



Lecture 2-9: Frequency Analysis in the Inner Ear

Overview

1. **Frequency specificity of hearing.** Simple experiments show that our hearing mechanism delivers messages to the brain that differ depending on the frequency content of the sound signal. For example a pure tone can be made inaudible, or **masked**, by the presence of a band of noise. This masking is greatest when the tone and the noise overlap in frequency. This suggests that individual frequency components of sounds are processed separately from each other. A suitable analogy is that of a **filterbank** – a set of band-pass filters each responding to a different frequency region. Masking only occurs when the tone and the noise are processed by the same filter.
2. **Structure and function of the cochlea.** The cochlea is a spiral chamber filled with fluid and divided along its length by membranes. Mechanical input from the **oval window** causes fluid flow along the **scala vestibuli**, through the **helicotrema**, and back down the **scala tympani** to the **round window**. The nerve cells that signal sound input are organised along the length of the cochlea in the **organ of Corti**. This sits on one of the dividing membranes, called the **basilar membrane**. Vibration of the basilar membrane in response to fluid flow in the cochlea causes transduction elements in the organ of Corti to register the presence and frequency content of the sound.
3. **Response of the basilar membrane to pure tones.** The size and mechanical properties of the basilar membrane vary along its length, being narrower and stiffer near the base and wider and more flexible near the apex. When a pure tone signal is applied, the cochlear fluid oscillates in phase with the stimulus, causing the whole basilar membrane to vibrate at the stimulating frequency. However, because the membrane varies along its length, there will be one place where the resonant frequency of the membrane matches the stimulus frequency and this place will show the maximum amount of vibration, see figure 2-9.1. Thus each frequency can be mapped to a single place of maximum vibration. This is called a **tonotopic** or **frequency to place** mapping. The pattern of vibration is shaped by the **travelling wave pattern** of the vibration on the basilar membrane: this is shallow on the high frequency side and steep on the low frequency side, see figure 2-9.2. By measuring vibration at particular points on the membrane for a range of stimulus frequencies we can plot out the frequency response of each place on the membrane. This also gives us evidence that each place on the membrane acts as a band-pass filter, see figure 2-9.3.
4. **Nerve transduction.** Within the organ of Corti are specialised vibration-sensitive cells called **hair cells**. These have projecting cilia that shear against the **tectorial membrane** when the basilar membrane vibrates, see figure 2-9.4. Bending of the cilia releases neurotransmitter which passes into the synapses of one or more nerve cells which fire to indicate vibration. The amount of firing is thus related to the amount of vibration, so that the overall pattern of nerve excitation from the organ of Corti also follows the place principle. Indeed we can plot the audiogram of a single nerve cell (called a **physiological tuning curve**, see figure 2-9.5) that reflects the band-pass analysis seen on the basilar membrane. Since neurotransmitter is only released when the cilia are bent in one direction, firing tends to be in phase with basilar membrane movement. This means that the temporal pattern of firing is **synchronised** to the phase of the stimulating waveform, at least for low-to-mid frequencies (below 5 kHz). This is called **temporal coding** of frequency, see figure 2-9.6.

Reading

- Hewlett & Beck, An introduction to the science of phonetics, Chapter 15: Pitch and quality, pp212-226. *Basic introduction to concepts.*
- Yost, Fundamentals of Hearing: An introduction (4th edition), Chapters 7-9. *Detailed and comprehensive description of frequency analysis.*

Learning Activities

You can help yourself understand and remember this week's teaching by doing the following activities before next week:

1. Draw a 'boxes and arrows' schematic diagram which summarises the processing of a sound signal through auditory system components from outside the head to firings on the auditory nerve.
2. Write a description of the two different ways in which information about the pitch of a pure-tone stimulus is encoded in the firing on the auditory nerve.
3. Research and summarise your findings on one method that has been used to measure psychophysical tuning curves in human subjects. PTCs are effectively audiograms of single regions of the basilar membrane.

If you are unsure about any of these, make sure you ask questions in the lab or in tutorial.

Reflections

You can improve your learning by reflecting on your understanding. Here are some suggestions for questions related to this week's teaching.

