

Figura 22.1 Il decorso della pressione sonora di un tono, di un suono e di un rumore. Il tono e il suono presentano un

periodo, mentre i rumori ne sono sprovvisti. Il suono presenta, oltre all'onda principale, anche i cosiddetti armonici.

The Nature of Sound

Sound pressure easier to measure

dB SPL =

$$20\log_{10}P(\text{measured})/P(\text{reference})$$

$$P(\text{ref}) = 2 \times 10^{-5} \text{ Pascals}$$

For Intensity

$$\text{dB} = 10\log_{10}I(\text{measured})/I(\text{ref} - 10^{-12} \text{W/m}^2)$$

So 3dB increase in intensity is doubling of sound energy.

The Nature of Sound

- Previous parameters describe pure-tones
- Real sound is mixture of pure tones
- Breakdown into component pure tones requires Fourier Analysis
- Performed by cochlea!

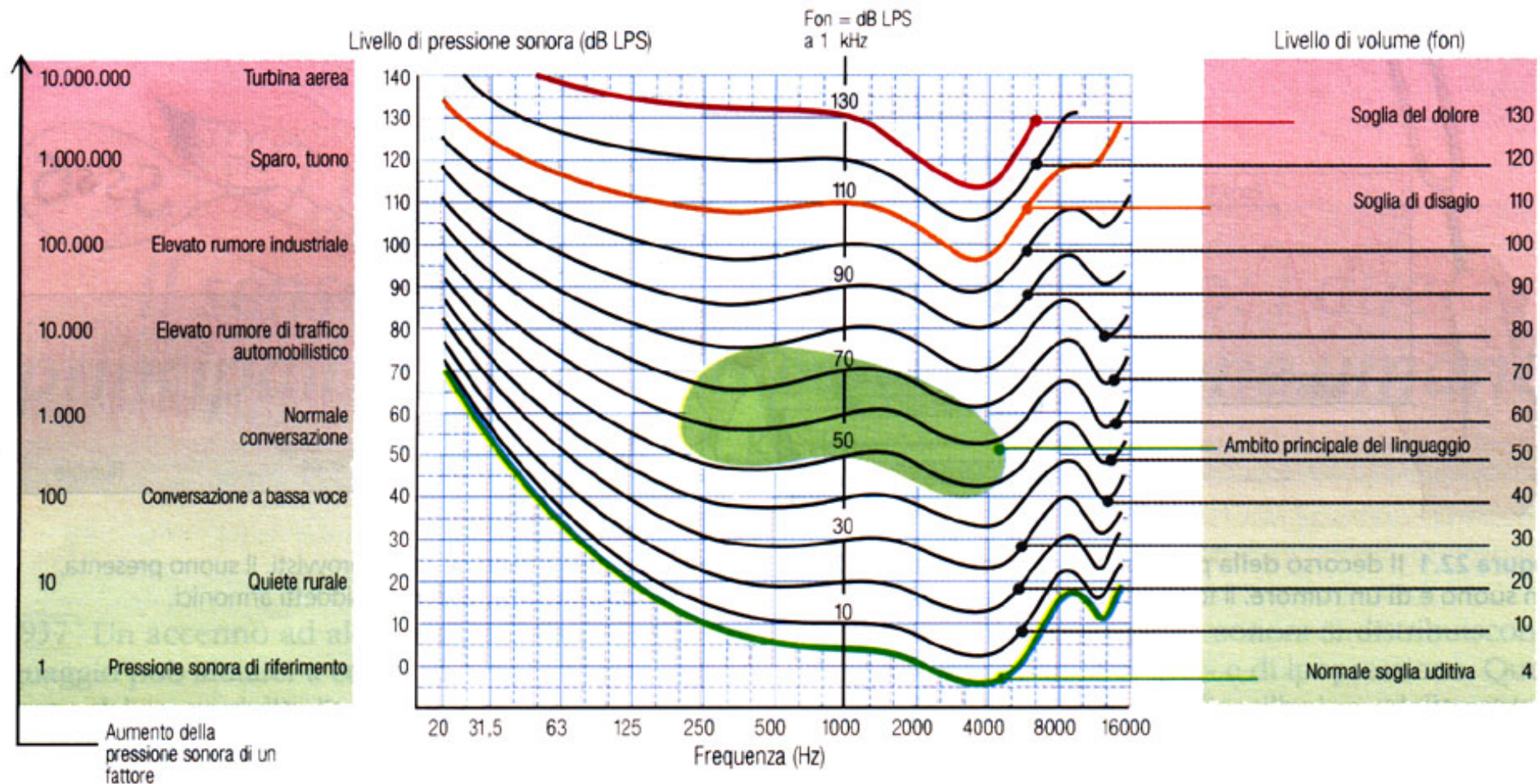
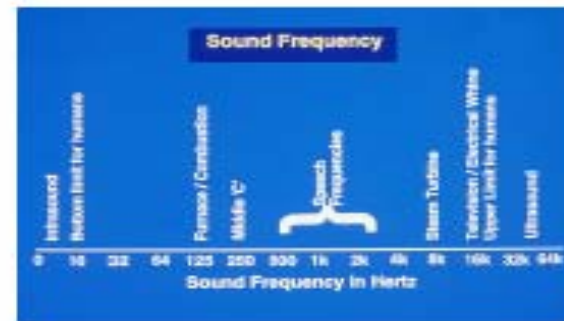


Figura 22.2 L'ambito uditivo dell'orecchio umano (secondo DIN). Oltre alla soglia uditiva sono riportate altre curve che presentano un medesimo livello di volume (isofone). A 1000 Hz i

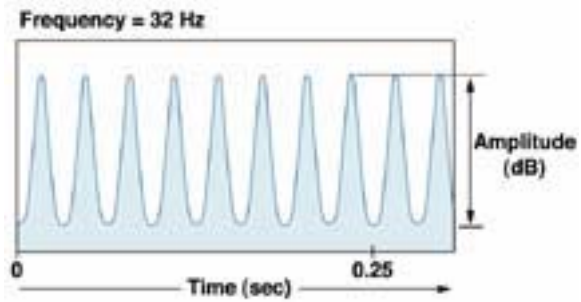
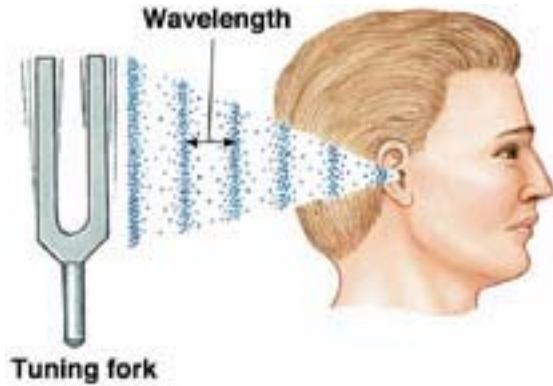
valori numerici dei livelli di volume risultano per definizione identici a quelli del livello di pressione sonora.

Hearing - Measurement

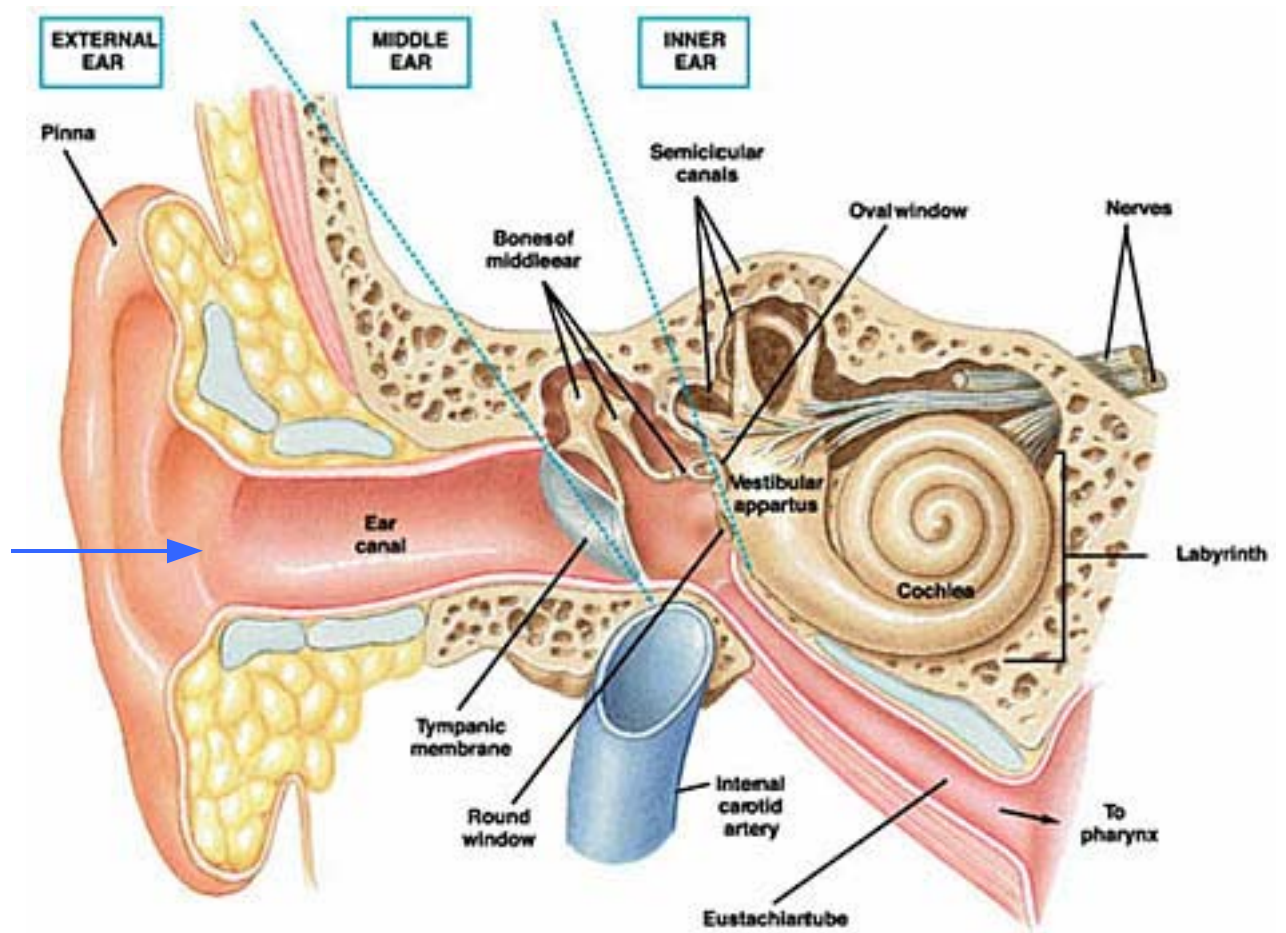
- Ear – Not equally sensitive to all frequencies (doubling=octave)
- Maximal sensitivity in “speech frequencies” – 500-4000Hz.
- Correction Factors – dB(SPL), dB(A), dB(HL) (10dB increase in sound level is perceived as doubling of volume)



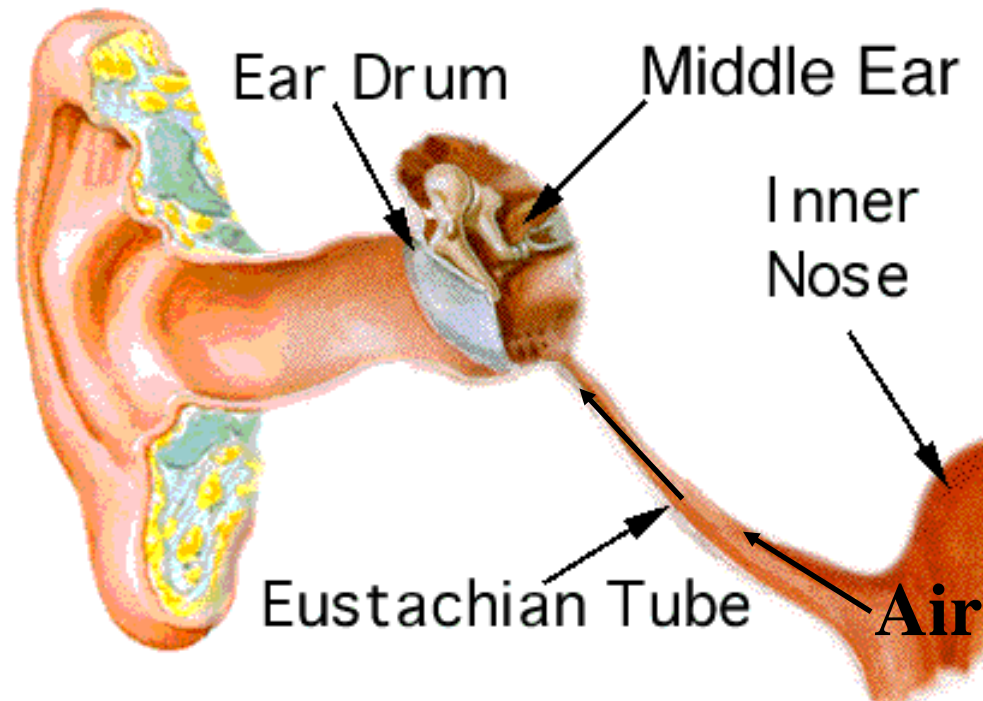
Anatomy of the Ear



Sounds waves in air



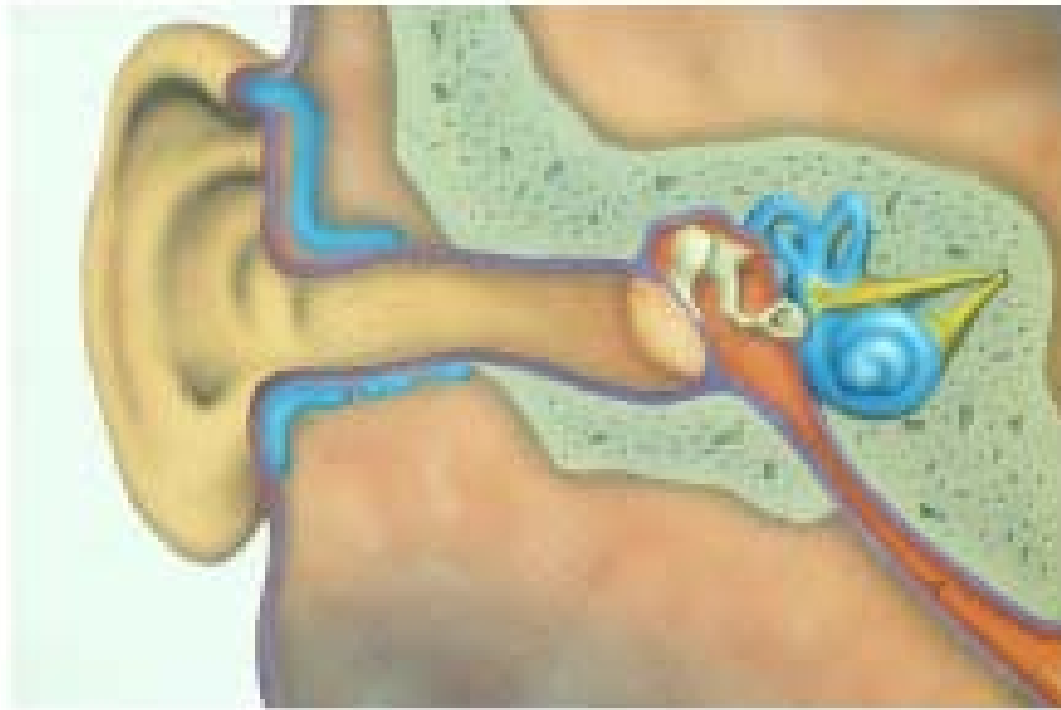
Eustachian tube



- Middle ear is sealed air filled cavity
- Ear drum compliance
- Gives ability to gather sound
- Selective valve that permits air to enter middle ear
- Connects back of nose to middle ear
- Equalises pressure outside and inside ear
- Permits normal hearing
- When pressure imbalance hearing decreases – reduced compliance
- Equalising pressure causes ‘pop’

Anatomically divided into 3 parts

- External: lateral to tympanic membrane
- Middle
- Inner: cochlea, utricle, saccule and semicircular



External Ear

- Lateral to tympanic membrane
- "Funnel"
- Convolutions – sound direction
- Intrinsic resonance – 3000Hz

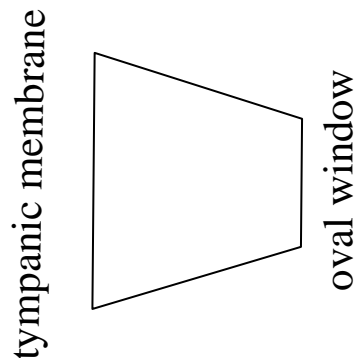


Middle Ear

- Air-filled space including eustachian tube and mastoid air-cells
- Ossicles (3) and muscles (2)
- Transformer mechanism (air/fluid interface)
 - Low intensity and high amplitude >>>
 - High Intensity but low amplitude

Amplification mechanisms: intensity.

1)



2) Bones of middle ear

Attenuation mechanisms

Tensor tympani and stapedium muscles are activated by V and VII motor nuclei to attenuate low frequency intensities.

