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Lecture - 7/29/99
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***Note: the figures for this lecture are all in the readings.

Hearing I: Lecture Notes

O. Introduction

We started the class by listening to a piece from Beethoven's Symphony No. 9. Beethoven began to lose his hearing at 30, and although he could no longer perform as a pianist, he continued to be able to compose music. Symphony No. 9 was written late in life after he had gone completely deaf.

I. What is sound?

- If a tree falls in the forest, does it make the sound of one hand clapping?
    - sound as a physical stimulus: pressure changes in the air (see Fig. 11.5)
        - **amplitude**: the height of a pressure wave
        - **frequency**: how many times per second the sine-wave repeats itself
    - sound as a psychological experience: hearing
        - **loudness** is related to amplitude: sounds get louder with an increase in amplitude
        - **pitch** is related to frequency: pitches get higher with an increase in frequency
            - In addition to an increase of pitch with increase in frequency, tones are organized into**octaves**. (see Fig. 11.9)
            - Each octave contains seven notes (A, B, C, D, E, F, and G). Two 'A' notes in different octaves sound similar. This similar-sounding quality is called **tone chroma**.
            - An 'A' note one octave above another note has a fundamental frequency twice that of the lower note. (e.g., A4 = 220 Hz, A5 = 440 Hz, A6 = 880 Hz, etc.,).
        - **harmonics**: Fourier components of a complex tone which are multiples of the fundamental frequency. (Fig. 11.8)
            - Two pure tones whose frequencies are multiples of each other blend into one in our perception producing a single tone at the fundamental (the lower) frequency.
            - Musical instruments hardly ever produce pure tones. Instead, when you pluck a string on a guitar, it will produce a vibration at some

        - fundamental frequency as well as several multiples (called harmonics).
        - Our perception of timbre is related to the harmonic composition of a tone (more on this later).
        - This is also the basis of a capella singing.
- Many animals use air/water vibrations for things other than hearing
    - bats use sonar to get around at night
    - whales can create such powerful vibrations that they stun their prey

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II. The Human Ear

- Please see pages 318-325 in the readings - they contain a very clear and complete explanation of ear anatomy and auditory transduction.
- Outer Ear
    - Figure 11.10
    - **pinna**: the outer fleshy part of the ear helps focus sound waves
    - **auditory canal** (that part of the ear you're not supposed to put q-tips in): has wax to protect from insects and hairs to keep a constant temperature. also serves to amplify sounds around its resonant frequency (2,000-5,000 Hz).
    - **tympanic membrane** (aka eardrum): a taut membrane at the end of the auditory canal that vibrates with the changes in airpressure at the ear
- Middle Ear
    - **ossicles**: three bones (the smallest bones in the body) that connect the tympanic membrane of the outer ear and the oval window of the inner ear. The three bones in order are **malleus**, **incus**, and**stapes**. (Figure 11.11)
    - The ossicles serve to amplify vibrations (about 22x) between the outer ear and inner ear. This is necessary since vibrations in the inner ear travel through fluid which is much more dense than air. The ossicles amplify in two ways:
        - concentrate vibrations of the large tympanic membrane onto the small footplate of the stapes (an amplification of about 17 times). (Fig. 11.13)
        - act as a fulcrum and so (because of the way they are hinged) benefit from the lever principle (another amplification of 1.3 times) (Fig. 11.14)
- Inner Ear
    - **cochlea**: a coiled liquid-filled structure. The liquid inside the cochlea vibrates because the stapes pushes on the oval window (at the base of the cochlea). The cochlea has three layers: **scala tympany**, **scala vestibuli**, and the **cochlear partition**. (Fig. 11.15)
    - Inside the cochlear partition is the **organ of corti** which is the site of auditory transduction (Fig. 11.16 & 11.17)
        - the organ of corti contains **inner hair cells** and **outer hair cells**
        - sits on top of the basilar membrane
        - is covered by the tectorial membrane
        - **auditory transduction**: when the basilar membrane moves up and down, the cilia of the inner hair cells (small hair-like projection off of the hair

cells) rub against the tectorial membrane. The bending of the cilia produces and electrical response in the hair cells.
        - outer hair cells help amplify vibrations of the basilar membrane (figure 11.37 in the text).

