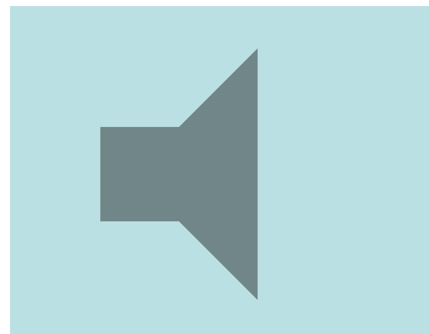


Press for sound check!

If no sound, check system volume control.

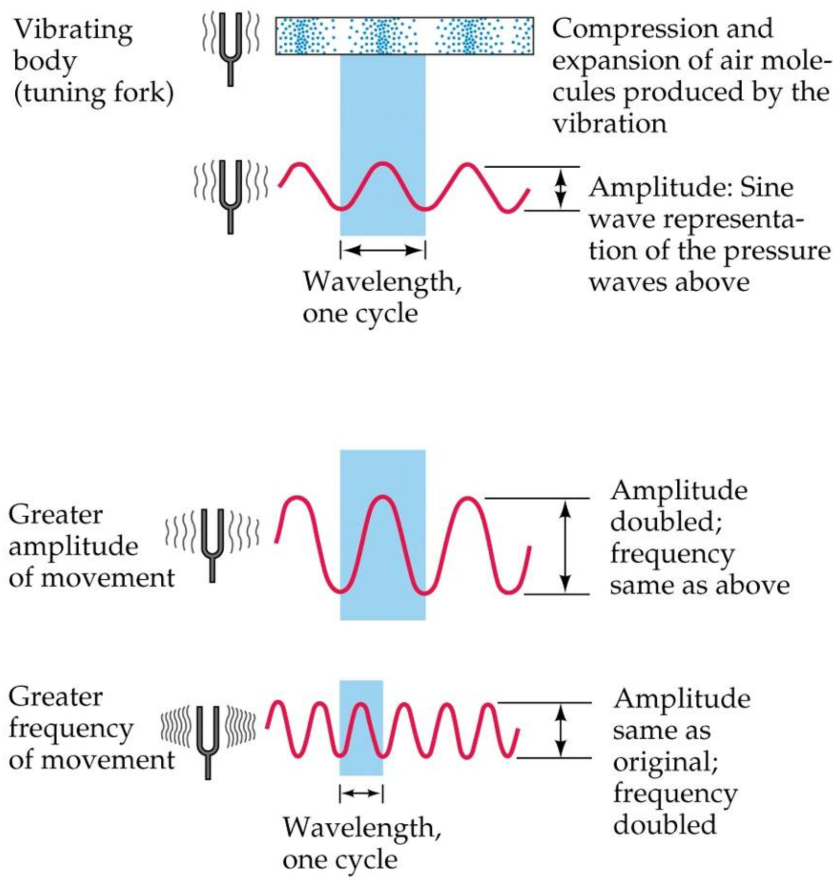
ECE 537

Oct. 31, 2014

Nov. 3 & 5, 2014

Sound

Amplitude and Frequency of Sound Waves

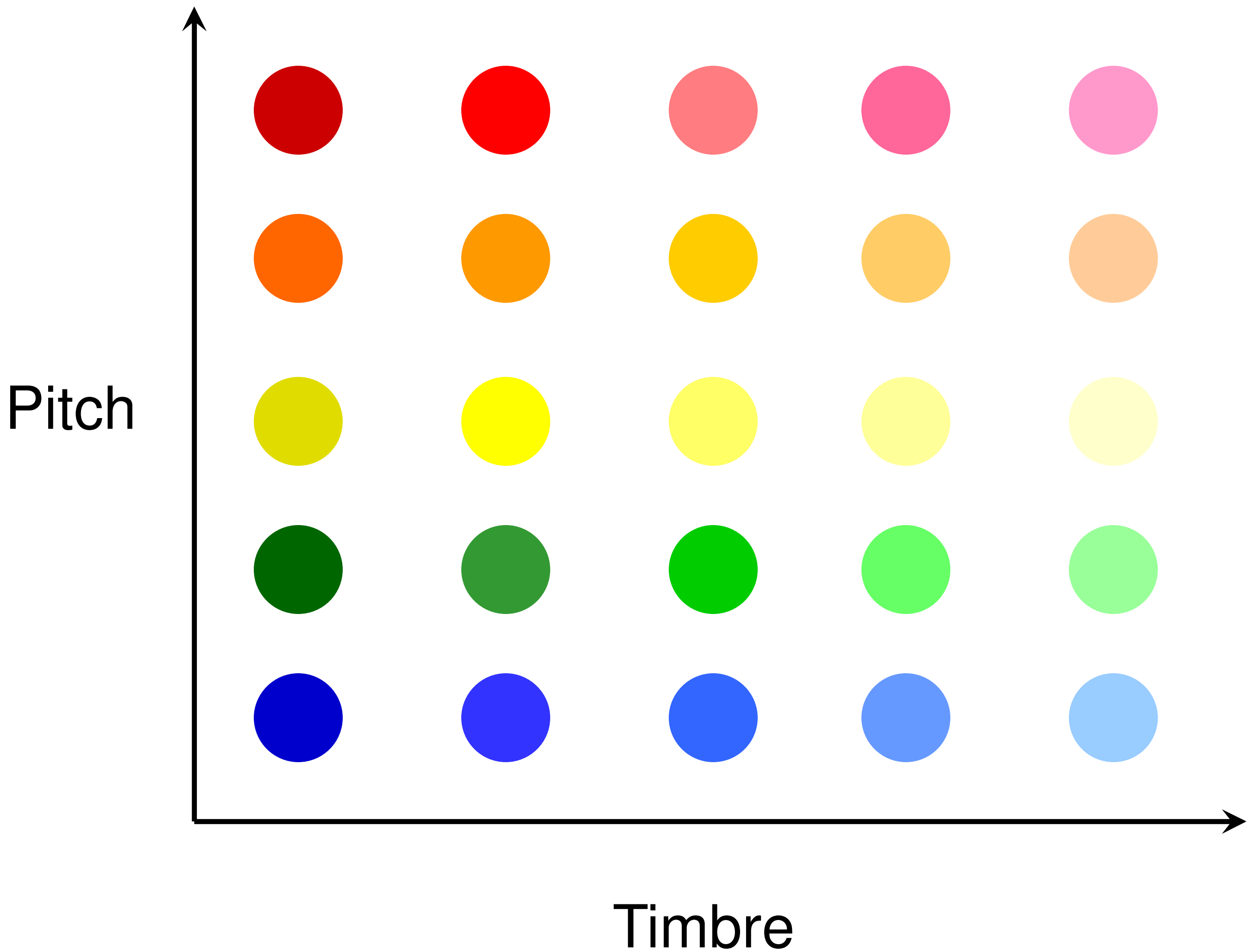


- Sound is the vibration of air molecules.
- A tuning fork produces a sinusoidal vibration