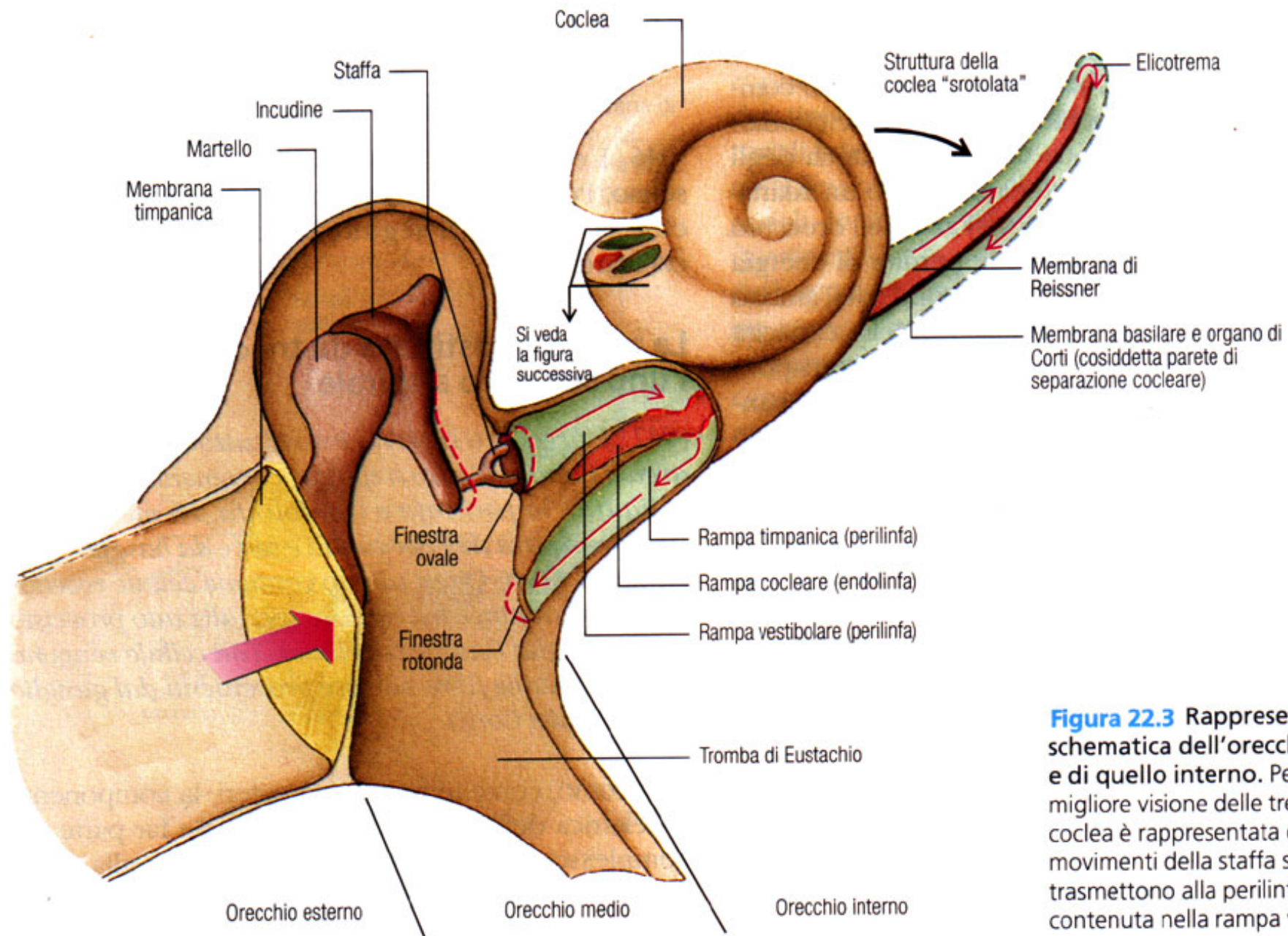


Figura 22.3 Rappresentazione schematica dell'orecchio medio e di quello interno. Per una migliore visione delle tre rampe la coclea è rappresentata distesa. I movimenti della staffa si trasmettono alla perilinfa contenuta nella rampa vestibolare.

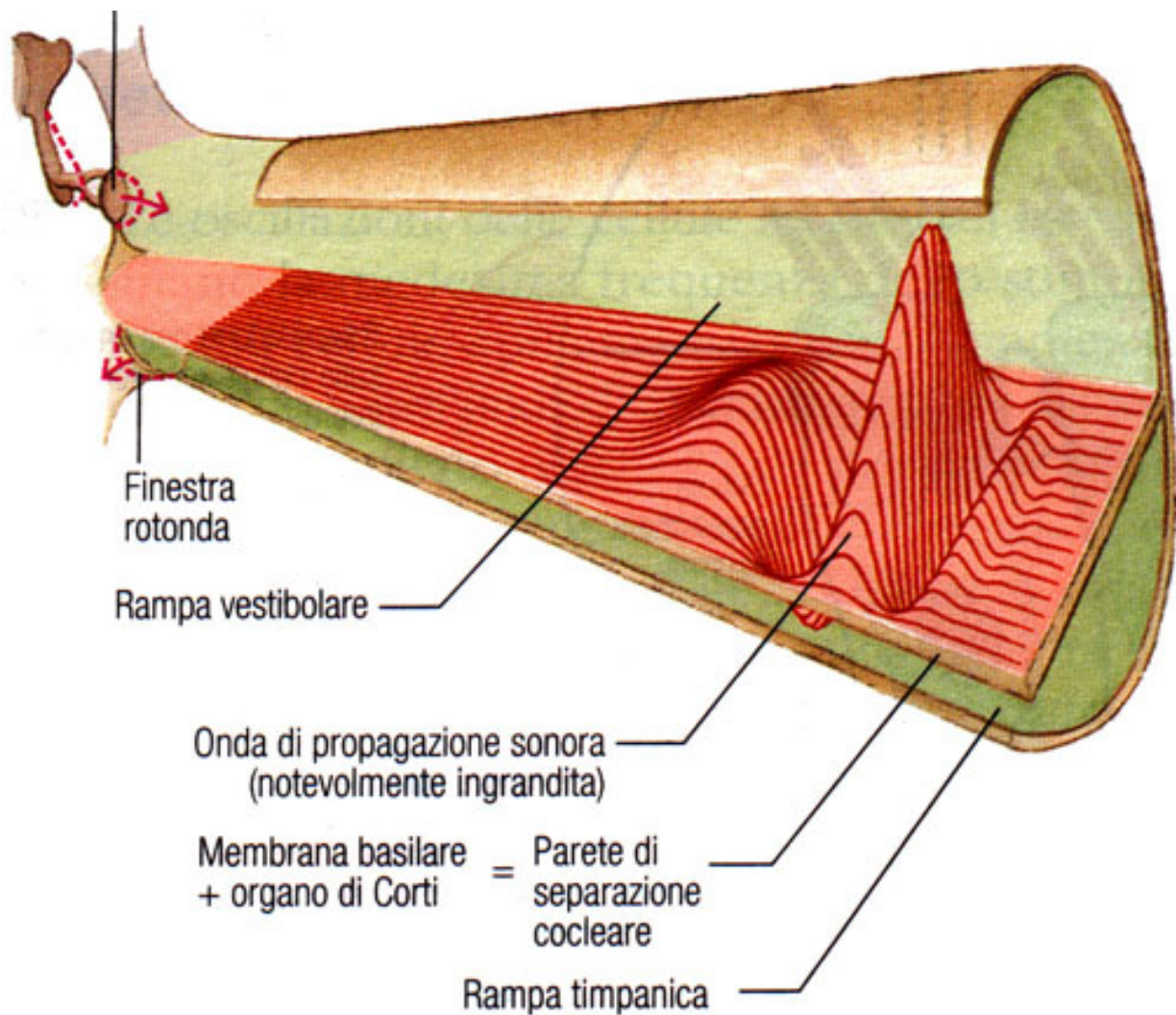
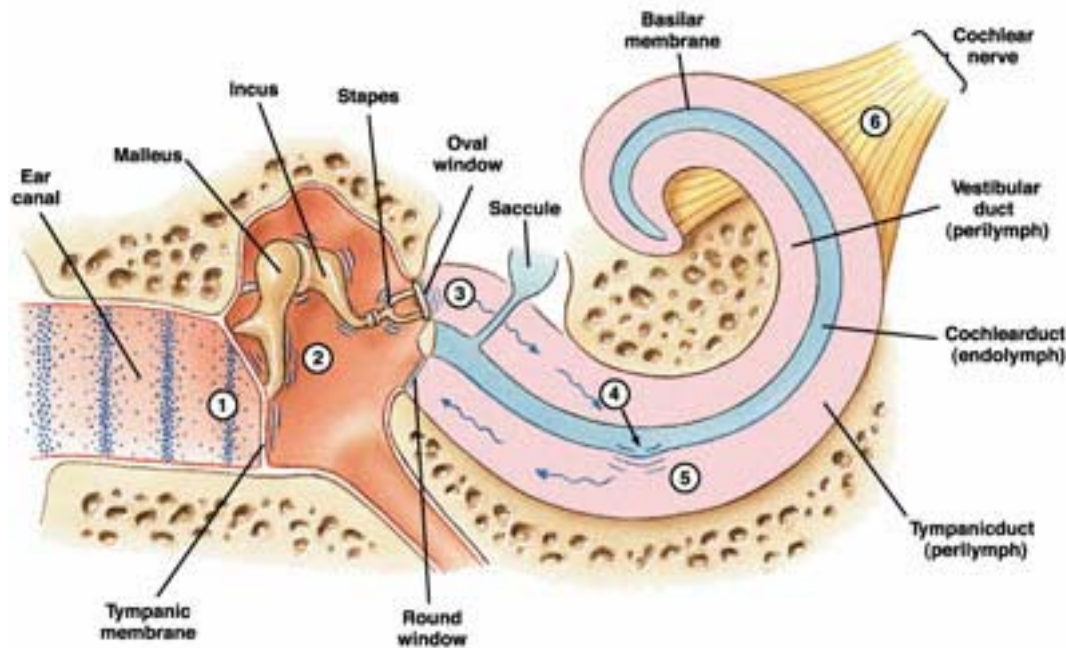


Figura 22.7 Un'onda di propagazione sonora che attraversa la coclea. A partire dalla staffa, l'onda si trasmette lungo la membrana basilare, quella tettoria e quella di Reissner in direzione dell'apice (elicotrema) della coclea. A scopo illustrativo l'ampiezza dell'onda rappresentata in figura è notevolmente ingrandita.

Sound Transmission

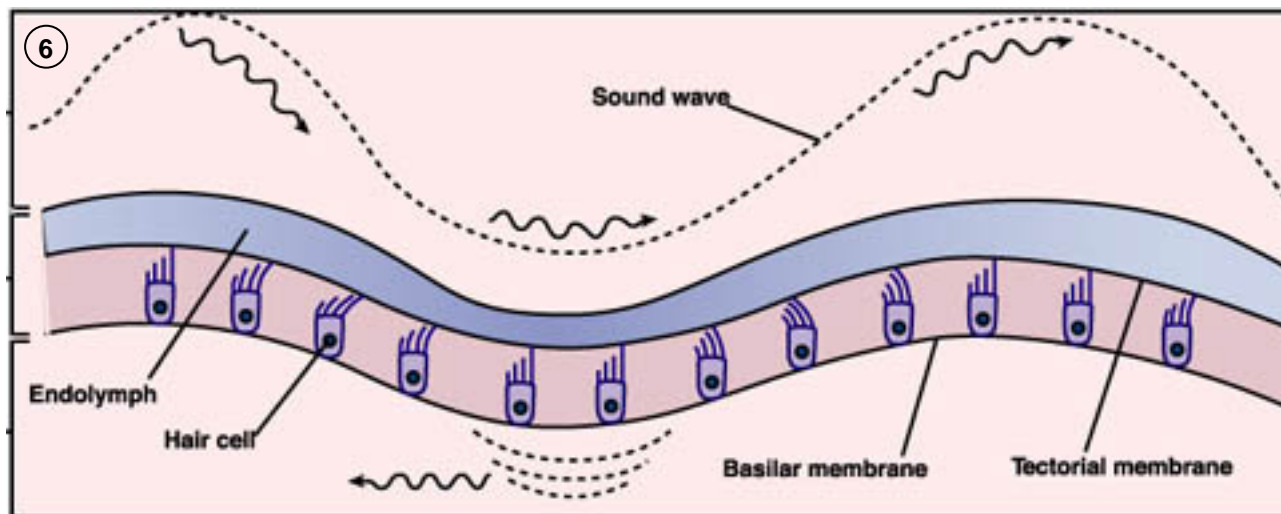


1. Sound waves in the air strike the tympanic membrane
2. Sound wave energy is transferred to bone of the middle ear which vibrate
3. The vibrations are transmitted via the oval window to the fluid within the vestibular duct and create a fluid wave within the cochlea
4. The fluid waves push on the flexible membrane of the cochlear duct
5. Sound waves are transmitted to the tympanic duct and dissipated back into air by the movement of the round window.
6. Deformation of the cochlear duct causes the tectorial membrane to move and activate the stereocilia of the hair cells.

Vestibular duct

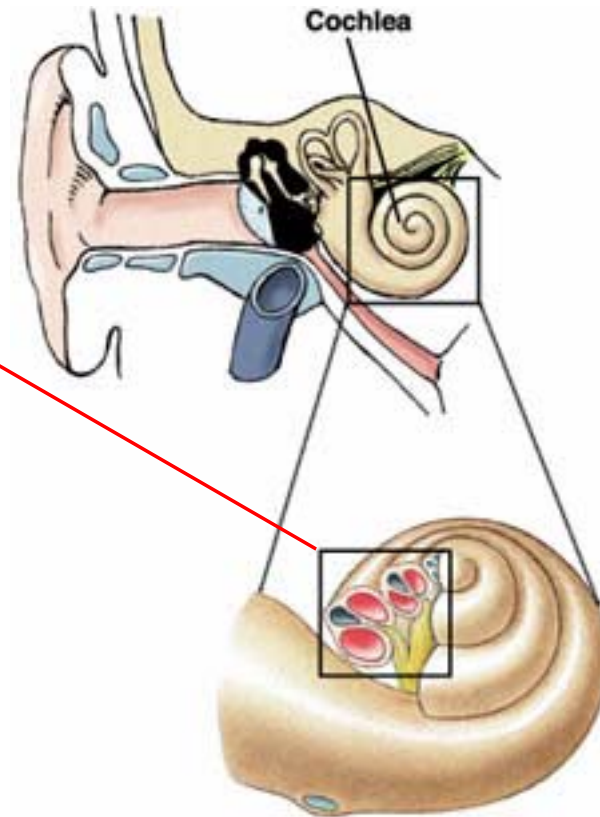
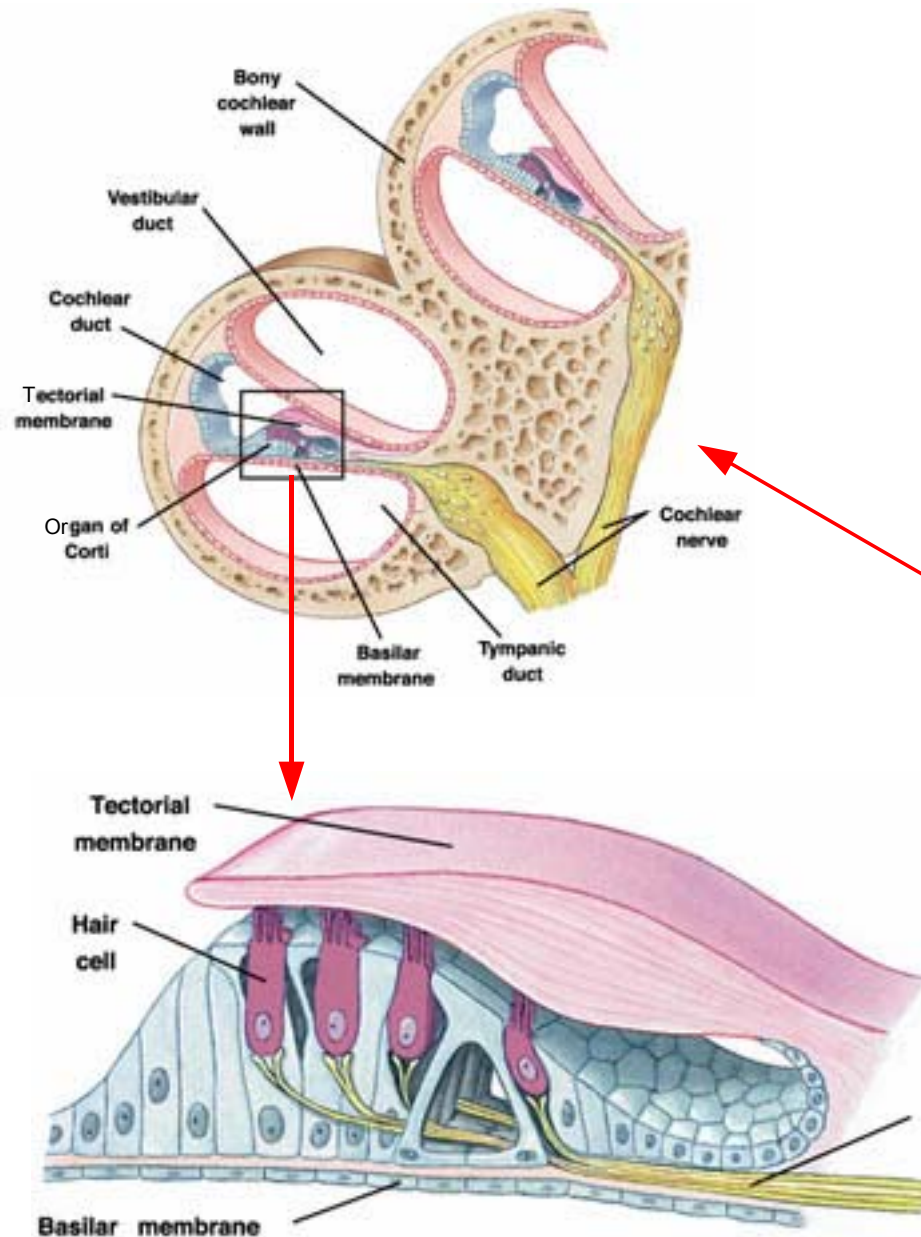
Cochlear duct

