Auditory Physiology

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Physics

Sound Waves

* sound sensation is produced when ***sound waves*** (longitudinal vibrations of molecules in external environment, i.e. alternate phases of condensation & rarefaction of molecules) ***strike tympanic membrane***.
* sound wave speed:

**air** (at 20 °C at sea level) - 344 m/s (1200 km/h, 770 miles/h).

fresh water (20 °C) - 1450 m/s.

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| **A** is record of pure tone.**B** has greater amplitude (**louder** than **A**).**C** has same amplitude as **A** but greater frequency (**pitch** is higher).**D** is complex wave form that is regularly repeated - perceived as musical sounds.***musical sounds*** are made up of wave with primary frequency (determines **pitch**) plus number of harmonic vibrations (***overtones***) that give sound its characteristic **timbre**; timbre variations permit us to identify sounds of various musical instruments even though they are playing notes of same pitch.Waves like that shown in **E,** which have no regular pattern (aperiodic), are perceived as ***noise***. | D:\Viktoro\Neuroscience\Ear. Otology\00. Pictures\Sound Waves.jpg |

**Loudness** correlates with **amplitude**.

**Pitch** correlates with **frequency**.

* pitch is also determined by other factors in addition to frequency (see below).
* *frequency affects loudness* (since auditory threshold is lower at some frequencies than others) and vice versa – *loudness affects pitch* (see below).

**Amplitude** of sound wave can be expressed in terms of maximum pressure change at eardrum, but relative scale (e.g. **decibel scale**) is more convenient:

* sound intensity in **bels** is *logarithm of ratio of intensity* of that sound and standard sound.
* 1 B = 10 dB

dB = 10 log (sound intensity / standard sound intensity)

* sound intensity is proportionate to sound pressure2

dB = 20 log (sound pressure / standard sound pressure)

e.g. 60 dB is sound pressure 1000 times the threshold

20 dB is sound pressure 10 times the threshold

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| * **standard sound** (adopted by Acoustical Society of America) corresponds to 0 dB at pressure level of 0.000204 dyne/cm2 - just at ***auditory threshold*** for average human.

N.B. remember that decibel scale is log scale:**0 dB** does not mean sound absence but sound level of intensity equal to standard (i.e. 0.0002 dynes/cm2);**0÷140 dB** range (threshold pressure ÷ pressure that is damaging to Corti organ) actually represents 107-fold variation in sound pressure.**atmospheric pressure** at sea level is 1 bar, and range 0÷140 dB is 0.0002-2000 μbar. | D:\Viktoro\Neuroscience\Ear. Otology\00. Pictures\Decibel scale of common sounds.gif |

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| Sound **frequencies** audible to humans range 20­÷20,000 Hz.* ***threshold*** *of human ear varies with sound pitch* - greatest sensitivity being in 1000-5000 Hz range (**maximal at 4000 Hz** – sensitivity at this frequency corresponds to 0 dB).
* pitch of average male voice in conversation is ≈ 120 Hz and average female voice ≈ 250 Hz.
* ***pitch discrimination*** is best in 1000-3000 Hz range and is poor at high and low pitches.
* number of pitches that can be distinguished by average individual is ≈ 2000 (trained musicians can improve on this figure considerably).
 | D:\Viktoro\Neuroscience\Ear. Otology\00. Pictures\Audibility curve.jpgHuman audibility curve: **middle curve** is that obtained by audiometry under usual conditions; **lower curve** is that obtained under ideal conditions; at 140 dB (**top curve**), sounds are felt as well as heard. |

Sound **pitch** depends on:

1. **Frequency** of sound wave (primary pitch determinant)
2. **Loudness** - low tones (< 500 Hz) seem lower and high tones (> 4000 Hz) seem higher as their loudness increases.
3. **Duration**: pitch cannot be perceived unless sound lasts > 0.01 s; with durations between 0.01 and 0.1 s, pitch rises as duration increases.

Extra-axial Auditory Physiology

Auditory Vibrations



Source of picture: William F. Ganong “LANGE Review of Medical Physiology”, 21st ed. (2003); Publisher: McGraw-Hill / Appleton & Lange; ISBN-10: 0071402365; ISBN-13: 978-0071402361 [>>](http://www.amazon.com/gp/product/0071605673)

Sound Conduction

**ossicular conduction** (pathway for *normal hearing*, so clinically is called **air conduction**) - via tympanic membrane and auditory ossicles.

**air conduction** (unimportant in normal hearing) - sound waves initiate vibrations of secondary tympanic membrane that closes round window.

**bone conduction** - vibrations of skull bones (e.g. extremely loud sounds, tuning forks applied directly to skull) – directly stimulate inner ear (bypassing external-middle ear).

Traveling Waves

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| * stapes footplate movement sets up traveling wave in perilymph of scala vestibuli.
* as wave moves up cochlea, its *height increases to maximum and then drops off rapidly* (very little of wave ever reaches helicotrema!);
	+ distance from stapes to this point of maximum height varies with frequency of initiating wave.
	+ **high-pitched sounds** generate waves that reach maximum height ***near base of cochlea***; **low-pitched sounds** generate waves that peak ***near apex***.
* peaks of fluid waves in scala vestibuli depress flexible **Reissner membrane** into scala media; consequently flexible **basilar membrane** is readily depressed into scala tympani (i.e. sound produces distortion of basilar membrane, and site at which this distortion is maximal is determined by frequency of sound wave).
 | D:\Viktoro\Neuroscience\Ear. Otology\00. Pictures\Traveling waves.jpg**Top:** *solid* and *short-dashed* lines represent wave at two instants of time; *long-dashed* line shows "envelope" of wave formed by connecting wave peaks at successive instants.**Bottom:** displacement of basilar membrane by waves generated by stapes vibration at shown frequencies. |

* fluid displacements in scala tympani are dissipated into air at round window.
* tops of hair cells (in organ of Corti) are held rigid by **reticular lamina**, and hairs of outer hair cells are embedded in tectorial membrane; when stapes moves, both membranes move in same direction, but they are hinged on different axes, so there is shearing motion that bends hairs.
* hairs of inner hair cells are not attached to tectorial membrane, but they are apparently bent by fluid moving between tectorial membrane and underlying hair cells.

