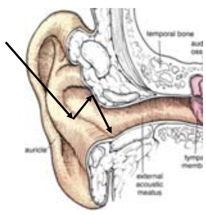
- In the ***median plane*** ⇒ sounds elicit neither ITDs nor ILDs
- Nevertheless, humans can localise the elevation of sound sources with reasonable accuracy

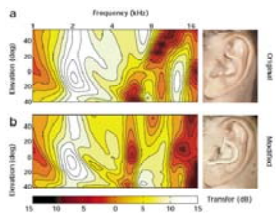




Spatial hearing

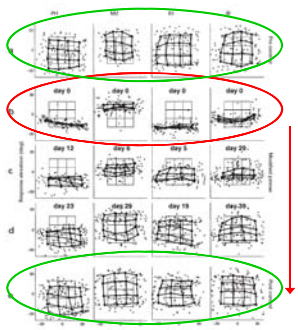
- In the median plane, sound location is conveyed by **spectral cues**
- Sound wave impinge on head and outer ear ⇒ reflections/deflections from various surfaces enhance some frequencies and attenuate others
- ➢ On its journey towards ear drum, sound acquires spectral "profile" ⇒ the shape of the profile depends on the direction of the sound
- ➢ ***Head-related transfer functions (HRTFs)***
- ➢ HRTFs depend on shape of outer ear ⇒ highly individual
- ➢ Being able to use the HRTFs for sound localisation means having learnt how they relate to sound location (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, performance gradually recovered to normal levels



→ Colour versions of handouts in large print:
ftp://ftp.ihr.mrc.ac.uk/pub/*katrin*

→ Further reading (books):

1. **C. J. Pack, The Sense of Hearing**
2. **W. A. Yost, Fundamentals of Hearing: An Introduction**

3. B. C. J. Moore, An Introduction to the Psychology of Hearing
4. W. A. Yost, A. N. Popper and R. R. Fay, Human Psychophysics
5. J. O. Pickles, An Introduction to the Physiology of Hearing

→ Websites:

i. http://www.brainconnection.com/topics/?main=anat/auditory-phys
ii. http://www.cf.ac.uk/biosi/staff/jacob/teaching/sensory/ear.html
iii. http://www.biols.susx.ac.uk/home/Chris_Darwin/Perception/Lecture_Notes/Hearing_Index.html