Tympanic duct



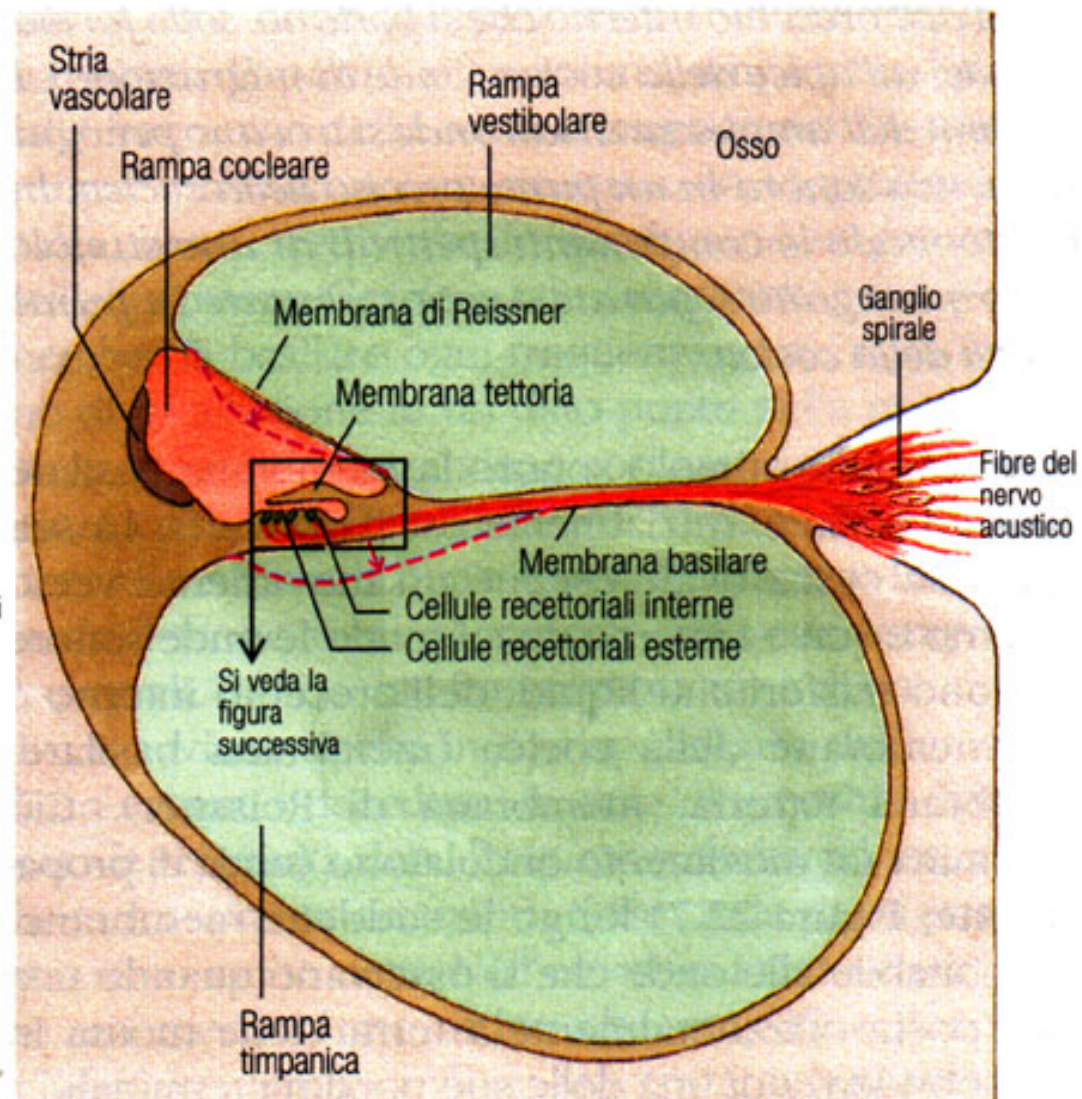
The Cochlea

The cochlea is the organ where sound waves are converted first into fluid waves, then into chemical signals and finally into action potentials



The movement of the tectorial membrane by sound waves moves the cilia on the hair cells and effects neurotransmitter release by the hair cells

Figura 22.4 Sezione trasversale della coclea. Le linee tratteggiate indicano le possibilità ondulatorie della membrana di Reissner e di quella basilare in caso di stimolazione sonora. La rampa vestibolare e quella timpanica contengono la perilinfa (in verde), mentre la rampa cocleare contiene l'endolinfa (in rosso).



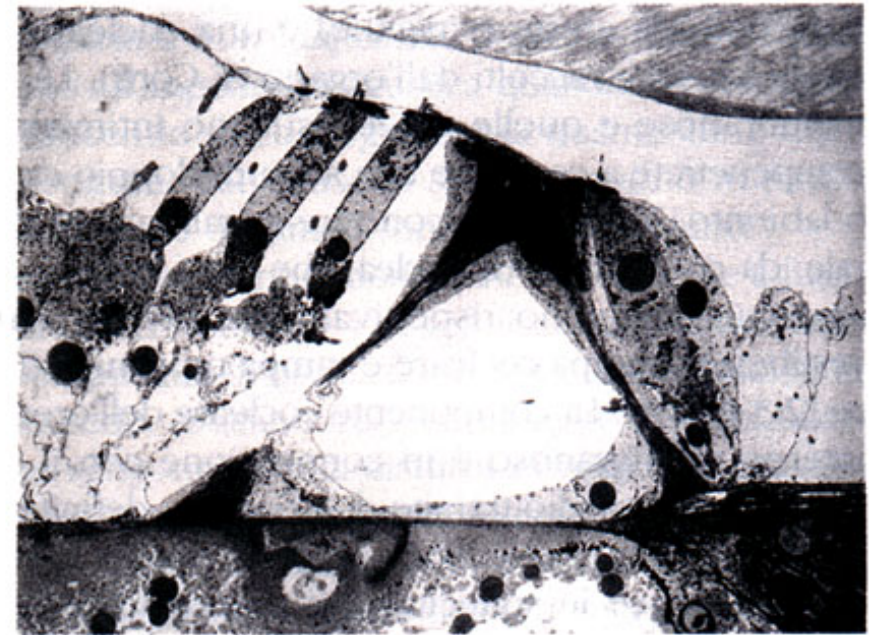
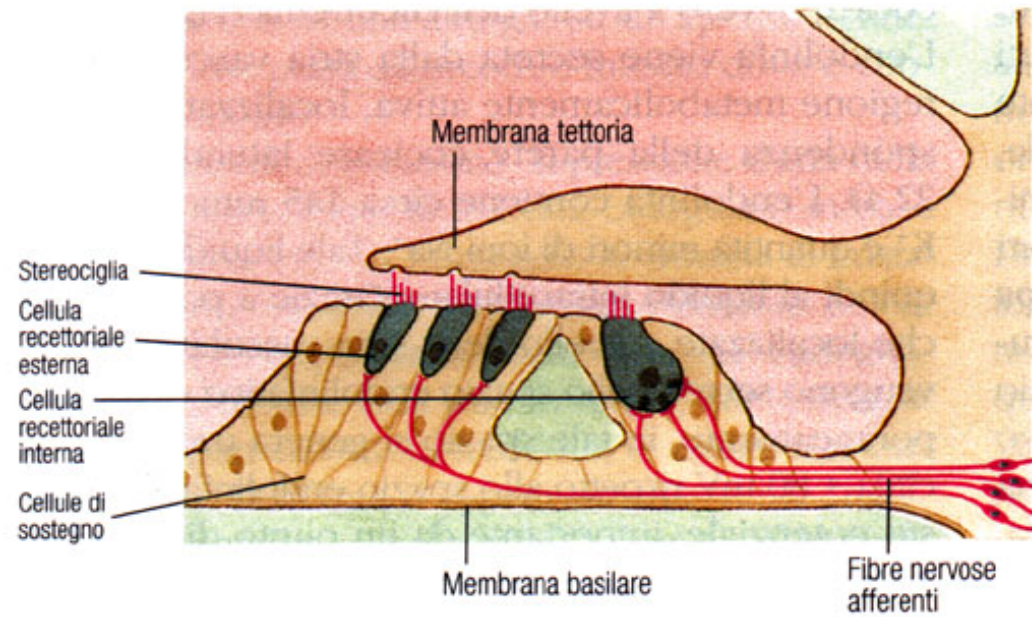


Figura 22.5 Sezione trasversale dell'organo di Corti, a sinistra. A destra si osserva l'organo di Corti come appare in

un'immagine al microscopio elettronico a trasmissione (H. Spöndlin, Innsbruck).

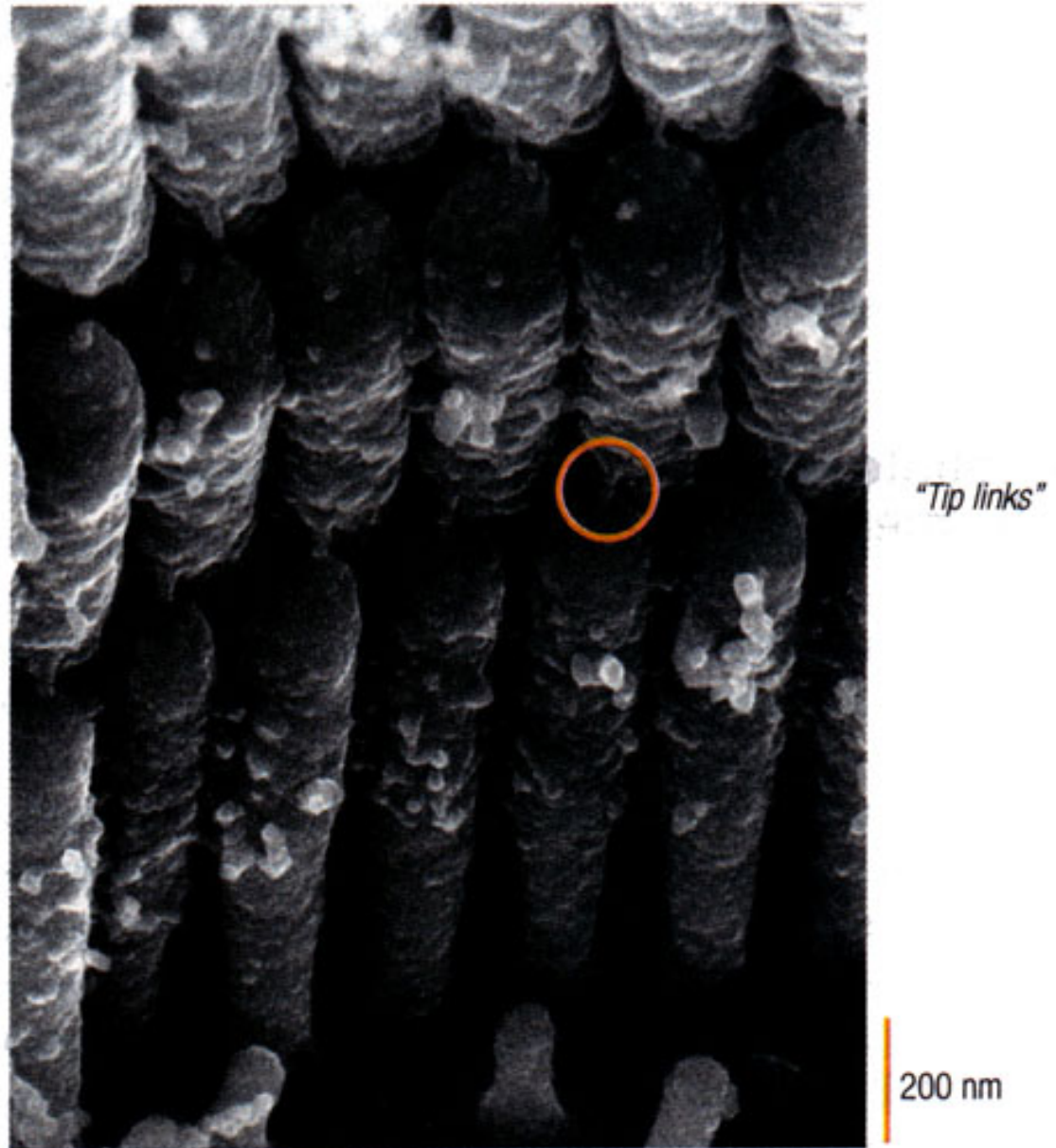


Figura 22.6 Stereociglia e "*tip links*" di una cellula recettoriale esterna. Immagine al microscopio elettronico a scansione di D. Furness e C. Hackney, Keele.

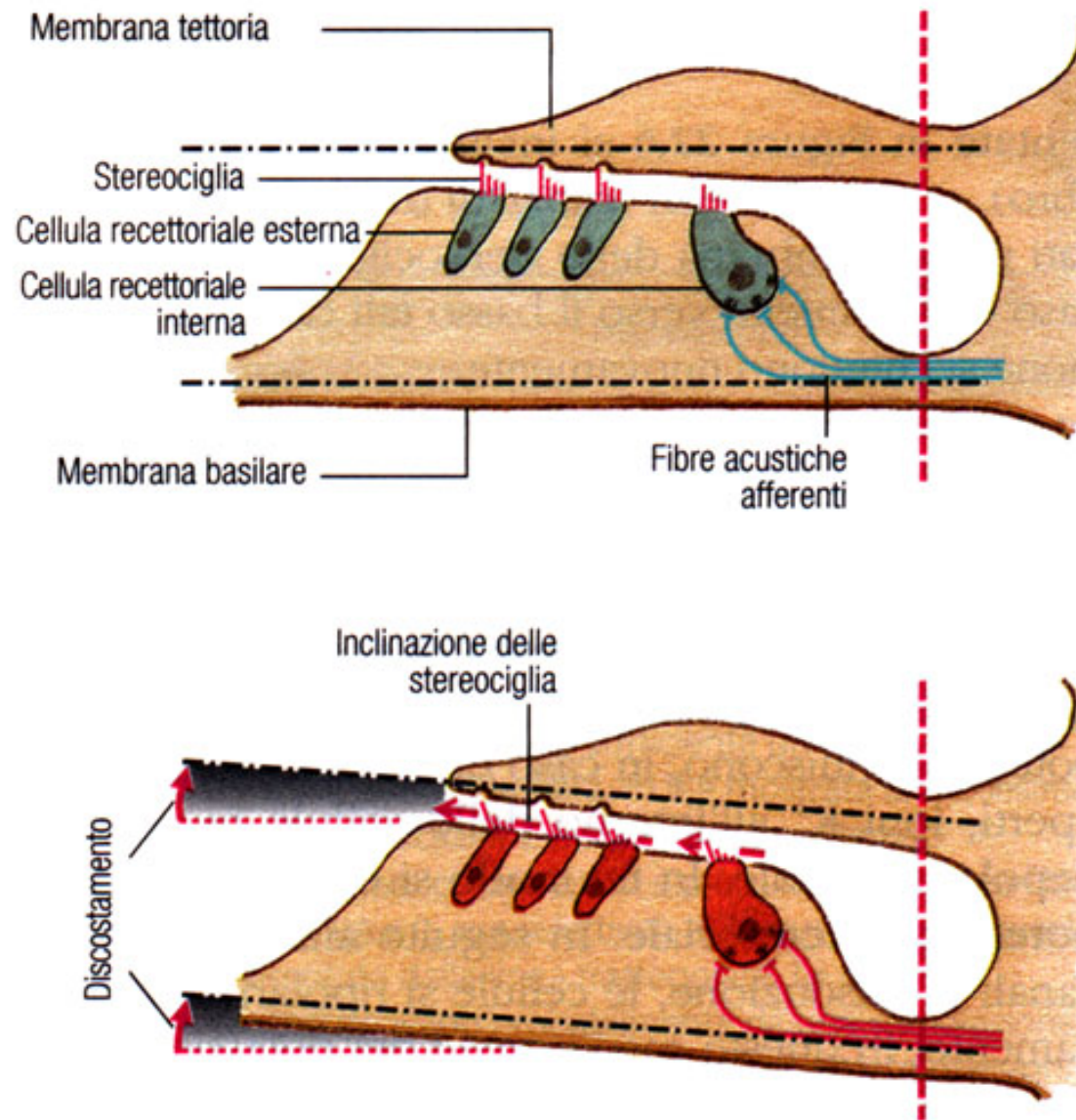
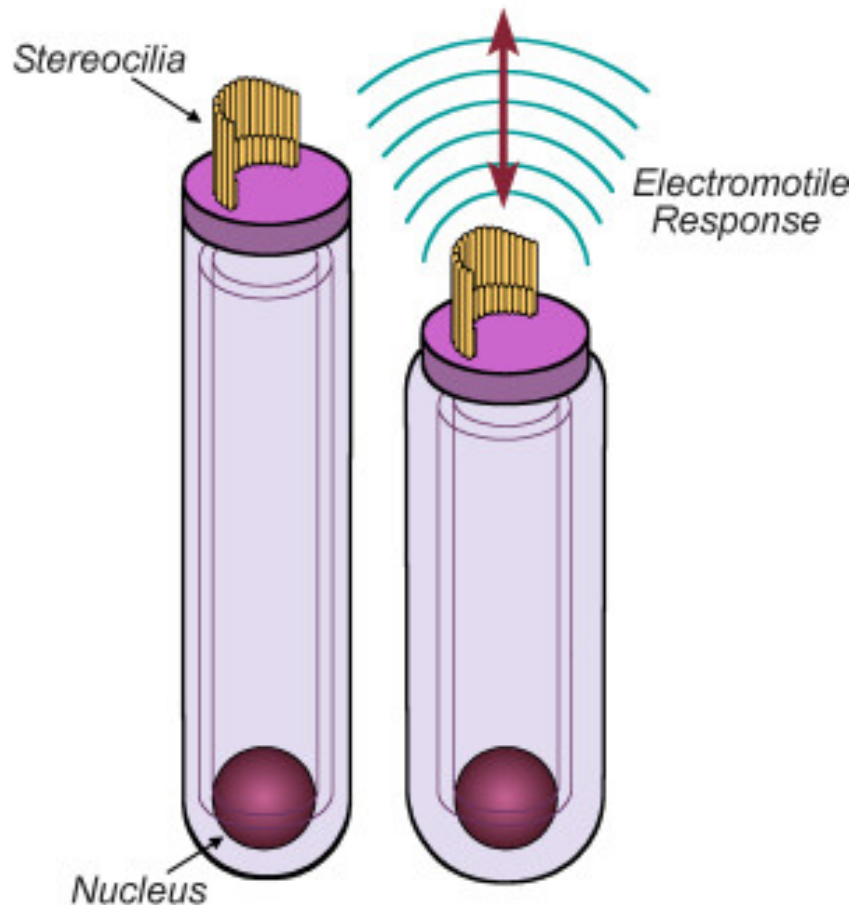


Figura 22.8 I movimenti delle stereociglia apicali in caso di movimenti ondulatori verso l'alto e verso il basso della membrana basilare e di quella tectoria.