Functions of Inner & Outer Hair Cells

Also see [p. Ear12a >>](http://www.neurosurgeryresident.net/Ear.%20Otology%5CEar12a.%20Hair%20cell%20function.pdf)

**inner hair cells** - *primary sensory cells* that generate action potentials in auditory nerves.

**outer hair cells** - *motile*, shortening when depolarized and lengthening when hyperpolarized.

* innervated by cholinergic efferents (from superior olivary complexes).
* *improve hearing* by increasing amplitude and sharpening peaks of vibration of basement membrane (though process by which they do this is controversial).
* sounds generated by these cells can be measured (**otoacoustic emissions**) – indicator of healthy cochlea.

Action Potentials in Auditory Axons

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| * major determinant of **pitch** perceived is **place in Corti organ that is maximally stimulated** (i.e. peak depression of basilar membrane);

*at low sound intensities*, each axon discharges to sounds of only one frequency (this frequency varies from axon to axon depending upon part of cochlea from which fiber originates).*at higher sound intensities*, individual axons discharge to wider spectrum of frequencies (particularly to frequencies lower than that at which threshold simulation occurs), because of wider basilar membrane vibrations.* sound **loudness** is encoded by **spike rate (frequency of action potentials)** in single auditory nerve fiber; also as *sound intensity increases* more axons (“neighbors” of given frequency) are activated.
 | D:\Viktoro\Neuroscience\Ear. Otology\00. Pictures\Spike rate in auditory nerve.gifRelation of *spike rate* in individual auditory axon to sound *frequency* and *intensity*. |

Auditory pathways retain **tonotopic organization** – orderly neuron arrangement by frequency sensitivity (analogous to retinotopic, somatotopic organizations); especially prominent in cochlear nuclei but becomes less precise in more rostral structures.

Auditory pathways are **bilaterally represented & redundant** – CNS lesions very rarely cause deafness (vs. vestibular pathways – highly lateralized system).

Intra-axial Auditory Physiology

Central Auditory Pathways → see [p. Ear23a >>](http://www.neurosurgeryresident.net/Ear.%20Otology%5CEar23a.%20Central%20Auditory%20Pathways.jpg)

Cochlear Nuclei

* response of individual second-order neurons in cochlear nuclei are like those of individual primary auditory nerve fibers.
* major difference is presence of sharper "cutoff" on low-frequency side in medullary neurons (i.e. greater specificity of second-order neuron to sound frequency).

Primary Auditory Cortex

* ***low tones*** are represented anterolaterally and ***high tones*** posteromedially in auditory cortex.
* it is **pitch** and not **frequency per se** that is coded in auditory cortex (i.e. processing of pure frequencies into pitch occurs at subcortical level).

Other Cortical Areas

* auditory pathways in cortex *resemble visual pathways* in that there is ***increasingly complex processing*** of auditory information along them.
* organized in two general paths (like visual pathways):
	1. **Dorsal-parietal pathway** concerned with **sound localization** ("where" pathway).
	2. **Ventral-temporal pathway** – **sound identification** ("what" pathway), including areas where neurons respond selectively to voices (analogous to face-selective areas in visual system).
* ***cortical lesions*** may not impair simple frequency discrimination, but impair complex sound features detection (incl. localization in space).

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| * auditory system is *modified by experience* and other factors; examples:
* individuals who become ***deaf*** before language skills are fully developed, viewing sign language activates auditory association areas outside primary auditory cortex.
* individuals who become ***blind*** early in life are demonstrably better at localizing sound than individuals with normal eyesight.
* ***babies*** rapidly develop enhanced neuronal responses to sounds unique to their native language after 6 months of age, whereas responses to sounds that are not unique gradually disappear.
* ***musicians*** have increased auditory areas activated by musical tones (in addition, violinists have altered somatosensory representation of finger areas; musicians also have larger cerebellums because of learned precise finger movements).
* **planum temporale** (portion of posterior superior temporal gyrus) is *regularly larger in left* than in right cerebral hemisphere, particularly in right-handed individuals - involved in language-related auditory processing; asymmetry is even greater, in musicians and others who have perfect pitch.
 | D:\Viktoro\Neuroscience\Ear. Otology\00. Pictures\Planum Temporale.jpgLeft and right planum temporale in brain sectioned horizontally along plane of sylvian fissure (shown in insert at bottom). |

Masking

- presence of one sound decreases individual's ability to hear other sounds - due to ***refractoriness*** (relative or absolute) of previously stimulated auditory receptors and nerve fibers.

* related to sound pitch.
* masking of background noise *raises auditory threshold* (i.e. because of background noise we hear other sounds less well).

Bibliography for ch. “Otology” → follow this [link >>](http://www.neurosurgeryresident.net/Ear.%20Otology%5CEar.%20Bibliography.pdf)

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