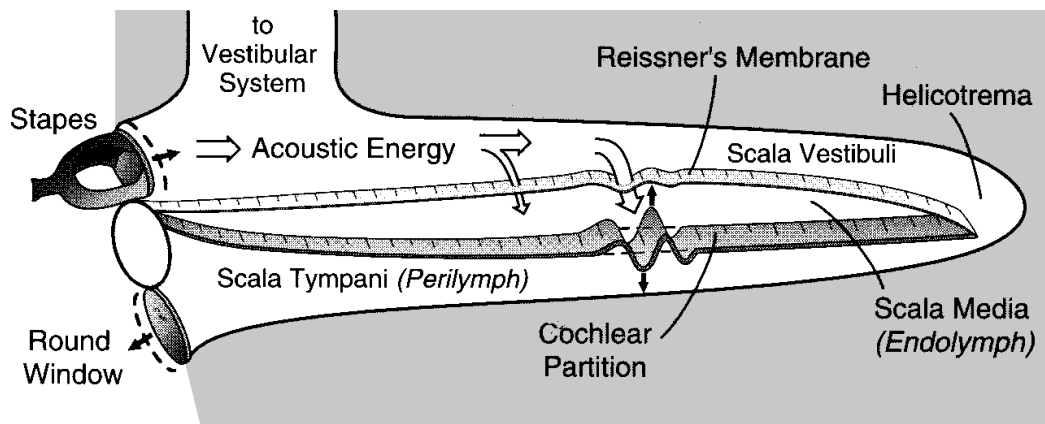
1. Think of some everyday examples of 'masking'.
2. What sets the limit for the highest frequency pure tone that we can hear? Why can dogs and bats hear higher frequencies?
3. What limits the size of the just noticeable change in the frequency of a pure tone?
4. Explain the shape of a typical physiological tuning curve for a nerve fibre. What controls the frequency at which it is most sensitive?
5. What is the difference between place coding and temporal coding of the frequency of a pure tone?
6. How do you think the place and temporal coding mechanisms might be used to establish the pitch of a complex tone?
7. How do you think the place mechanism might be used to establish the timbre of a complex tone?

Examination Question

These is a question from a past exam paper. You may like to write an outline answer or discuss in tutorial.

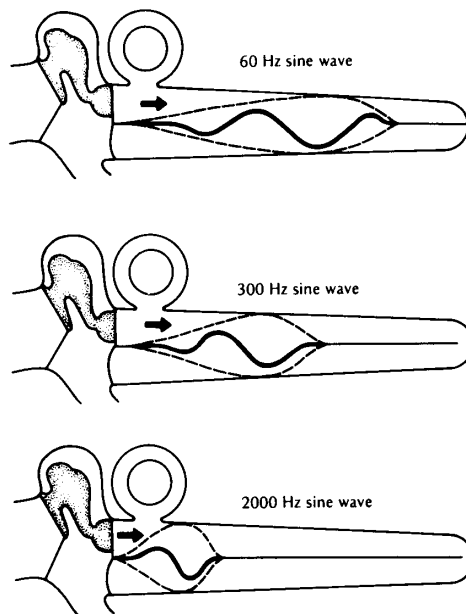
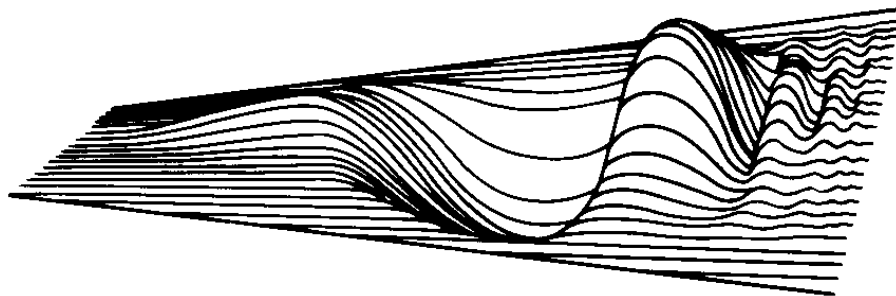
1. Give a step-by-step explanation of the processing of a pure tone by the peripheral auditory system from sound into neural firing. Be sure to include in your answer the filtering by the outer and middle ear, properties of cochlear transduction and neural encoding. [2008]

Figure 2-9.1 *Vibration of the Basilar Membrane in Response to a Pure Tone*



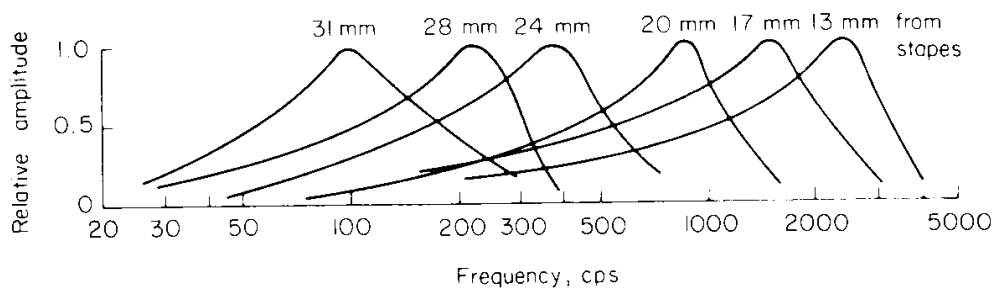
From Geisler, C. D. (1998) *From Sound to Synapse: Physiology of the Mammalian Ear* (Oxford, New York).