Outer hair cells



The Outer Hair Cell

- Cylindrical shaped
- Have stereocilia at top
- Nucleus at the bottom
- When stereocilia are bent by sound waves an electromotive force occurs
- Cell changes shape – lengthens then shortens
- Pushes against the tectorial membrane
- Amplifies vibrations in the basilar membrane allowing us to hear very quiet sounds

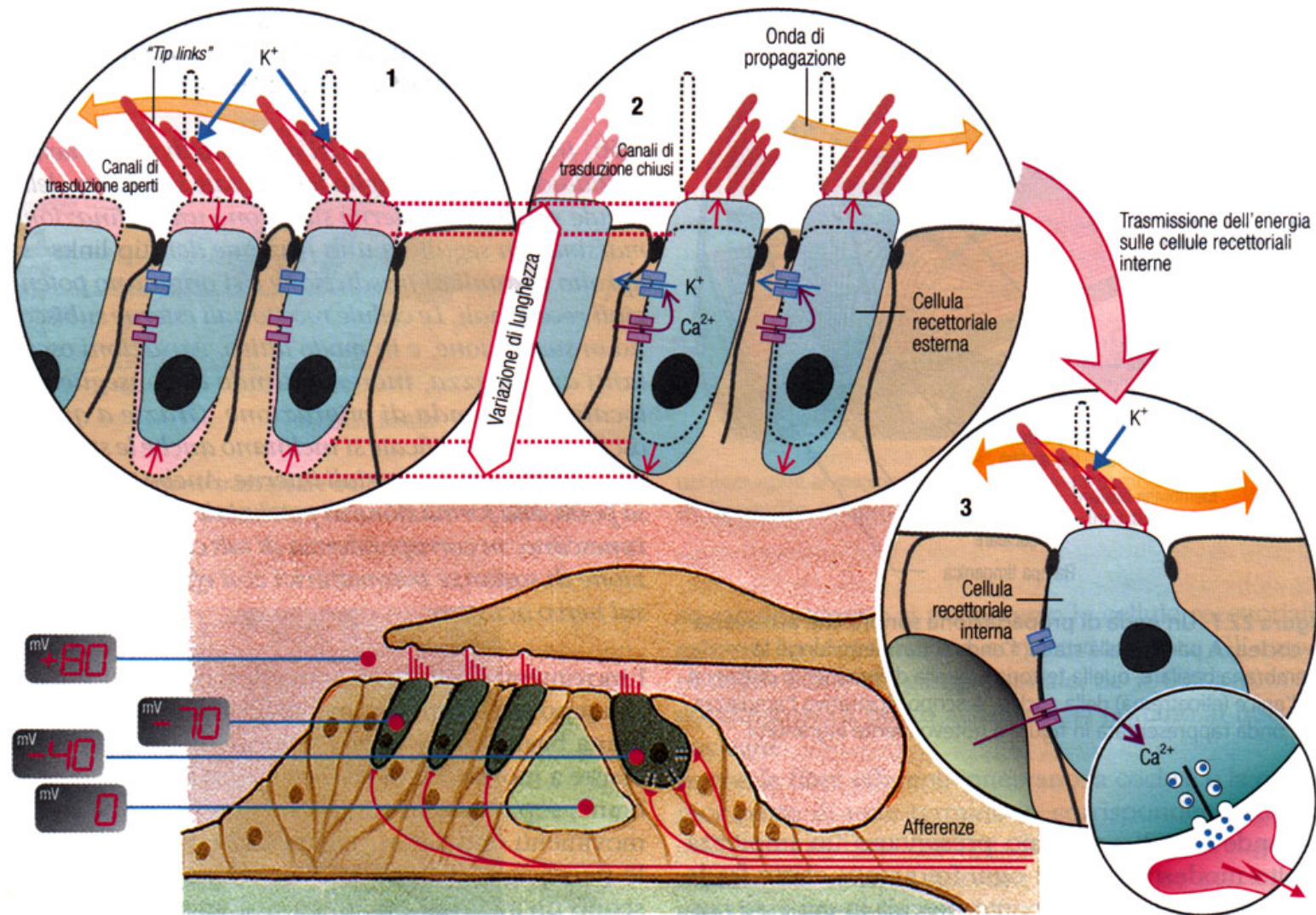
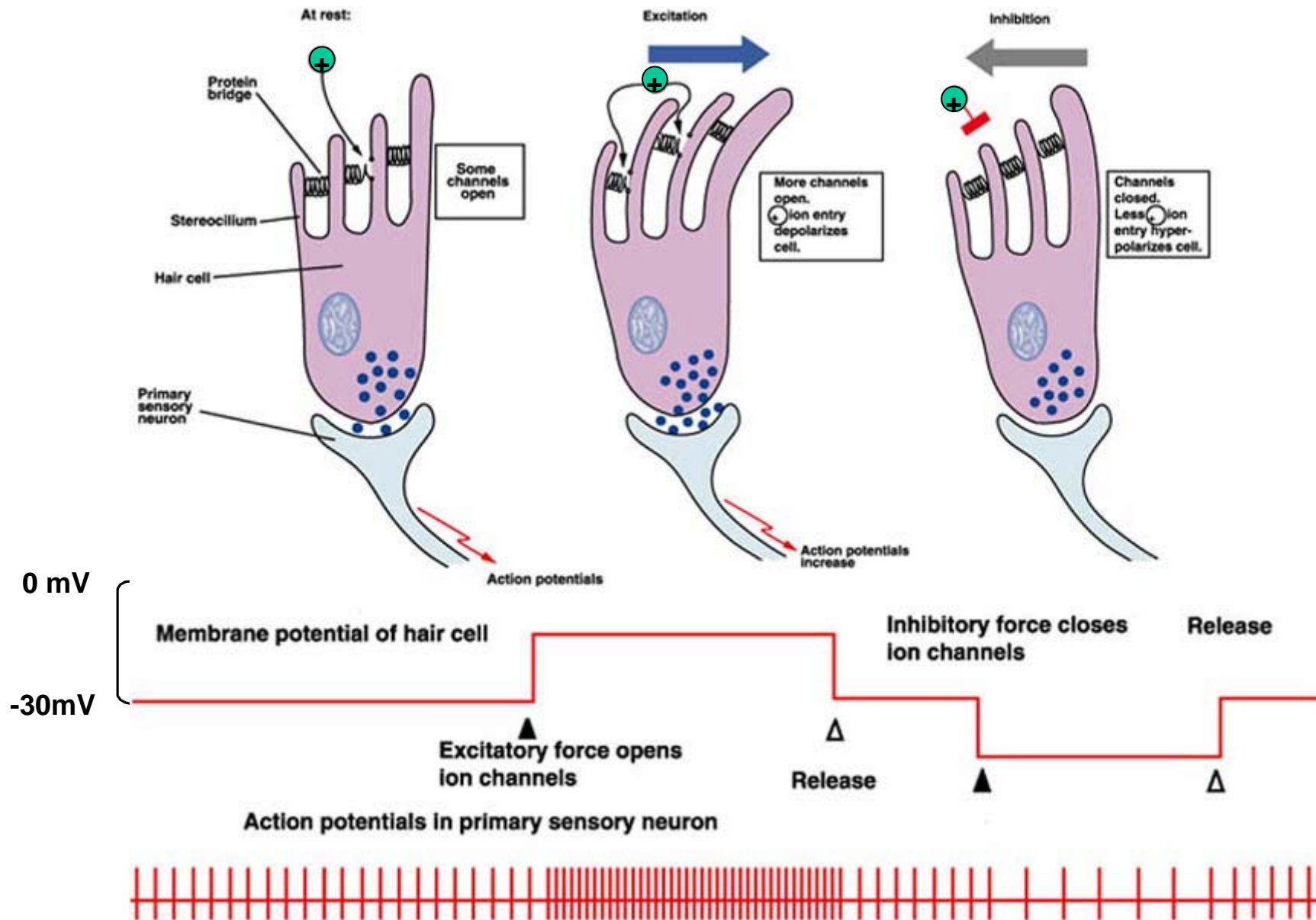


Figura 22.9 Schema complessivo del meccanismo di trasduzione. L'onda di propagazione sonora porta inizialmente alla stimolazione delle cellule recettoriali esterne. In seguito all'inclinazione delle stereociglia localizzate sull'apice di tali cellule, i "tip links" si tendono, causando l'apertura dei canali di trasduzione (1). Ioni K^+ fluiscono dallo spazio endolinfatico all'interno delle cellule recettoriali esterne lungo il gradiente del potenziale, depolarizzandole. L'inclinazione delle stereociglia in

direzione opposta richiama i "tip links" e i canali di trasduzione si chiudono, ripolarizzando le cellule recettoriali (2). A causa delle periodiche variazioni del potenziale di membrana, le cellule recettoriali esterne iniziano a oscillare, generando energia meccanica, che amplifica localmente l'onda di migrazione. Tale energia di oscillazione si trasmette alle cellule recettoriali interne (3) che vengono a loro volta stimulate.

Transduction in the Hair Cells



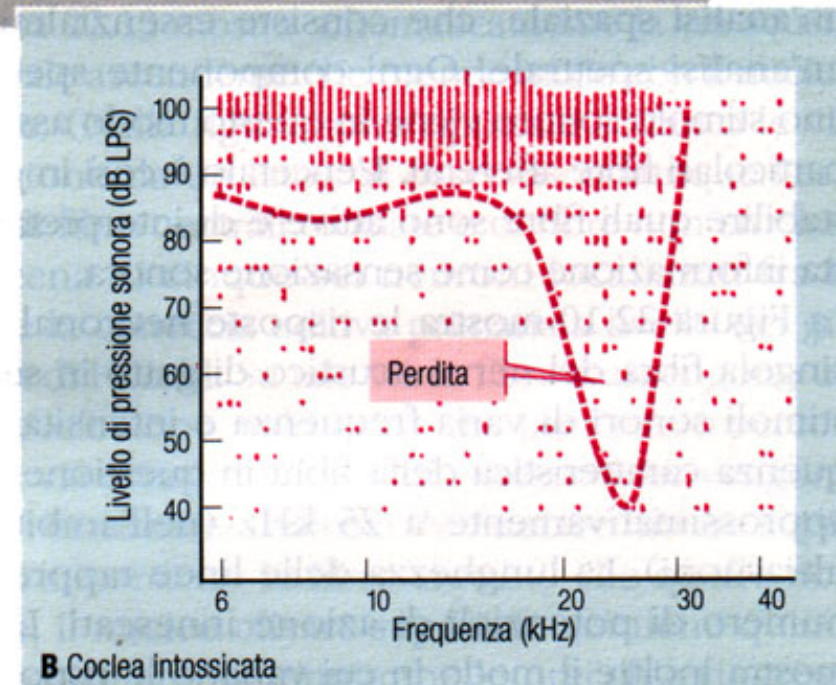
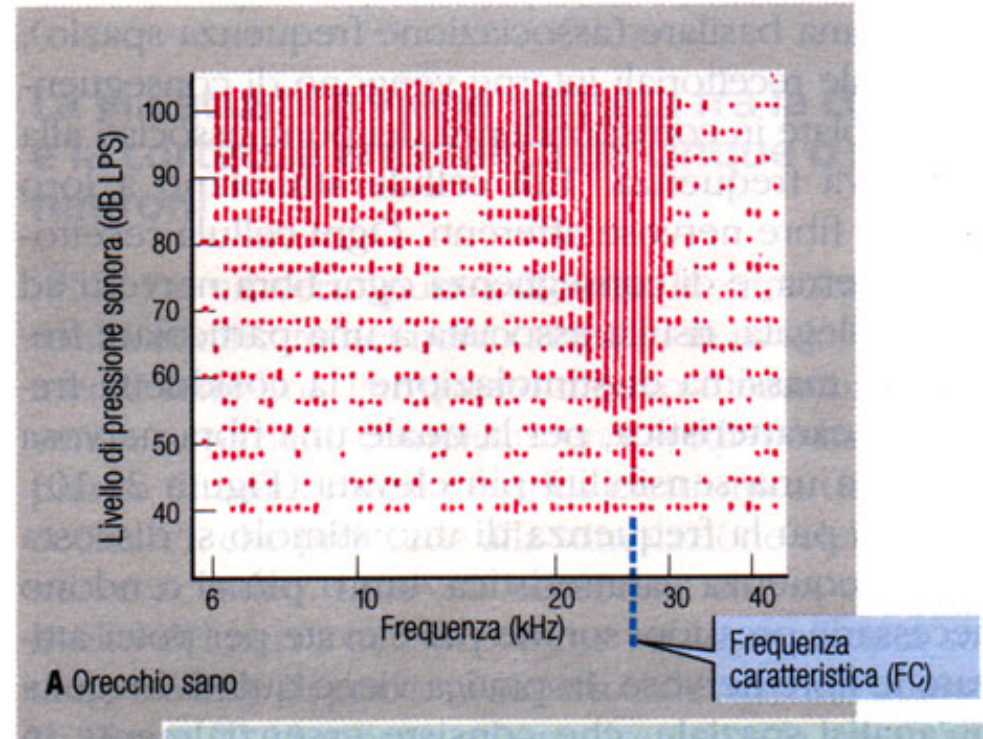


Figura 22.10 Le risposte neuronali di una fibra del nervo acustico. Un orecchio sano (A) di gatto viene stimolato con di varia frequenza e intensità. La lunghezza delle linee esprime il numero di potenziali di azione originatisi per ogni stimolo. Nell'ambito inferiore di intensità non si ha risposta al tono e la registrazione mostra soltanto un'attività spontanea. Alla frequenza caratteristica (FC) risulta sufficiente un basso livello di pressione sonora per attivare la fibra. In B è mostrata la stessa fibra in seguito all'intossicazione della coclea con farmaci ototossici. L'amplificatore cocleare non è più funzionante e perde la sua sensibilità e la sua selettività di frequenza. In B la perdita è rappresentata dalla linea tratteggiata. Le risposte neuronali rimanenti derivano probabilmente da una stimolazione diretta delle cellule recettoriali interne in caso di elevate pressioni sonore (secondo [18]).

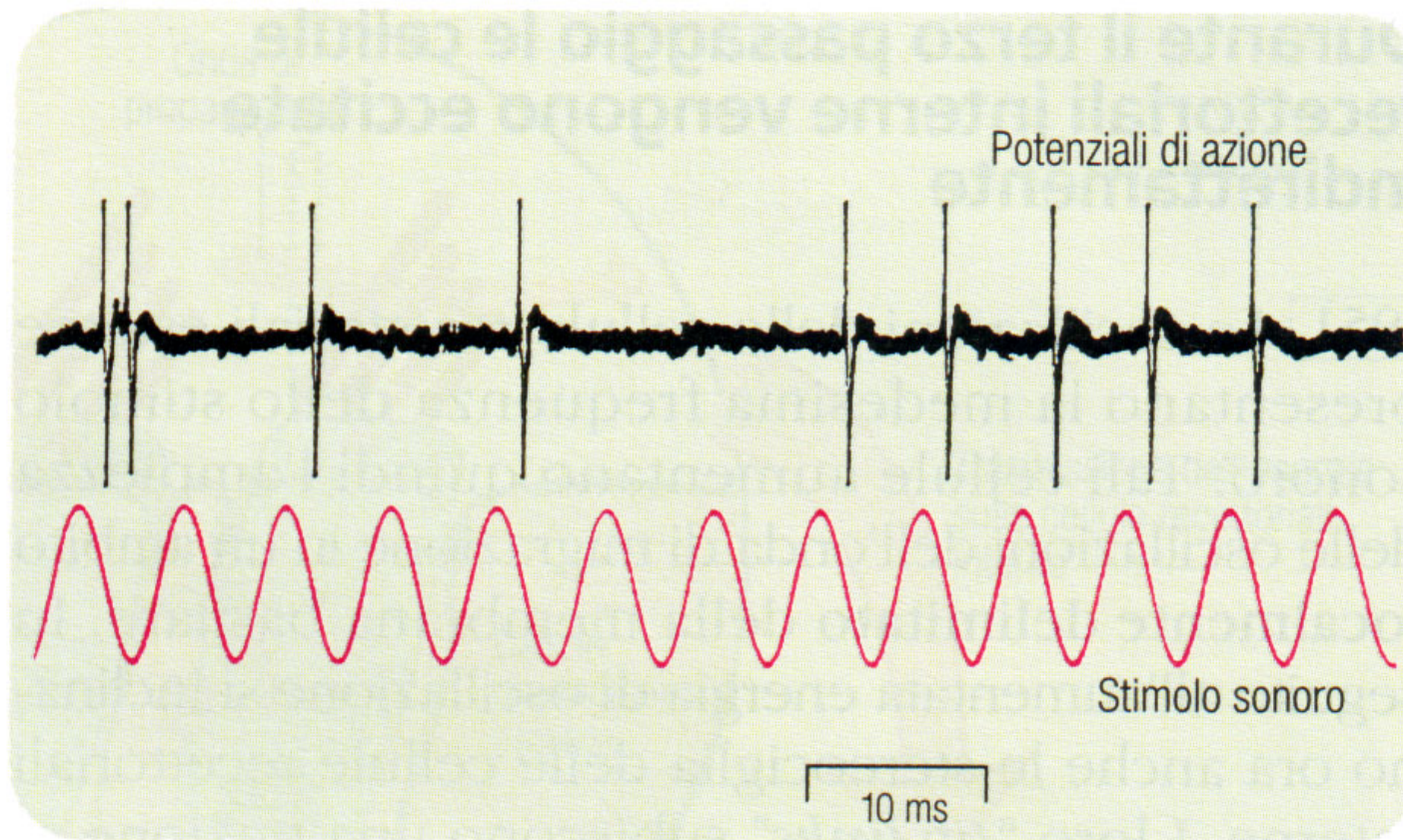


Figura 22.11 Scariche accoppiate alla fase in una fibra nervosa del nervo acustico. I potenziali di azione si originano sempre in determinate fasi dello stimolo sonoro oppure mancano del tutto. In caso di elevata intensità sonora si possono generare a volte anche più potenziali di azione (a sinistra). La distanza temporale fra i singoli potenziali di azione ammonta in genere a un multiplo del periodo del suono.

