# MEDS 371, Systems Neuroscience
# University of Connecticut Health Center

## A4. Peripheral Auditory System
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**Reading**: This syllabus and Purves et al. chapter 13

**Goals**: To understand the structure and function of the peripheral auditory system and the neural encoding of the stimulus frequency and intensity

## Introduction

As an initial step in an overall understanding of the hearing processes, this lecture will deal with standard terminology of auditory stimuli and of the structure and function of the peripheral auditory system, which consists of the outer ear, the middle ear, and the cochlea.

Vibration of a physical structure produces a sound wave which represents a change in the pressure over time and space. Some device such as a tuning fork vibrates sinusoidally and produces a sound which has a pure pitch. The perceived pitch is determined by the frequency of a sound. The frequency is measured in hertz (Hz) and has the meaning of cycles of vibration per second. The period of a sound is the reciprocal of the frequency and is measured in seconds or milliseconds. The perceived loudness is determined by the sound pressure level (SPL) in decibel (dB). The dB SPL is a logarithmic scale of sound pressure amplitude, P, defined as follows:

$$\text{dB SPL} = 20 \times \log(P/\text{ref.}),$$

where ref. is the reference pressure, 20 micro-pascal (µPa).

Normal human hearing covers a range of frequencies from about 20 Hz to about 20,000 Hz. The threshold of human hearing is the lowest for middle frequencies in the range of 2000-5000 Hz and is approximately 0 dB SPL. On either side of this middle range of frequency, the threshold of hearing increases. Conversational speech sounds typically have frequencies of 100-5000 Hz and levels of 50-70 dB SPL. Exposure to intense sounds above about 90 dB SPL can damage hair cells (particularly outer hair cells) of the cochlea causing permanent hearing loss.

## Middle Ear

The main function of the middle ear is to reduce the impedance mismatch between the low impedance of the air and the high impedance of the fluid in the cochlea. A large mismatch of the impedance causes most of the sound stimulus energy to be reflected at the air-fluid boundary instead of being transmitted into the cochlea. Maximum energy transmission at the boundary occurs if the impedances are the same. If it were not for the middle ear, the ratio of the cochlear impedance to the air impedance would be about 140. The middle ear action reduces this impedance ratio to about 30.

The middle ear achieves this action of impedance transformation by the following mechanisms: (1) the area of the eardrum is much larger than the area of the stapes footplate. This leads to higher pressure inside the stapes footplate relative to the pressure at the eardrum. (2) The ossicles move like a lever such that the incus and the stapes move less than the malleus. This amplifies the force.

## Middle-Ear Muscle Reflex

There are two middle-ear muscles. The tensor tympani muscle is attached to the malleus and is innervated by the trigeminal (5-th) nerve. The stapedius muscle is attached to the stapes and is innervated by the facial (7-th) nerve. These middle-ear muscles contract in a reflex action during vocalization or when loud sounds are applied. Contraction of the middle-ear muscles makes the ossicular chain stiffer and attenuates the stimulus intensity entering the cochlea. The middle-ear muscle reflex thus provides some degree of protection from loud sounds but not perfectly. The middle-ear reflex is an example of a brain-stem reflex and is analogous to the pupillary reflex of the visual system.

## Cochlear Mechanics

Sound stimulation sets the eardrum and the middle-ear bones in motion. Vibration of the stapes leads to traveling wave propagation along the length of the cochlea. The round window provides release of pressure allowing the stapes to move in and out of the cochlea containing an incompressible fluid.

The cochlear mechanical response exhibits tonotopic organization, i.e., there is an orderly relationship between the stimulus frequency and the position of the basilar membrane that responds maximally. The physical basis for the cochlea's frequency analysis is that the stiffness of the basilar membrane and the organ of Corti changes systematically along the length of the cochlea. The stiffness is maximum near the basal end (near the stapes) and minimum at the apical end (near the helicotrema). In addition, the mass of the organ of Corti is minimum at the basal end and maximum at the apical end. These properties make the basal end tuned to a high frequency and the apical end tuned to a low frequency.

The threshold amplitude of basilar-membrane displacement required to produce hearing is approximately 1 nanometer (nm), or 10 angstroms (Å). Recall that1 Å is the diameter of a hydrogen atom. A tuning curve of basilar membrane is a plot of dB SPL required to produce a constant displacement (e.g., 10 Å) versus frequency. Under a normal condition, such a curve shows a sharp tuning and high sensitivity (i.e., low threshold). The tuning and sensitivity of the mechanical response of the basilar membrane is affected by impairment of the function of the cochlea such as damage of the outer hair cells.

## Hair Cells

Hair cells are mechanoreceptors that transduce mechanical stimulus of hair-bundle displacement into electrical response of receptor potential. Displacement of the hair bundle toward the tallest stereocilia leads to depolarization of the hair cell membrane potential. Under this condition (i.e., hair bundle being displaced toward the tallest stereocilia), ion channels located at the tips of stereocilia are opened as a result of stretching the tip links. A two-pencil version of the "tip-link model" of hair cell transduction can illustrate this mechanism as will be demonstrated during the lecture. Opening of the ion channels at the tips of the stereocilia leads to an increase in the electrical conductance at the apical part of the cell. This leads to an increase in the current flow (mainly carried by $K^+$ ion) from the endolymph into the hair cell, which in turn leads to a depolarization of the hair-cell membrane and entry of $Ca^{++}$ ions into the hair cell. This leads to an increased release of excitatory neurotransmitter at the synapse between the hair cell and the afferent nerve ending. This, in turn, leads to an increase of the firing rate (i.e., excitation) of the afferent cochlear neuron.