Figure 2-9.2 Travelling Wave Pattern



From Yost (1994)

Figure 2-9.3 Basilar Membrane Acting as Bank of Band-Pass Filters



The way to interpret this graph is to think of how each **place** on the basilar membrane is set in vibration by a **range** of sinusoidal frequency components. It will vibrate best at one frequency, but other frequencies will cause it to vibrate to a lesser extent.

Figure 2-9.4 Structure of the Organ of Corti

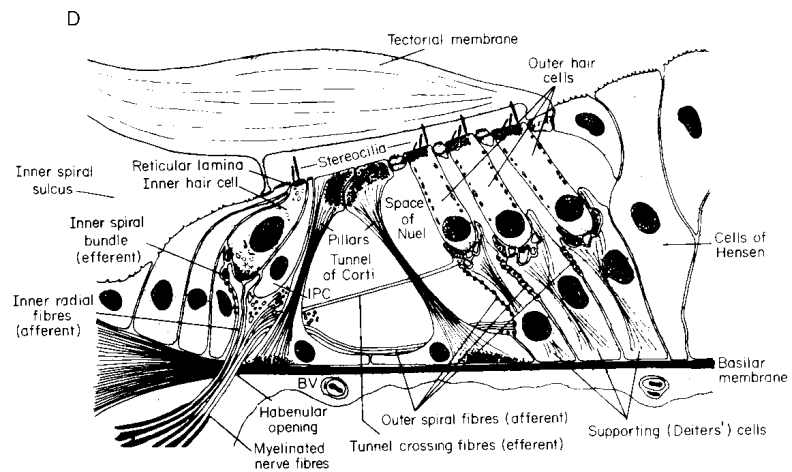


Figure 2-9.5 Physiological Tuning Curve

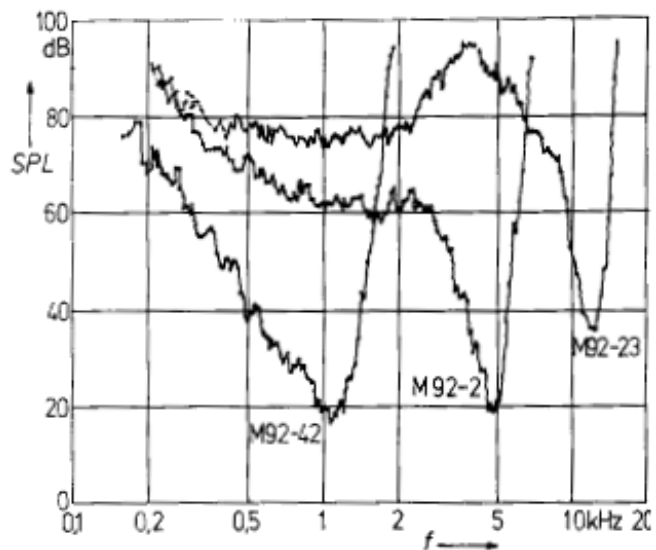
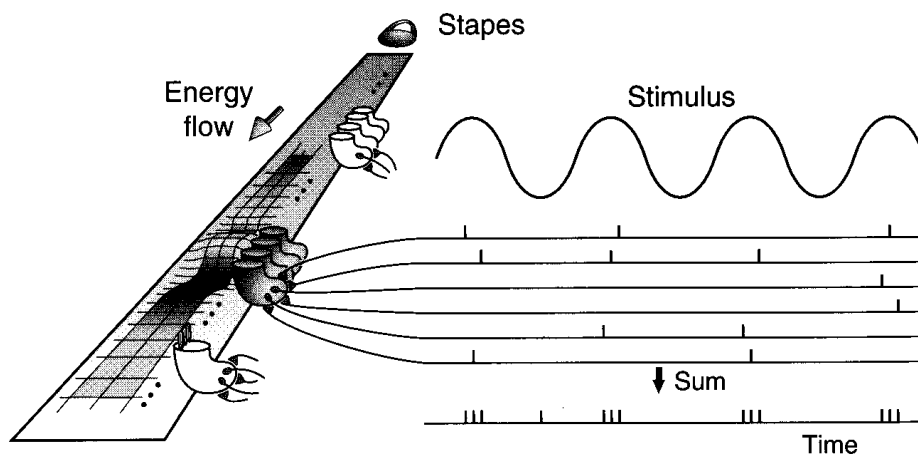


Figure 2-9.6 Temporal Properties of Nerve Firing



From Geisler (1998)