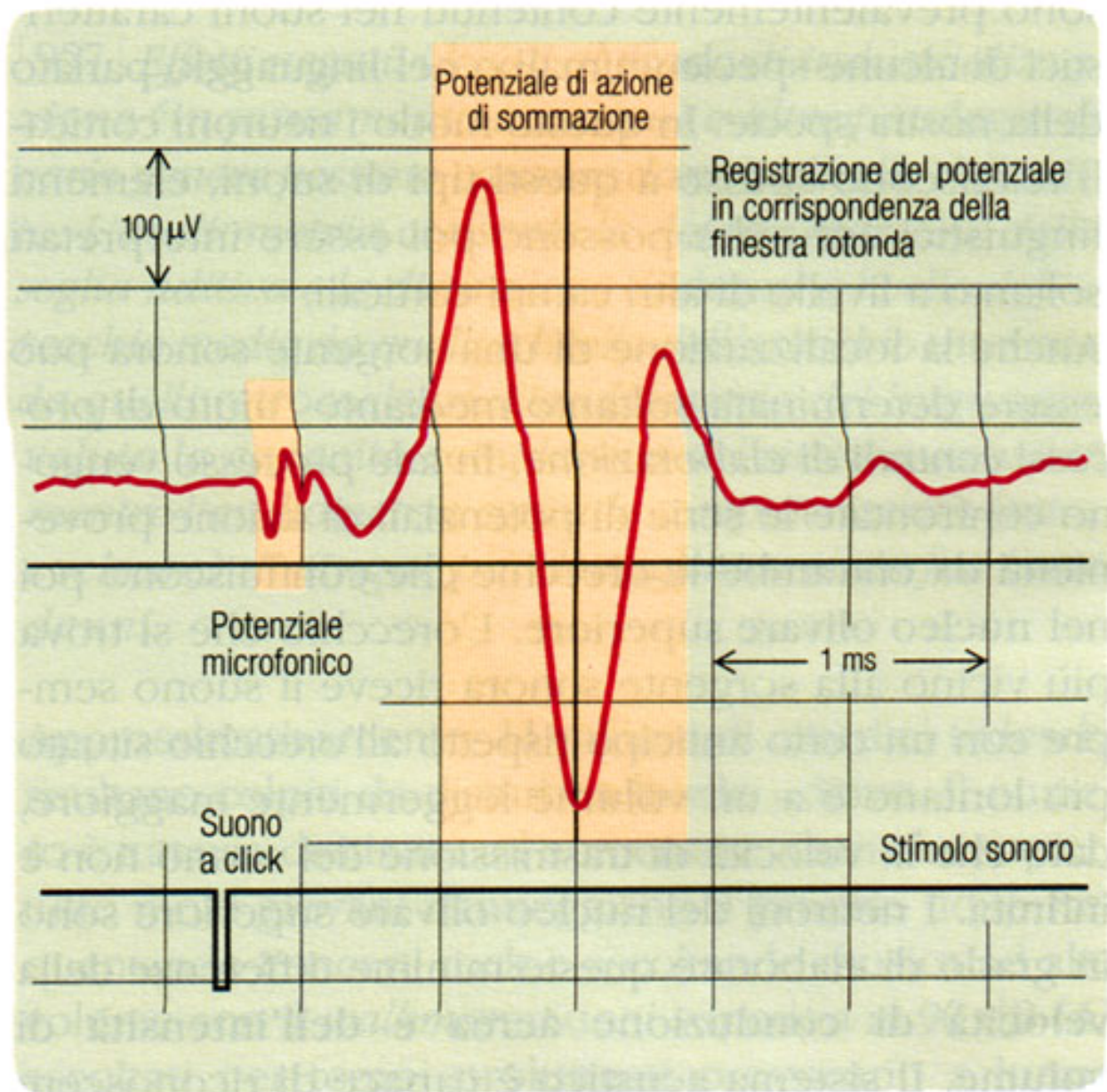


Figura 22.12 Potenziale microfonico e potenziale di azione di sommazione in seguito a stimolazione con un suono a clic, registrato in corrispondenza della finestra rotonda.

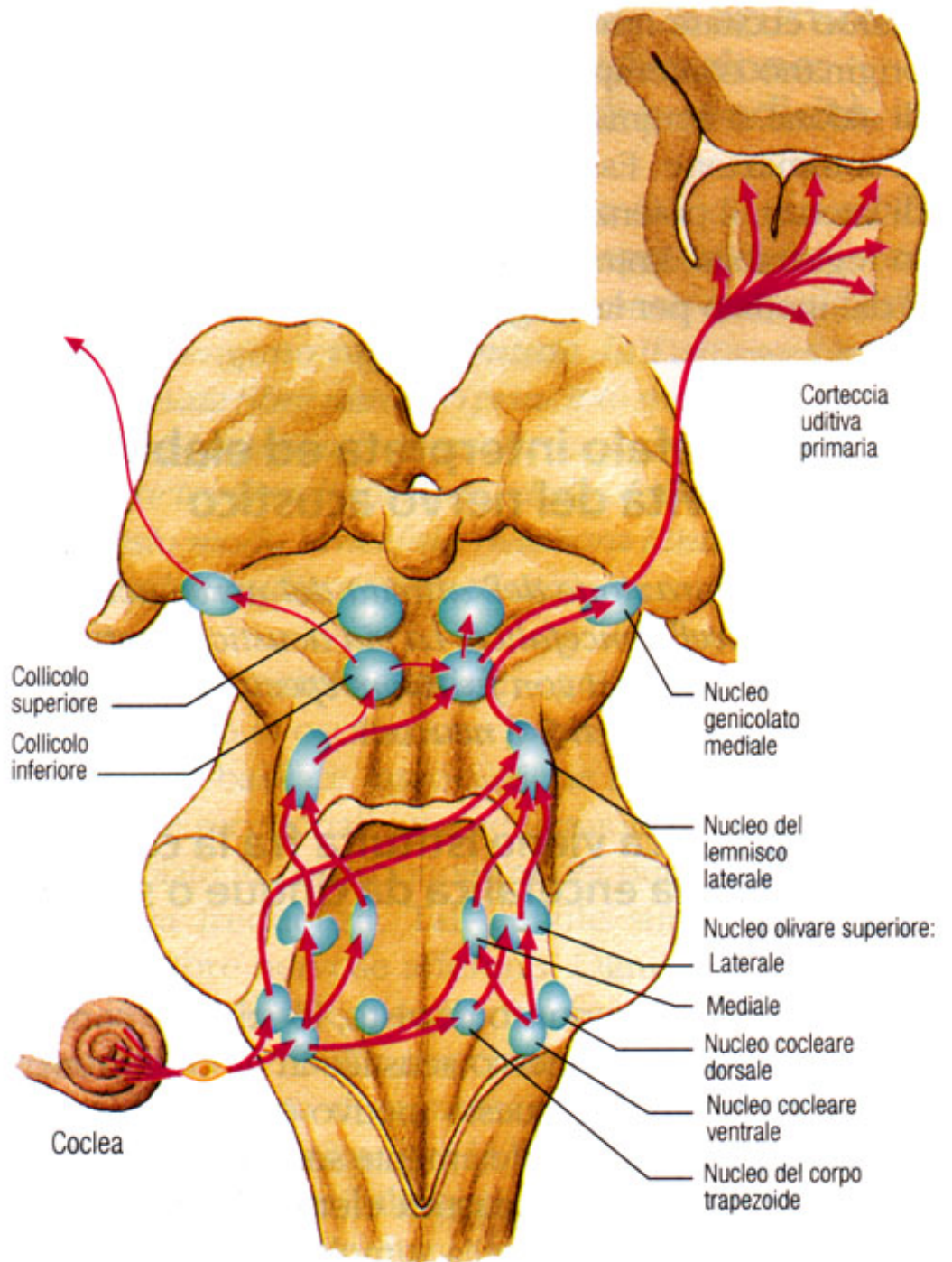
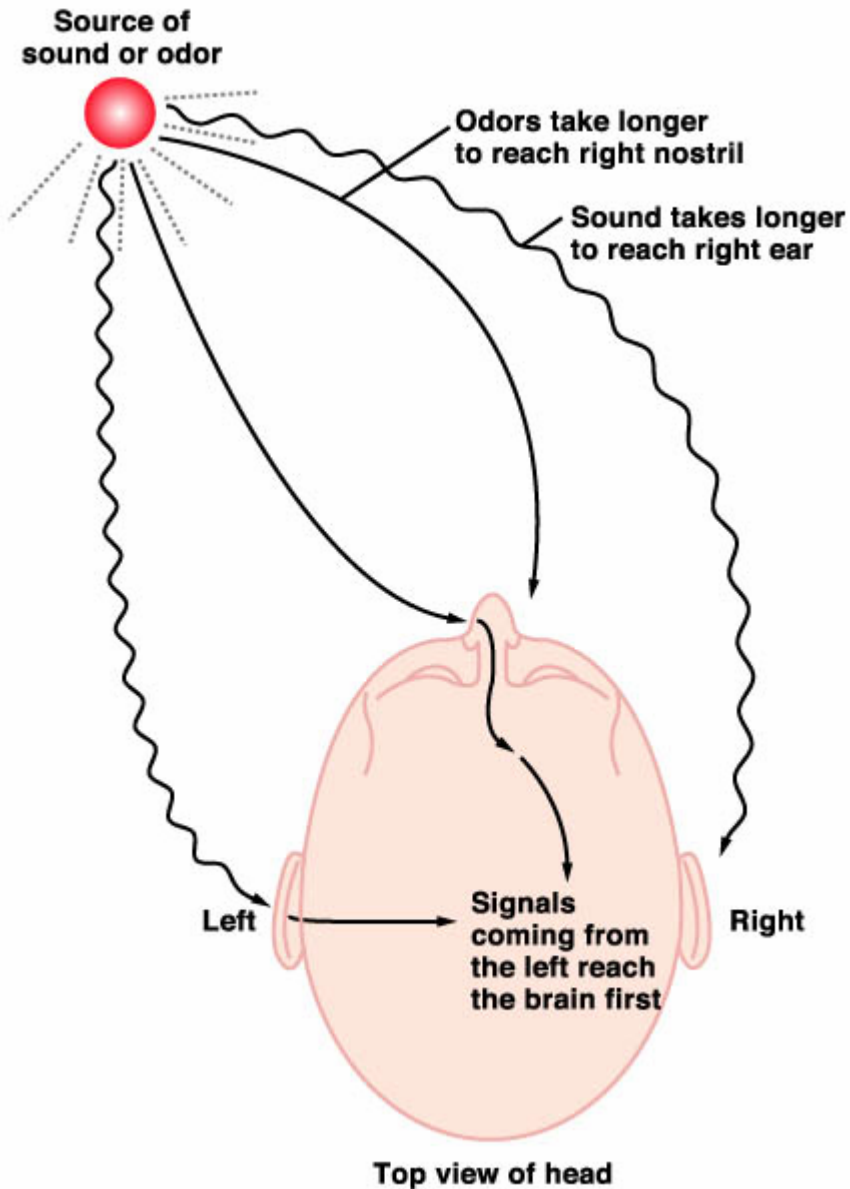


Figura 22.13 Rappresentazione schematica della via u
 Per motivi di semplificazione in figura sono indicate soltanto
 corrispondenti a un orecchio. Si notino comunque, a livello
 nucleo olivare superiore, le frecce che indicano la provenier
 bilaterale.

Localisation of Sound



The localisation of a sound source is an integrative task that requires simultaneous input from both ears.

Since the output from the cochlear nuclei cross over from each side, the cortex receives auditory input from both ears.

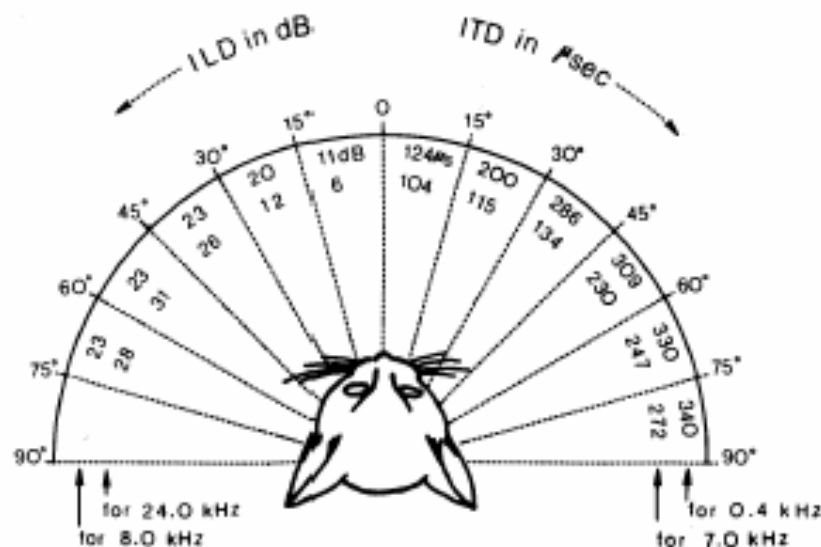
Unless sound is coming directly from the front (or following an equal path) the sound will not reach both ears simultaneously nor at the same amplitude.

The brain uses time, phase and amplitude differences between the input from each ear to compute the sound source.

Head or ear movement can refine the location and hence the cortex can derive a 3D representation of the sound source.

Binaural cues for sound localization

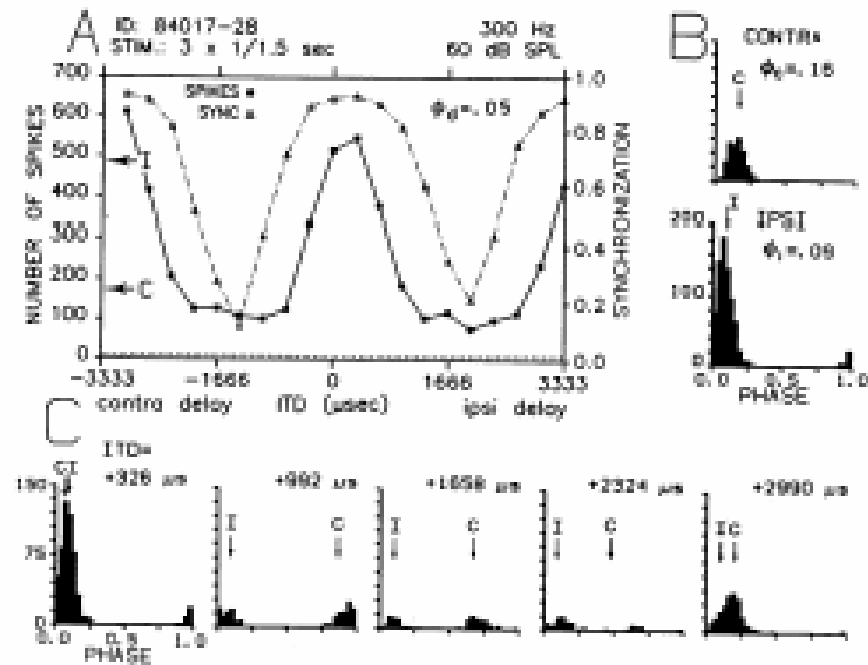
- Two main binaural cues are available:
- Interaural time differences (ITD)
- Interaural level differences (ILD).
- ITD depends primarily on the distance between the ears.
- In cats, ITD varies with azimuth from about -400 ms to $+400$ ms. In humans, the ITD range is about ± 700 ms.



- The ILD cue is strongest at high frequencies (> 5 kHz in cats, > 2 kHz in humans).
- Sound localization also depends on spectral features (peaks and notches) introduced by the filtering action of the pinna.

Neurons in MSO act as coincidence detectors

- MSO neurons respond best to a particular ITD for tone stimuli. For pure tones, introducing an ITD results in an interaural phase difference (IPD).
- MSO neurons phase lock to monaural and binaural stimulation.
- The best IPD corresponds to the difference in responses phases for monaural stimulation of the ipsilateral and contralateral ears. This result shows that MSO neurons act as binaural coincidence detectors.
- At the least favorable IPD, the binaural response is smaller than responses to monaural stimulation of either ear. This is consistent with, but not necessarily evidence for, inhibitory binaural interactions.



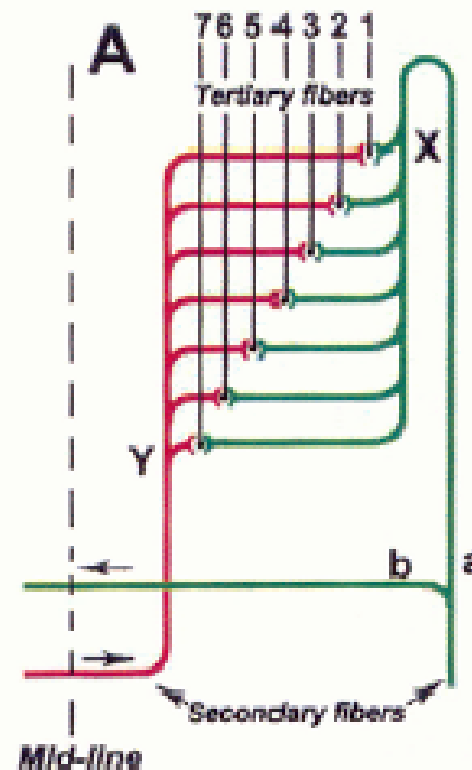
[Yin and Chan \(1990\)](#)

Features of the Jeffress model (1948)

Monaural channels ("secondary fibers"), which originate from left and right cochlear nuclei, converge on a binaural nucleus ("tertiary fibers") and contain temporal information in their discharge pattern about the waveform of the acoustic stimulus.

