THE AUDITORY SYSTEM

1. Physical Stimulus: Sound
   - Vibration of an object leads to compressions & rarefactions of the material in the object
   - This can be transferred and transmitted to other media (like air)

Cliché: If a tree falls in the forest, and no one is there, does it make a sound…?

Can describe the sound in terms of physical properties:
   a) Frequency (Hertz, HZ)

   b) Wavelength (meters, m)

   c) Amplitude (decibels, dB)

   d) Complexity (spectrum, etc.)

$P_{\text{threshold}} = 0.0002 \text{ dynes/cm}^2$  
$= 20 \mu\text{Pa} = \text{SPL}$

6 dB change means a doubling in intensity
2. Perceptual Attributes (Psychological experience of physical attributes)

a) Frequency ☞ Pitch

b) Amplitude ☞ Loudness

c) Complexity
   i. “richness”
   ii. “brightness”
   iii. “timbre”

Key point: there is a physical stimulus, with physical attributes that are essentially incontrovertible; there are also perceived, psychological descriptions of the stimulus that can change for a number of reasons

Both top-down and bottom-up processes at work in affecting perception of sounds
3. Anatomy of the Auditory System
Outer ear, middle ear, inner ear/cochlea, auditory nerve, auditory pathway, auditory cortex

a) Outer ear
   i. Pinna (“ears”)

   ii. External auditory canal

   iii. Eardrum – tympanic membrane

b) Middle ear
   i. Ossicles (malleus, incus, stapes)

   ii. Acoustic reflex

c) Inner ear (cochlea)
   i. Cochlea (anatomy only, today)
d) Auditory neural pathway
   i. Cochlear nerve

ii. Central auditory pathway (up to auditory cortex)

Acronym Mnemonic:
4. Functioning of the cochlea
   a) Basic transduction process
      
      i. RATE theory
      
      ii. PLACE theory (Traveling wave along basilar membrane)
      
      iii. Combination

With only 3500 inner hair cells, how can we determine all the complex sounds?
b) Hair cell functioning

i. Inner hair cells

ii. Outer hair cells

iii. “Characteristic frequency” of auditory nerve fiber
5. Auditory Cortex
   a) Pathway (recall from previous lecture)
      i. Primary Auditory Receiving Area (A1)
      ii. “Core” = A1 + some surrounding areas
      iii. Secondary auditory cortex
      iv. Auditory association cortex

   b) Tonotopic map

   c) Columnar arrangement

   d) Plasticity of perception

(See next page)
In previous chapters we have seen that there is ample evidence that the types of stimuli to which neurons respond is shaped by the stimuli that the animal experiences. Recent experiments by Rainer Klinke and coworkers (1999) have demonstrated a connection between how much stimulation is received by the cortex and the functioning of the cortex. They used kittens who were deaf because their organ of Corti had degenerated shortly after birth, due to a genetic defect. Because of this degeneration, no nerve impulses reached the auditory cortex in these animals.

The purpose of Klinke's experiments was to see how providing stimulation to the auditory cortex would affect its functioning compared to similar animals whose auditory cortex had received no stimulation. Klinke and coworkers provided this stimulation by implanting a stimulating electrode in the kitten's auditory nerve, which was still intact. This electrode was attached to a microphone that picked up sound stimuli in the environment and caused the electrode to fire and stimulate the auditory nerve.

In the behavioral part of the experiment, Klinke presented a tone to signal the dispensing of food pellets. Within one to three weeks, the kittens responded to the tone by stopping whatever they were doing to get the food pellets. Figure 10.48 shows a video sequence in which a tone was presented while the kitten was eating. Upon hearing the tone, the cat left its food to collect the much more desirable food pellets.

The behavioral experiments showed that the electrode enabled the kittens to hear. But what is particularly significant about this experiment is that, as training progressed, the electrical response of the cat's auditory cortex increased significantly. Not only did long-latency responses develop, indicating high-level processing, but the size of the auditory area expanded, so it became seven times larger than the auditory area of control animals that had been implanted with electrodes that were never activated. The difference between the cortical responding of the experimental and control animals shows that without stimulation, the auditory cortex does not develop, but with stimulation development occurs.

Other experiments, with normal animals, have also shown a connection between cortical stimulation and the response of the cortex. For example, owl monkeys were trained to discriminate between two frequencies near 2,500 Hz. After

(continued)

![Figure 10.48](image)

Video sequence showing a cat that has stimulating electrodes implanted in its auditory nerve. It is eating on the left and then responds to a tone, which has activated the stimulating electrode. (From Klinke et al., 1999.)

The Plasticity of Perception (continued)

the training had caused a large improvement in the monkey's ability to tell the difference between frequencies, a tonotopic map of the primary auditory cortex (AI) was determined (Recasens et al., 1993). The results, shown in Figure 10.49, indicate that, compared to a monkey that had no discrimination training (Figure 10.49a) the trained monkey (Figure 10.49b) had much more space devoted to neurons that respond best to 2,500 Hz. Thus, the kitten experiments show that stimulation of the auditory cortex causes the size and general responsiveness of the auditory area to increase, and the monkey experiments show that training in a specific task can cause changes in the firing of individual neurons.

![Figure 10.49](image)

(a) Normal owl monkey

(b) Monkey trained on 2,500-Hz task

(a) Tonotopic map of the owl monkey's primary auditory receiving area (AI), showing areas that contain neurons with the characteristic frequencies indicated. The gray area contains neurons with CF = 2,500 Hz. (b) Tonotopic map of an owl monkey that was trained to discriminate between frequencies near 2,500 Hz. The gray areas indicate that there is an expansion of the area that contains neurons with CF = 2,500 Hz.