Displacement of the hair bundle in the opposite direction (toward the shortest stereocilia) produces opposite effects, i.e., closing of the ion channels, hyperpolarization of the cell membrane potential, and a decrease of the firing rate (i.e., suppression) of the afferent cochlear neuron.

## Innervation Patterns

There are two types of hair cells in the mammalian cochlea, inner hair cells (IHC) and outer hair cells (OHC). There are two type of afferent cochlear neurons, Type I and Type II neurons. The cell bodies of both types of cochlear neurons are located in the spiral ganglion of the cochlea. Most of the cochlear neurons (about 95 %) are Type I, and a very small fraction of cochlear neurons (about 5 %) are Type II. Each Type I cochlear neuron innervates only one IHC. Each Type II cochlear neuron innervates many OHC.

## Response of Cochlear Neurons

A cochlear neuron increases firing rate when the ear is stimulated by sounds. Each of the cochlear neurons shows a sharp tuning of frequency selectivity and a best frequency. A particular cochlear neuron responds best to a tone if the tone's frequency is at the neuron's best frequency. On either side of the best frequency, the threshold rises steeply as the frequency is moved away from the best frequency. The resulting V-shaped curve in a plot of threshold (in dB SPL) versus frequency is called a tuning curve of cochlear neuron. The best frequency of a cochlear neuron is determined by the position of the hair cell along the length of the cochlear partition which is contacted by the cochlear neuron.

## Phase Locking of Cochlear Neurons' Discharges

A cochlear neuron cannot maintain the firing rate of one spike for every cycle of a tone of a middle or high frequency (e.g., above 1000 Hz). Often there are many cycles of a stimulating tone in which a cochlear neuron skips firing. However, if the neuron fires, the spikes tend to occur preferentially at a particular phase within each cycle of the stimulating tone. This tendency of a cochlear neuron’s response is called the **phase-locking** of spike discharges and is observable for stimulus frequencies below about 5000 Hz.

There are two possible roles played by phase locking of spike discharges. Phase-locking of spike discharges in certain populations of neurons of the auditory pathways (e.g., cochlear neurons, certain cochlear-nucleus neurons and certain neurons of the superior olivary complex) plays an important role in binaural processing underlying **sound localization**. Another consequence of the phase-locking of spike discharges is that the interval between successive spikes tend to be integer multiples of the period of the stimulating tone (visible in the interspike interval histograms) and thus the stimulus **frequency** can be encoded (or represented) by the phase-locking of spike discharges (further discussed below).

## Pitch Perception: Frequency Coding

The phase-locking of spike discharges of cochlear neurons provide a code for stimulus frequency which is called a **temporal code** . The temporal code for frequency is present in addition to the more easily understood place code. The **place code** is provided by the tonotopic organization of the cochlear response which represents the frequency in terms of the place along the cochlea. The perception of pitch is believed to be mediated by both the place code and the temporal code for a range of middle frequencies. The place code is dominant for high frequencies and the temporal code is dominant for low frequencies.

## Loudness Perception: Intensity Coding

When a sound stimulus such as a pure tone is made more intense (i.e.,when the dB SPL of the tone is increased), the spike discharge rates of cochlear neurons are increased and, at the same time, more of the cochlear neurons are brought into excitation. Both of these effects, i.e., an increase in the discharge rates of cochlear neurons and an increase in the number of excited cochlear neurons provide a code for sound stimulus intensity which is related to loudness perception.

## Hypothesis of Functional Role of the OHC and IHC Subsystems

One may consider that it is paradoxical that there are about 3.5 times more OHCs than IHCs in the cochlea and yet the OHCs receive only about 5 % of the total afferent cochlear neural population. This unusual situation represents one of the major puzzles in the current understanding of the auditory system. Isolated OHCs have been observed to exhibit contraction and extension of their cell bodies under electrical and chemical stimulation. It has been hypothesized (Kim, 1984; Neely and Kim, 2008) that the role of the OHCs is to amplify the mechanical response of the cochlear partition by means of a motile mechanism powered by metabolic energy. The hypothesis further postulates that the OHCs, the Type II cochlear ganglion neurons and medial olivocochlear neurons form part of a brain-stem reflex arc ( or a feedback loop) that we call the OHC subsystem. According to this hypothesis, the function of the OHC subsystem is <u>not</u> to transmit the usual auditory information to the brain <u>but</u> to amplify mechanical response, and to produce a sharp tuning and wide dynamic range, and to provide a biomechanical gain control adapting the ear properly as the sound pressure level is varied over a range of 100 dB.

The enhanced sensitivity, tuning and wider dynamic range produced by the OHC subsystem is conferred to the IHC subsystem. Details of the auditory information, such as the phonetic contents of speech, the speaker's identity, psychological mood of the speaker, are transmitted to the brain through the IHC subsystem (including 95 % of the cochlear neurons), according to this hypothesis.

## Types of Hearing Loss

Conductive hearing loss refers to hearing loss due to disorders in the middle ear which interferes with sound conduction and attenuates the excitation entering the cochlea. Examples in this category are otitis media and otosclerosis. Sensorineural hearing loss refers to hearing loss due to disorders in the sensory apparatus and/or in the neural structures. Examples in this category are degeneration of hair cells by acoustic trauma or Meniere's disease. Mixed hearing loss refers to hearing loss due to disorders both in the conductive system and in the sensorineural system. An example is presbycusis, where hearing loss begins at about 30 years of age and gradually increases with age. In this case, the hearing loss begins from the high-frequency end and spreads gradually to lower frequencies over time.

References

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