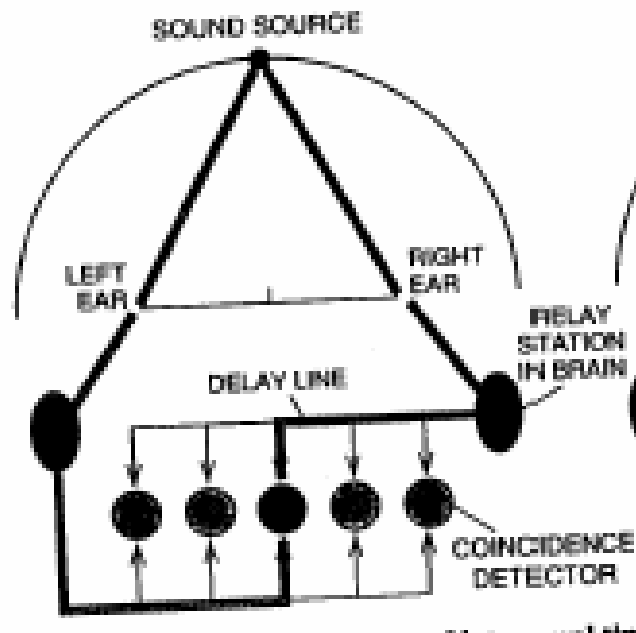
Cells in the binaural nucleus only fire when receiving coincident spikes from their monaural afferents.

The monaural channels project with ladder-like branching patterns running in opposite directions to the tertiary cells.

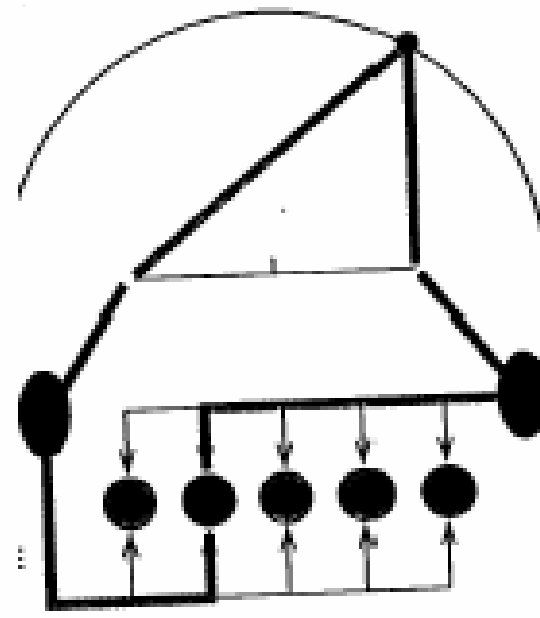


Coincidence detectors make use of delay lines

Frontal sound source

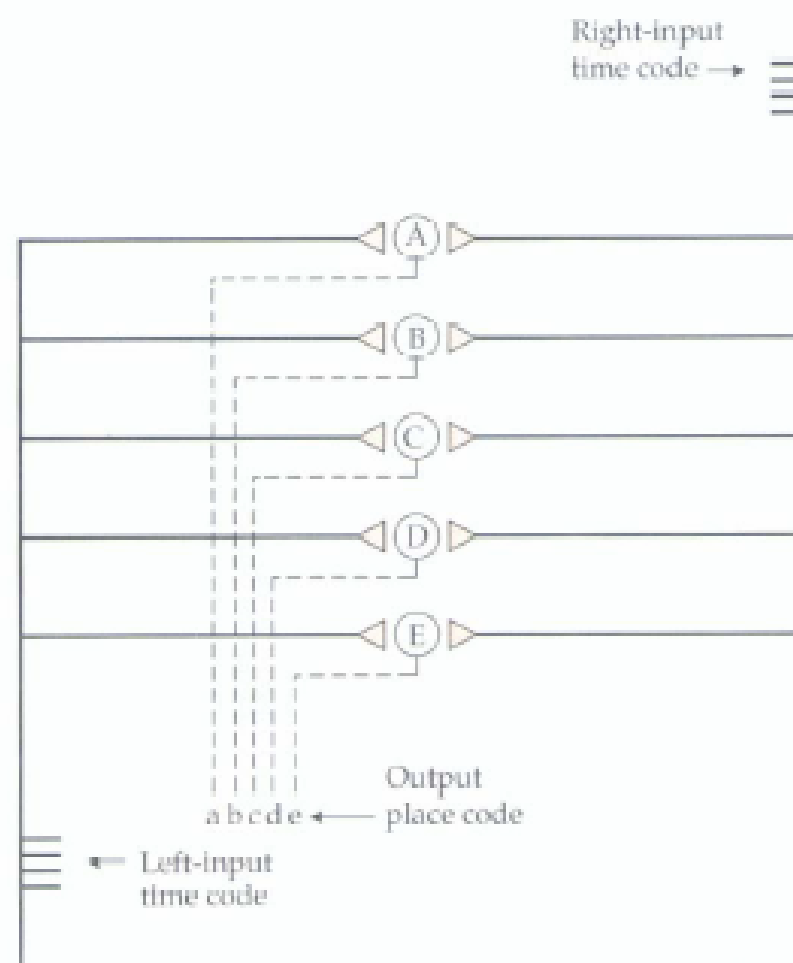


Right sound source

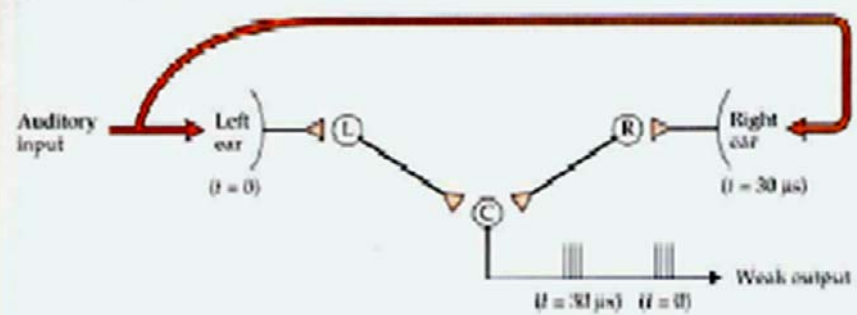


Jeffress's model was modified by Konishi.

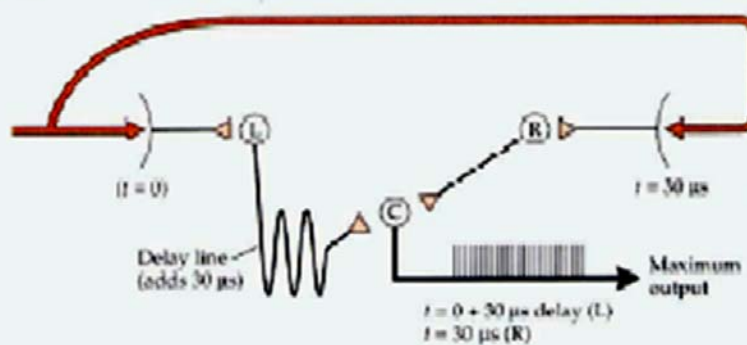
Time codes (via coincidence detectors) are converted to place codes.



(A) No delay line

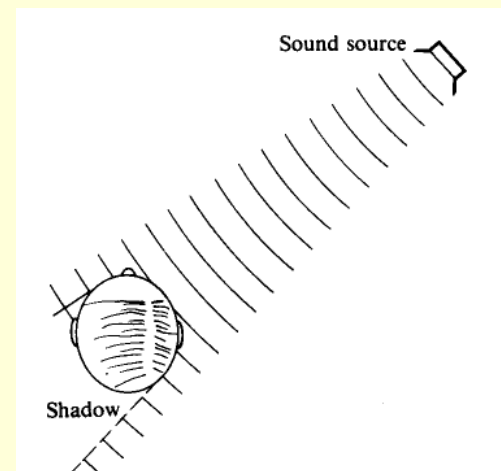
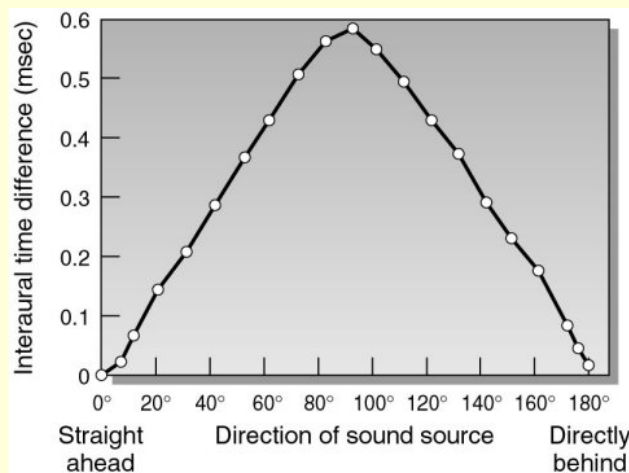


(B) Delay line

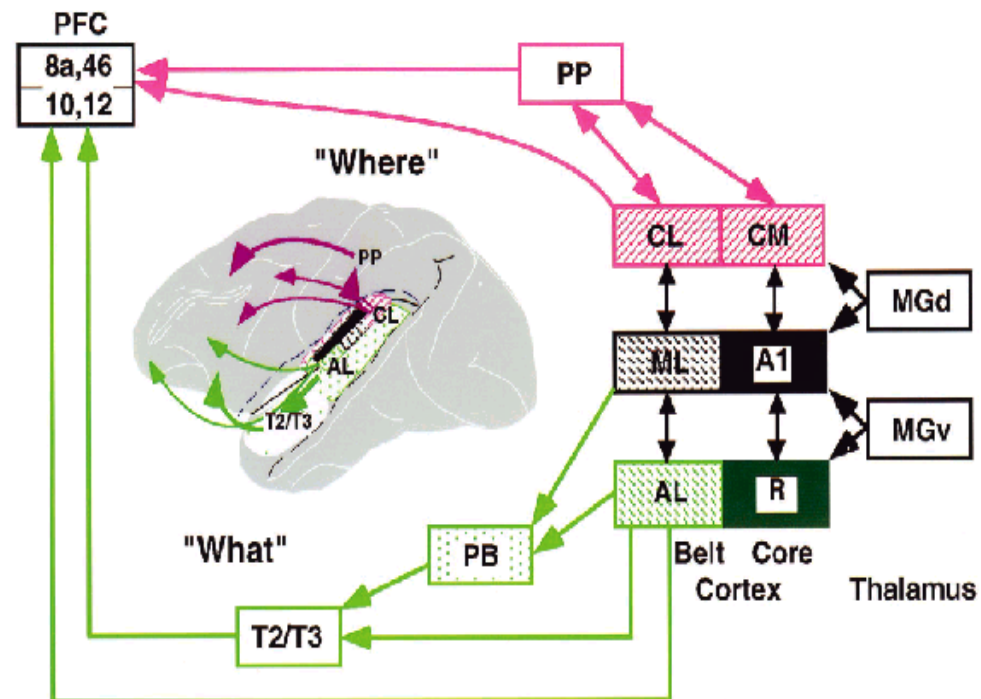


□ Localization of Sound

- At low frequencies (< 1000 Hz), detect phase difference
 - wave crest hits one ear before the other
 - “shadowing” not very effective because of diffraction
- At high frequencies (> 4000 Hz), use relative intensity in both ears
 - one ear is in sound shadow
 - even with one ear, can tell front vs. back at high freq.



Neurobiology of homologous brain systems: primate neuroanatomy and neurophysiology



(Rauschecker & Tian, *PNAS*, 2000)

Pure-Tone Audiogram

- Psycho-acoustic test
- Concept of "threshold" and influencing factors
- International standard
- dB(HL) or dB(ISO)



PTA - Method

- Test – 0.25, 0.5, 1, 2, 4 & 8 kHz
- 3 and 6 kHz in medico-legal setting
- Incremental presentation (5dB min.)
- Ascending versus Descending technique
 - Usually descending



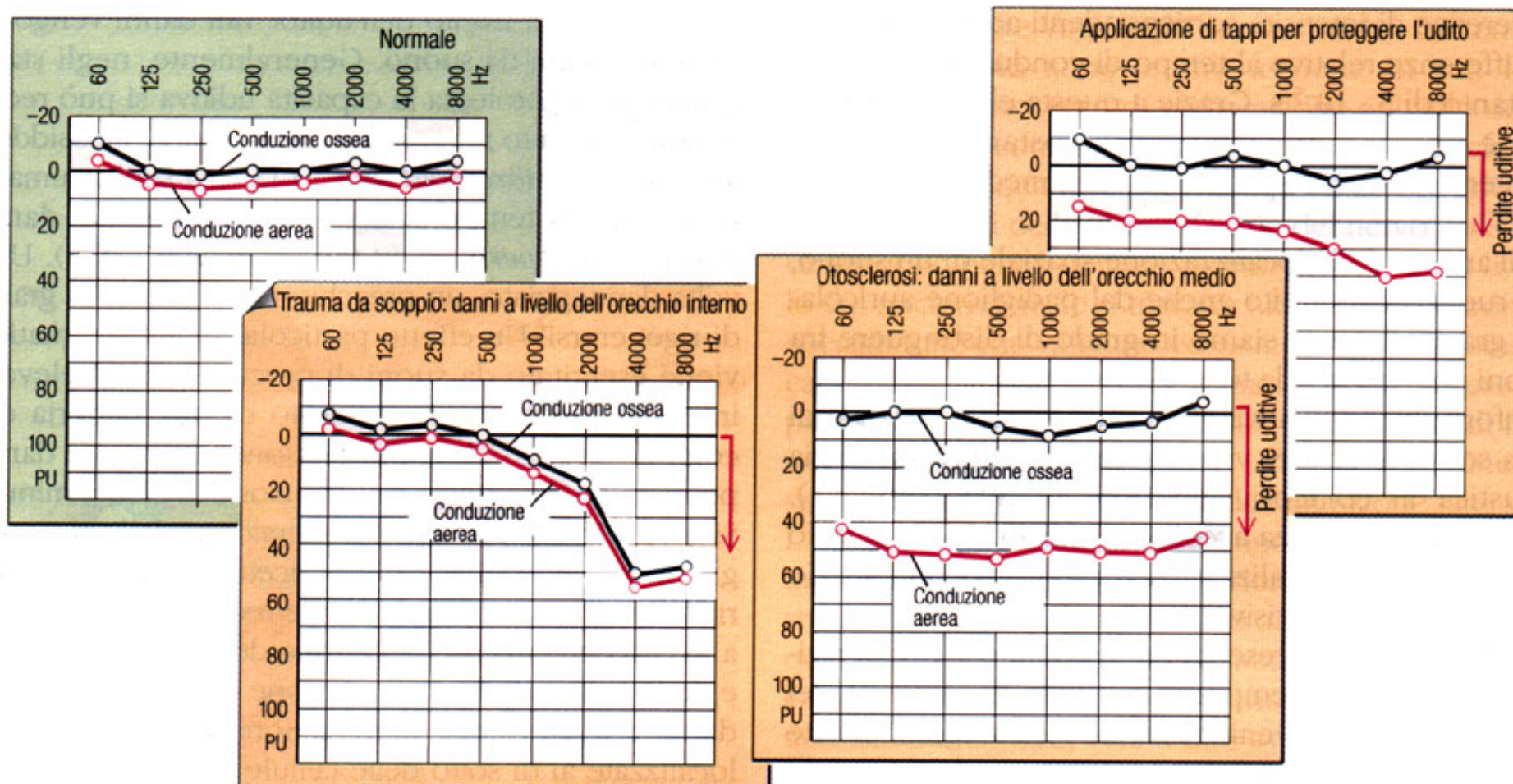


Figura 22.14 Audiogrammi di soglia ottenuti da soggetti con orecchie sane e da soggetti con orecchie danneggiate. In caso di disturbi a livello dell'orecchio interno (ad esempio trauma da scoppio), i valori patologici di misurazione risultano uguali per la conduzione aerea e per quella ossea. In caso

di disturbi localizzati in corrispondenza della trasmissione del suono (ad esempio otosclerosi) risulta peggiorata soltanto la conduzione aerea. In alto a destra è rappresentato l'effetto protettivo svolto in un soggetto sano da tappi per le orecchie. PU = perdita di udito.