III. Pitch Perception

- How does the firing of hair cells signal different pitches?
- Place code for pitch
    - big idea: different frequencies are signaled by neurons that are located in different places in the auditory system
    - Bekesy studied the basilar membrane to discover that:
        - the motion of the basilar membrane is a **traveling wave** (Fig. 11.25)
        - the **base** of the basilar membrane (near the oval window) is three or four times narrower than the **apex** (the far end of the cochlea).
        - at the base, the basilar membrane is 100 times stiffer than it is at the apex.
    - using this information, Bekesy constructed models of the traveling wave motion of the basilar membrane
    - he discovered that different frequencies of sound would lead to a different **envelope** of vibration on the basilar membrane with a different peak of displacement for each frequency. (Fig. 11.28)
    - therefore, different frequencies of sound would get a peak vibration in different places on the basilar membrane. The point of peak vibration of the basilar membrane would presumably cause the most bending of the cilia and elicit the most response from the hair cells in that part of the cochlea.
    - high frequencies would cause greatest vibration near the base, and low frequencies would cause greatest vibrations near the apex.
    - **tonotopic map**: measuring electrical responses from different points on the cochlea revealed that there is indeed a tonotopic map - cells in different spots on the cochlea respond to different frequencies, with high frequencies near the base, and low frequencies near the apex. (Fig. 11.29)
    - **frequency tuning**: microelectrode recording revealed that individual cells are responsive to different frequencies of vibration. A cell's **characteristic frequency** is the frequency that that neuron is most sensitive to. (Fig. 11.30)
    - *COOL* The cochlea works as a frequency analyzer (it does what fourier transform does). It analyzes incoming sound into its constituent frequency components and translates the components into separated areas along its length. (Fig. 11.38)
- Timing code for pitch
    - big idea: different frequencies are signaled by the frequency of firing of neurons in the auditory system
    - big problem: neurons have a refractory period which allows them to fire a maximum of 500 times per second (500 Hz). How would such neurons be able to

signal higher frequencies? (people can hear frequencies of up to 20,000 Hz) It was looking bad for the timing code until Wever discovered the cochlear microphonic.

    - **The cochlear microphonic** is a small electrical signal that can be measured by an electrode placed near the hair cells of the cochlea. We now know that the cochlear microphonic arises from the sum of electrical potentials in the hair cells of the cochlea. Mimicks the form of the sound pressure waves that arrive at the ear. Low frequency tones result in low frequency modulations of the cochlear microphonic electrical signal. High freq tones result in high freq modulations of the electrical signal. Combination (sum) of high plus low freq tones results in sum of high plus low freq modulations in cochlear microphonic electrical signal. In fact, cochlear microphonic is a shift-invariant linear system that obeys scalar, additivity, and shift-invariance rules.
    - a simple version of the timing code can't work, but if neurons work together according to the **volley principle**, it's possible to produce a timing code even for higher frequencies (see figure 11.41 in the text). Wever suggested that while one neuron alone could not carry the temporal code for a 20,000 Hz tone, 20 neurons, with staggerred firing rates, could. Each neuron would respond on average to every 20th cycle of the pure tone, and the pooled neural responses would jointly contain the information that a 20,000 hz tone was being presented. (Fig. 11.41)
    - **phase locking**: an observed phenomenon (in support of the volley principle) where neurons fire in synchrony with the phase of a stimulus. No individual neuron could fire at each peak, but a bunch of phase-locked neurons working together can produce a burst of activity at each peak, and so the firing frequency of a collection of neurons can indeed mimic the frequency of the stimulus. (Fig. 11.42)
- Periodicity pitch
    - Suppose we have a 400 Hz fundamental plus its harmonics (800, 1,200, 1,600, 2,000). This should sound like a pitch of 400 Hz with a rich timbre.
    - What happens when we remove the fundamental frequency (the 400)? The percieved pitch of the tone doesn't change. This is called **periodicity pitch** or the **effect of the missing fundamental**. (Fig. 11.44)
    - Why is this a problem for place-coding for pitch?
    - Why is this useful?
        - music is recognizable even on crappy stereos that can't reproduce the fundamental frequencies
        - voices are recognizable on the phone, even though phones can't reproduce the fundamental frequency of the human voice
        - construction of pipe organs