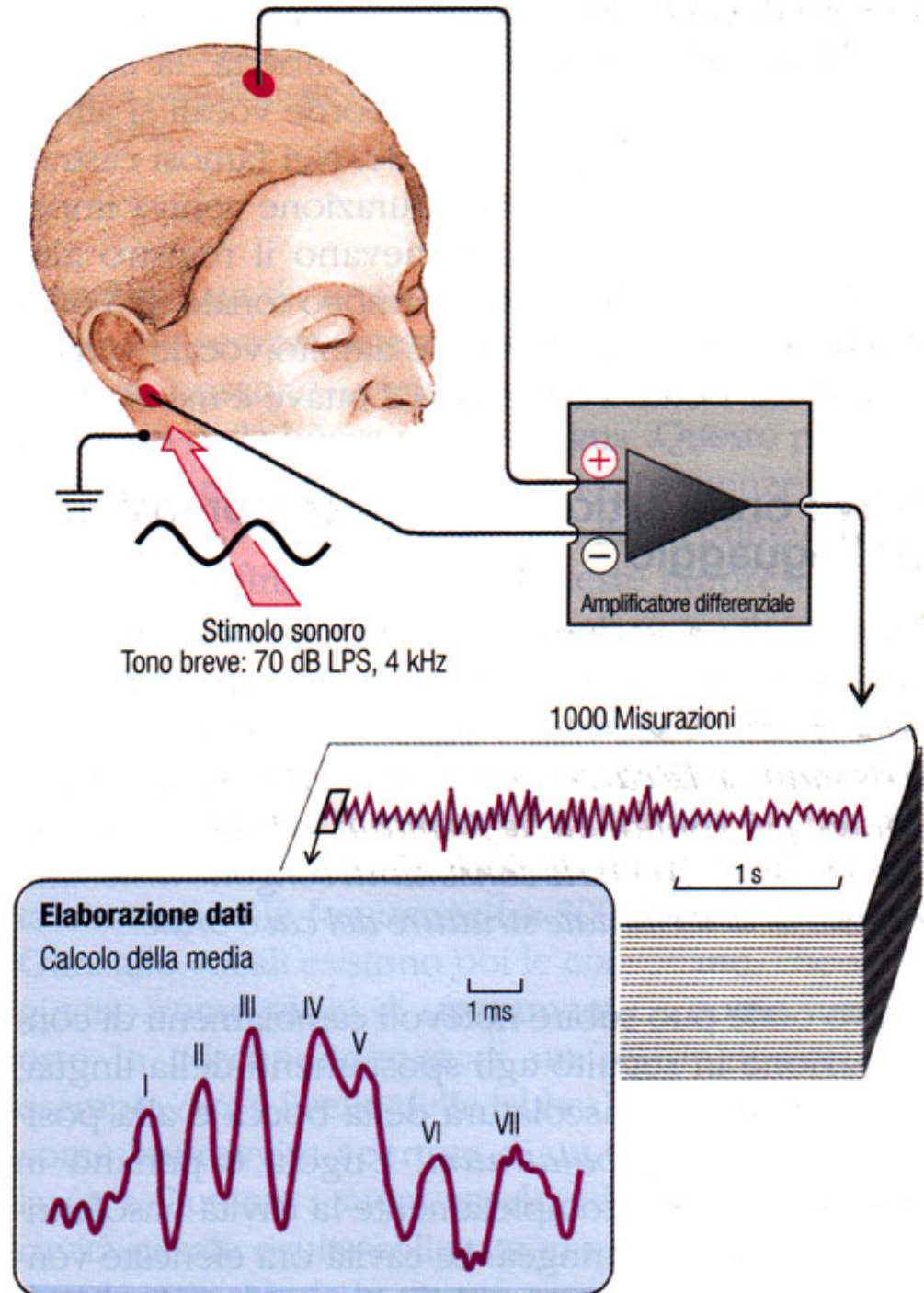
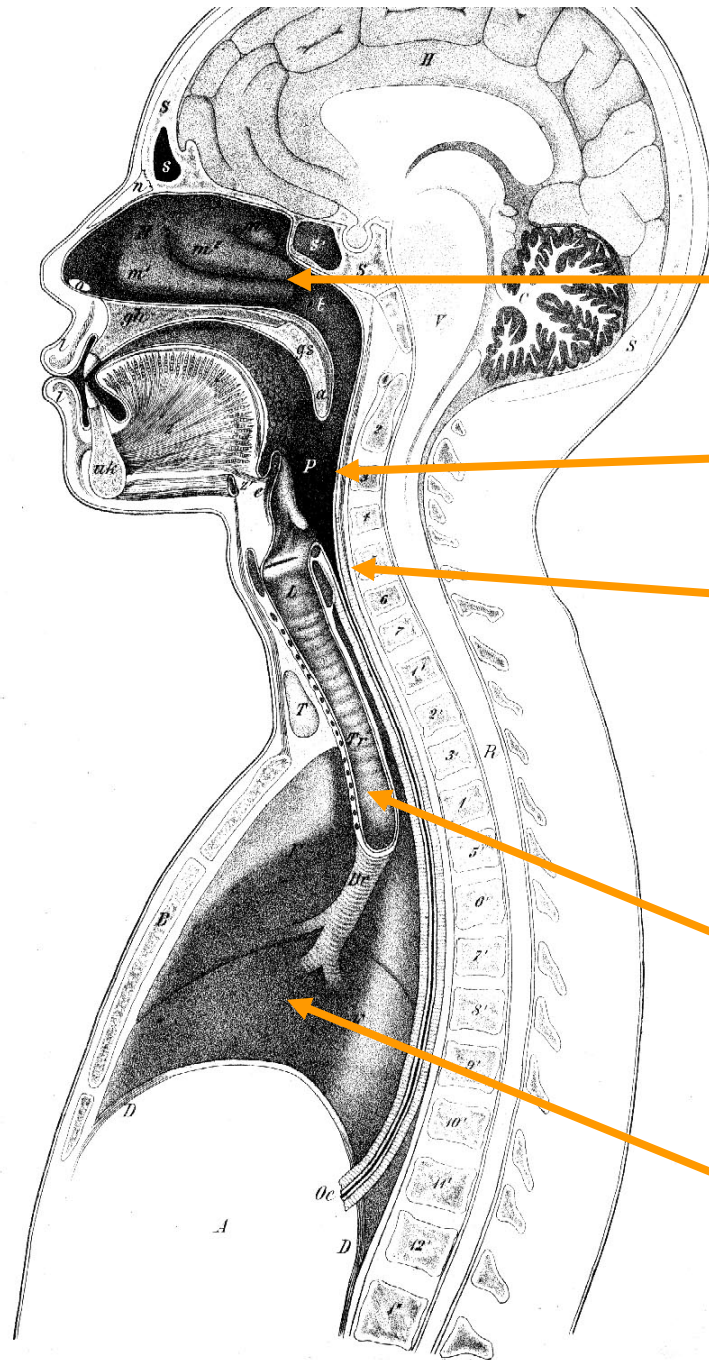


Figura 22.15 Registrazione di potenziali acustici evocati. L'elettroencefalogramma viene derivato fra il vertice del cranio e il lobo dell'orecchio, e le risposte a 1000 stimoli vengono portate a un valore medio da un computer. Si ottengono così curve a picchi (in basso), che rispecchiano l'attività delle vie di conduttività e dei nuclei localizzati nel tronco cerebrale. Anche onde tardive che derivano dalle aree corticali (non rappresentate in figura) possono ancora essere registrate (secondo [Bastani 1999](#)).

Sagittal section of the vocal tract
(Techmer 1880).



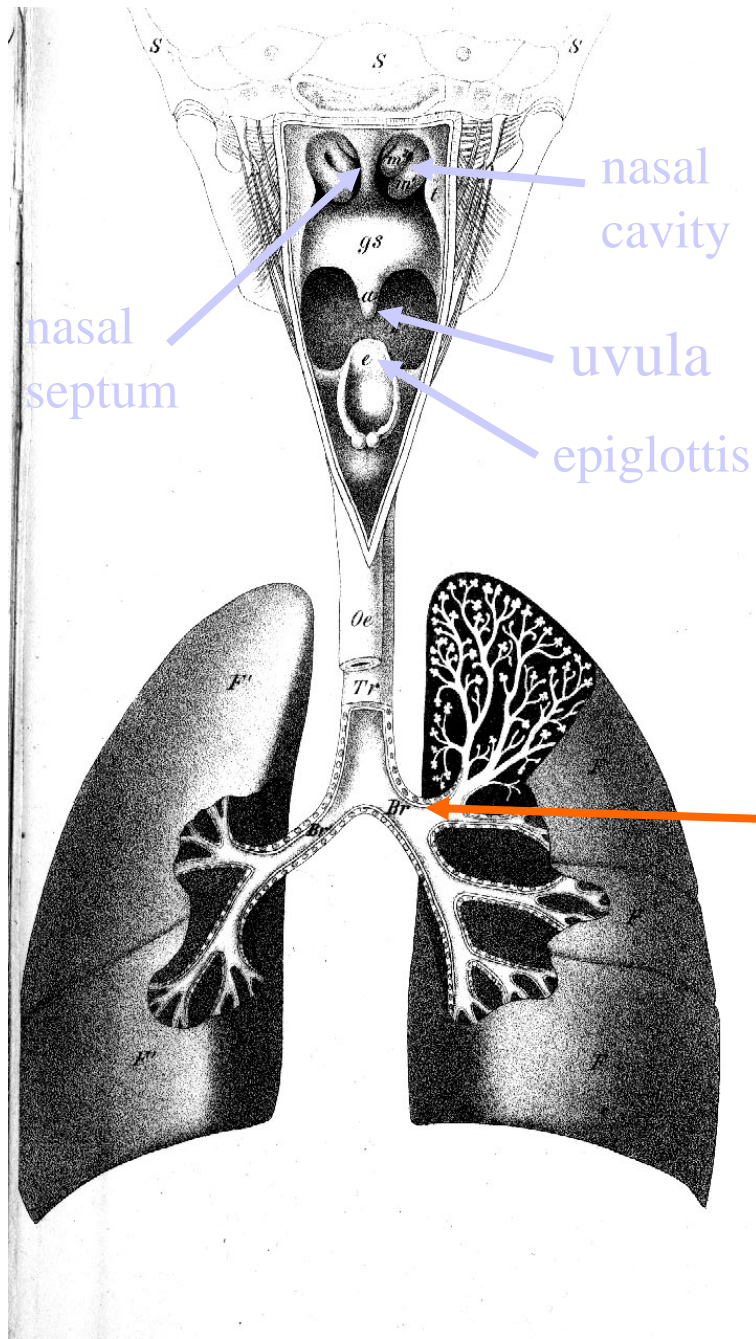
Nasal Cavity

Pharynx

Vocal Cords (within the Larynx)

Trachea

Lungs



View of Speech Organs viewed from behind (coronal section)

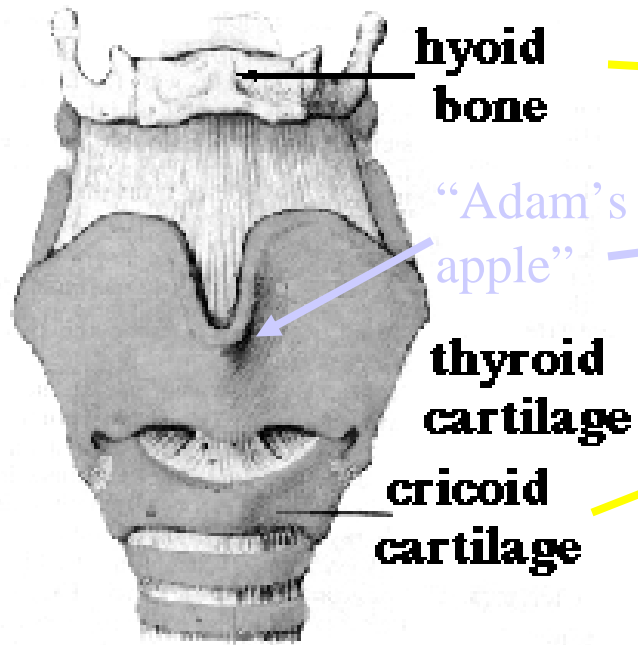
nasal septum

nasal cavity

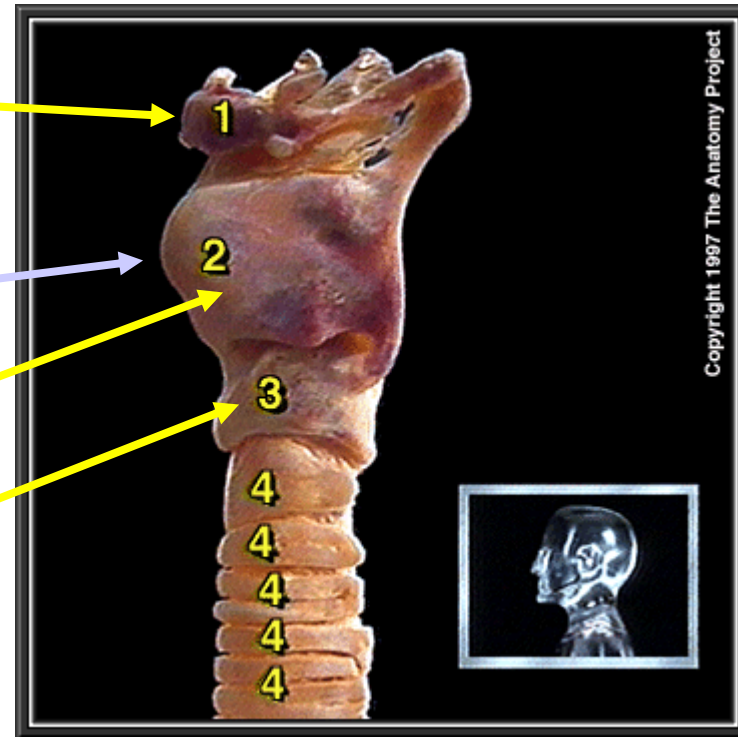
uvula

epiglottis

Bronchi

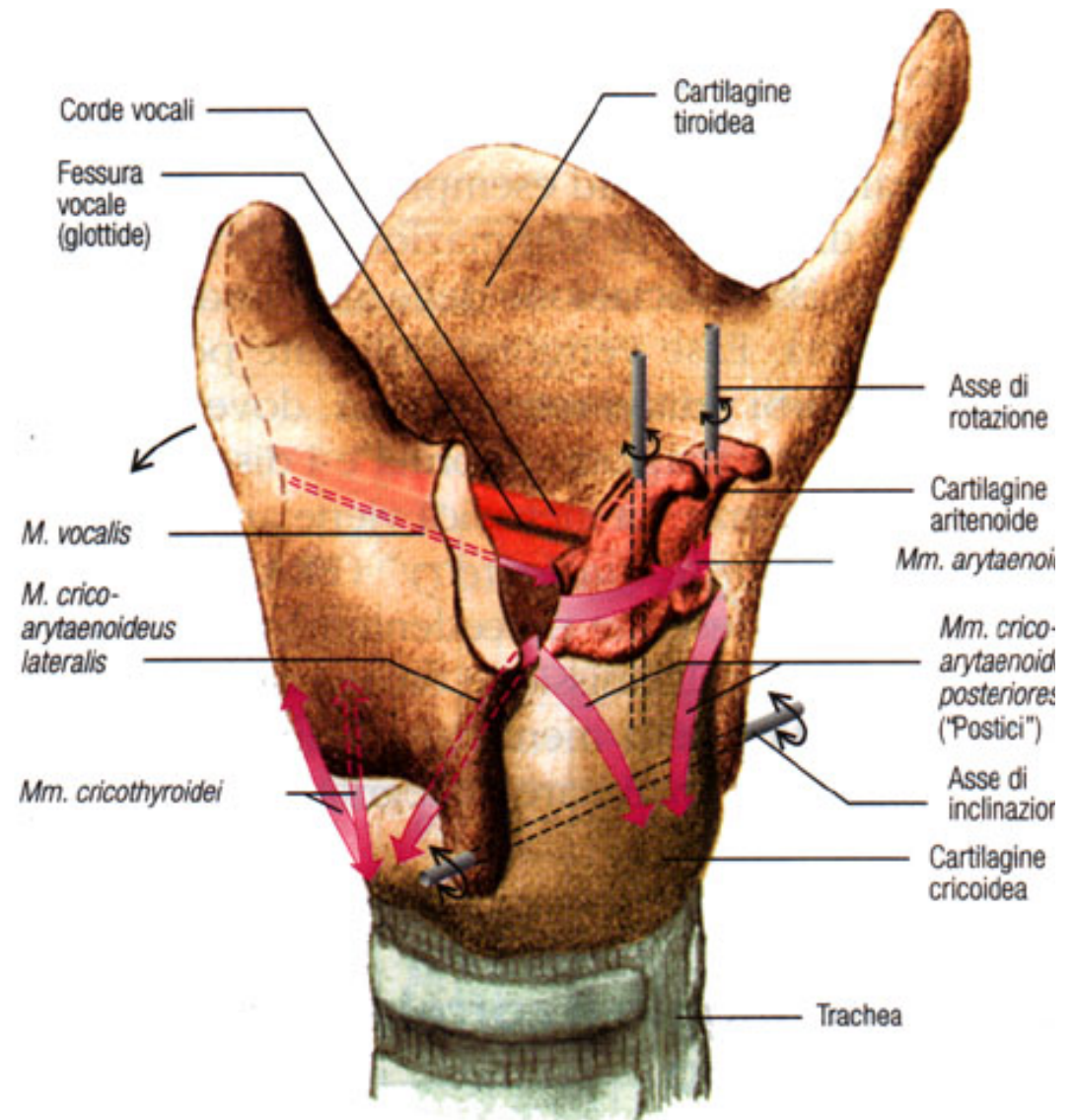
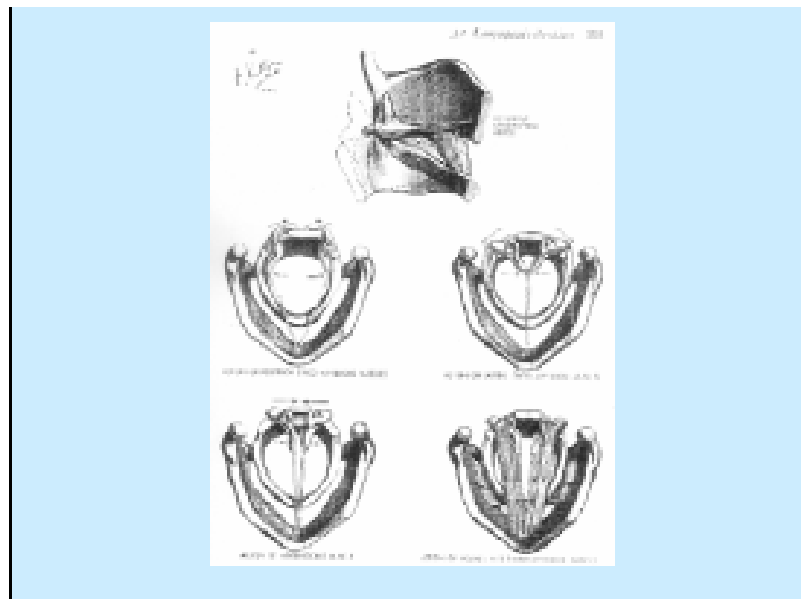


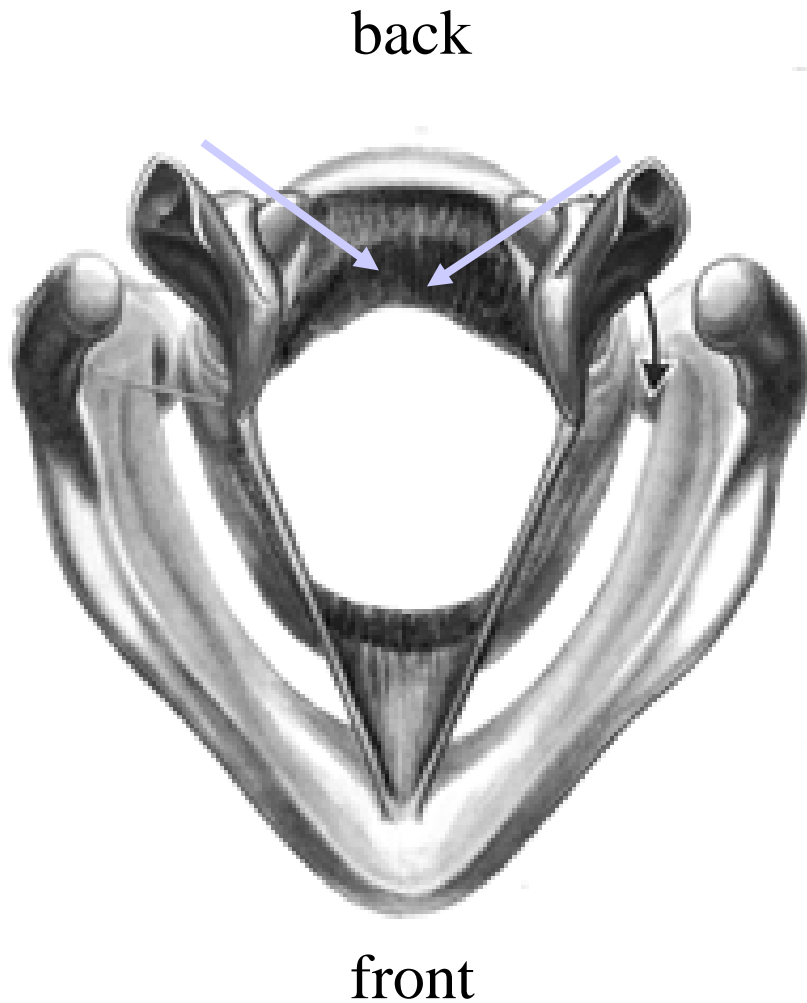
Larynx: front view



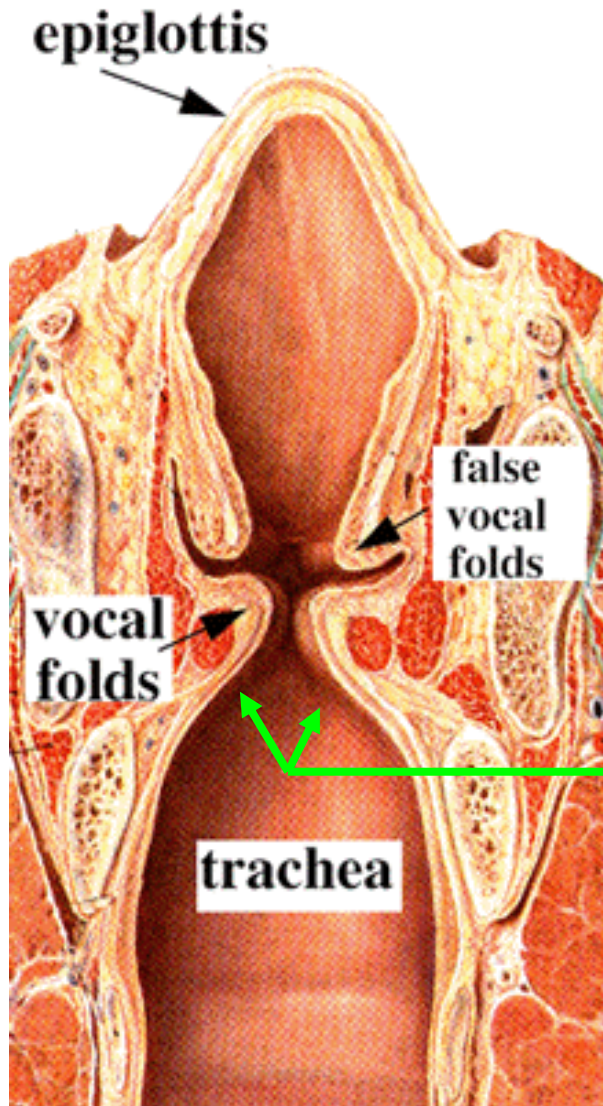
Larynx: oblique side view

Figura 22.16 La muscolatura laringea e la sua funzione. Le corde vocali si applicano ai processi delle cartilagini aritenoidi, che possono ruotare intorno al loro asse longitudinale. È inoltre indicato l'asse di inclinazione della cartilagine tiroidea.



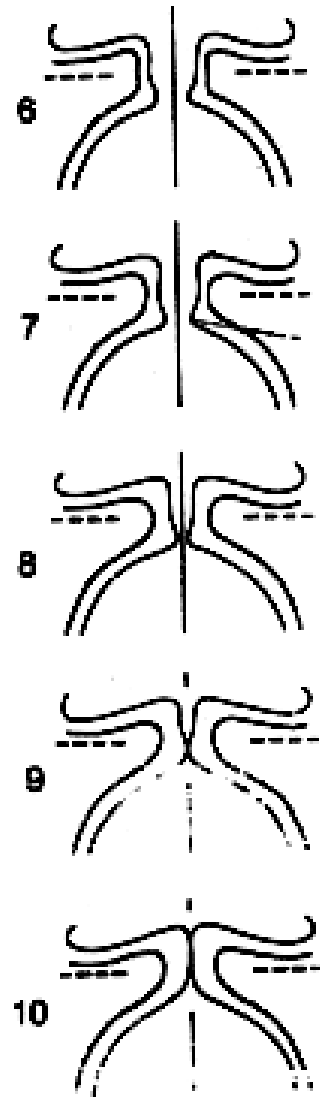
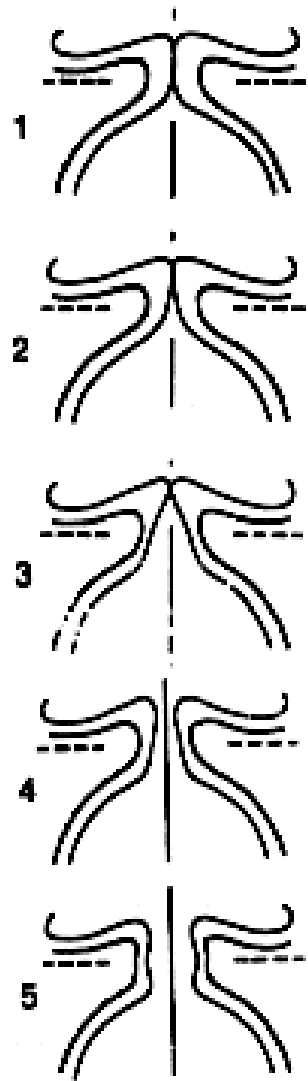


Vocal cords (without overlaying muscles and tissue) seen from above. The cords are attached to the inside of the thyroid cartilage at the front and to the moveable arytenoid cartilages at the back. The cords may be brought toward the midline when the arytenoid cartilage “rock” inward (red arrows).



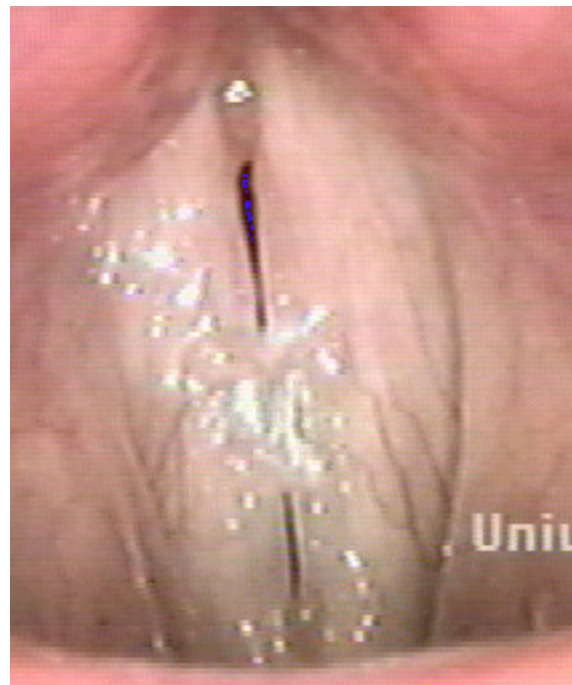
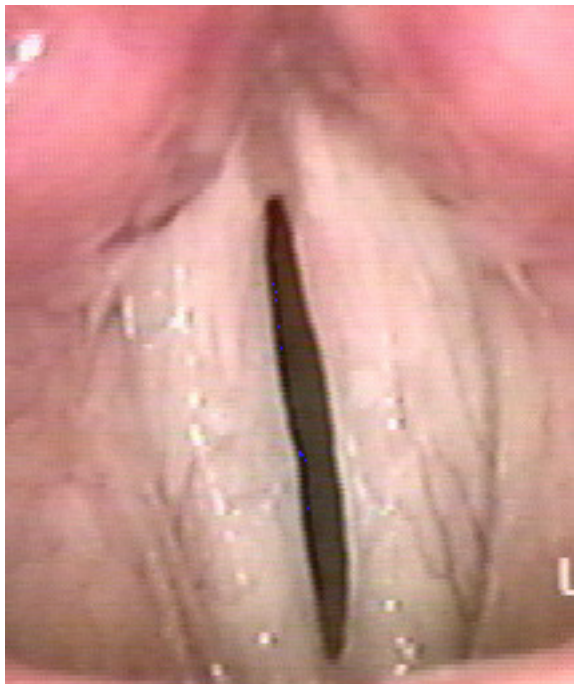
Coronal slice through the larynx; rear portion removed, leaving front portion. (Viewed from behind.)

[Aside: conus elasticus, mentioned in an earlier slide, is here.]



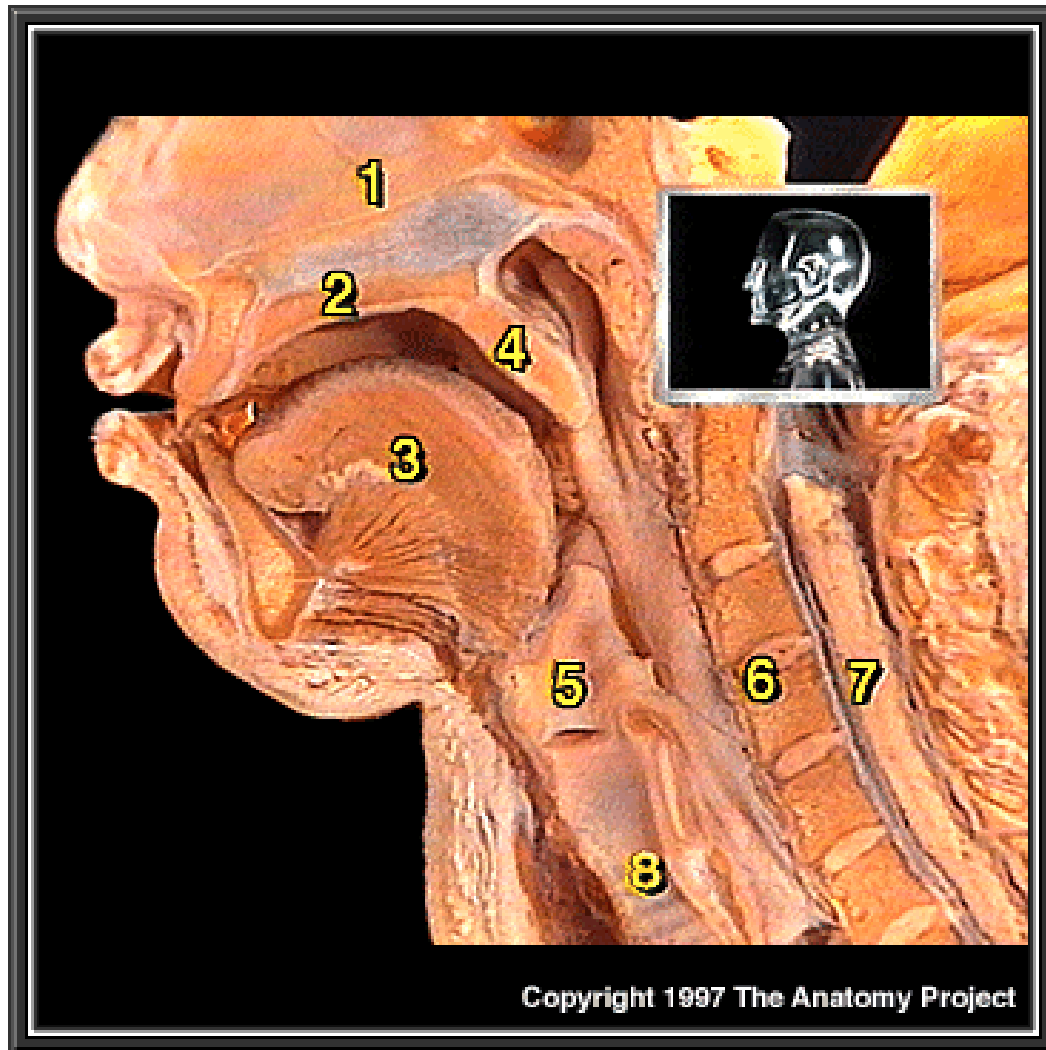
Movement of the vocal cords during one vibratory cycle (seen in coronal section).

Posterior



Anterior

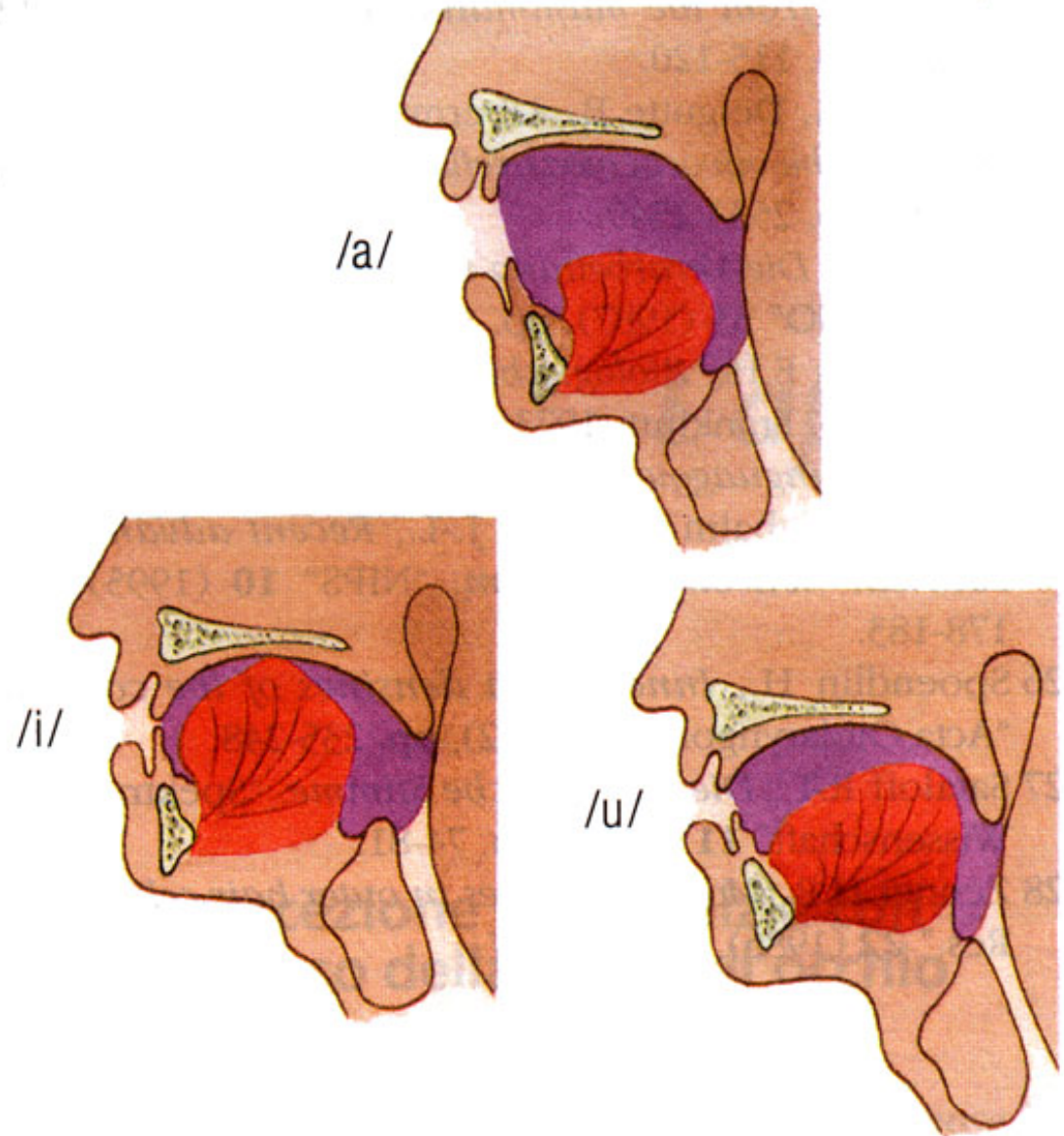
Different phases of one vibratory cycle of the vocal cords.



The soft palate (velum) is a “veil” of tissue with several muscles attached to it so that it can be elevated and lowered. It is thus a valve regulating the passage of air (and for speech, sound) into nasal cavity.

In neonates the velum and epiglottis overlap, as they do in the adults of many mammalian species.

Figura 22.17 Le varie posizioni di articolazione nel cavo orale. Grazie alle varie posizioni assunte dalla lingua, nel cavo orale si formano spazi diversi con tipiche frequenze di risonanza. In figura sono illustrate le posizioni per la formazione delle vocali /a/, /i/ e /u/.



Muscular control of phonation

- Lateral control of the glottis
 - adduction (for protection and voiced sounds)
 - abduction (for breathing and voiceless sounds)
- Longitudinal control of the glottis
 - tension settings of the vocalis muscle
 - control of fundamental frequency (F0)

Voice quality

- Phonation type (lateral tension)
 - Tense (pressed) voice *pressad*
 - Normal (modal) voice *modal*
 - Flow phonation *flödlig*
 - Breathy voice *läckande*
- Vocal intensity
 - Interaction between subglottal lung pressure and lateral (adductive) tension