- The number of cycles each second is the frequency (Hertz)
- We hear frequencies between 20 Hz and 20,000 Hz

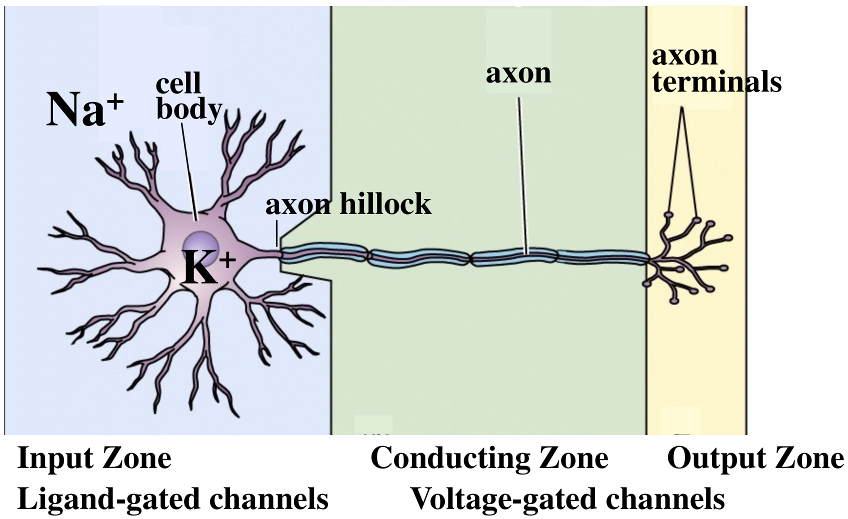
Pitch

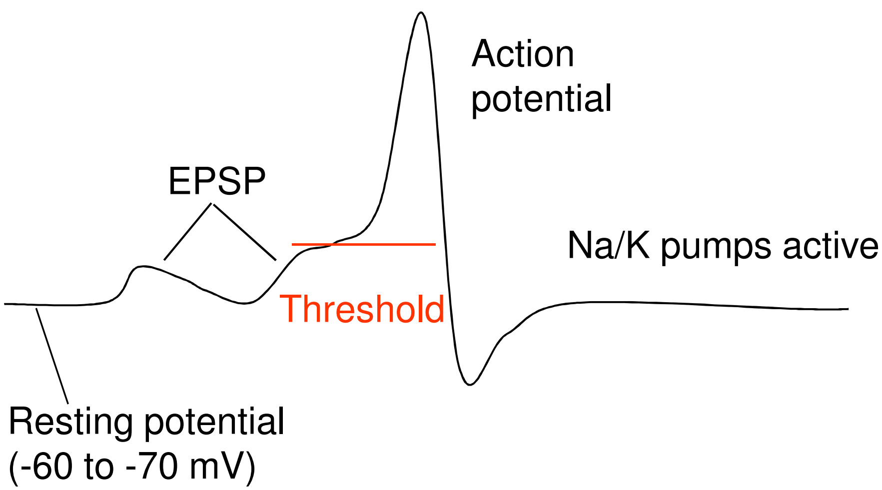
- Pitch is the perceived frequency of a sound
- Defined as “that attribute of auditory sensation in terms of which sounds may be ordered on a musical scale.”
- Very similar to actual frequency for pure tones

Pitch vs Timbre



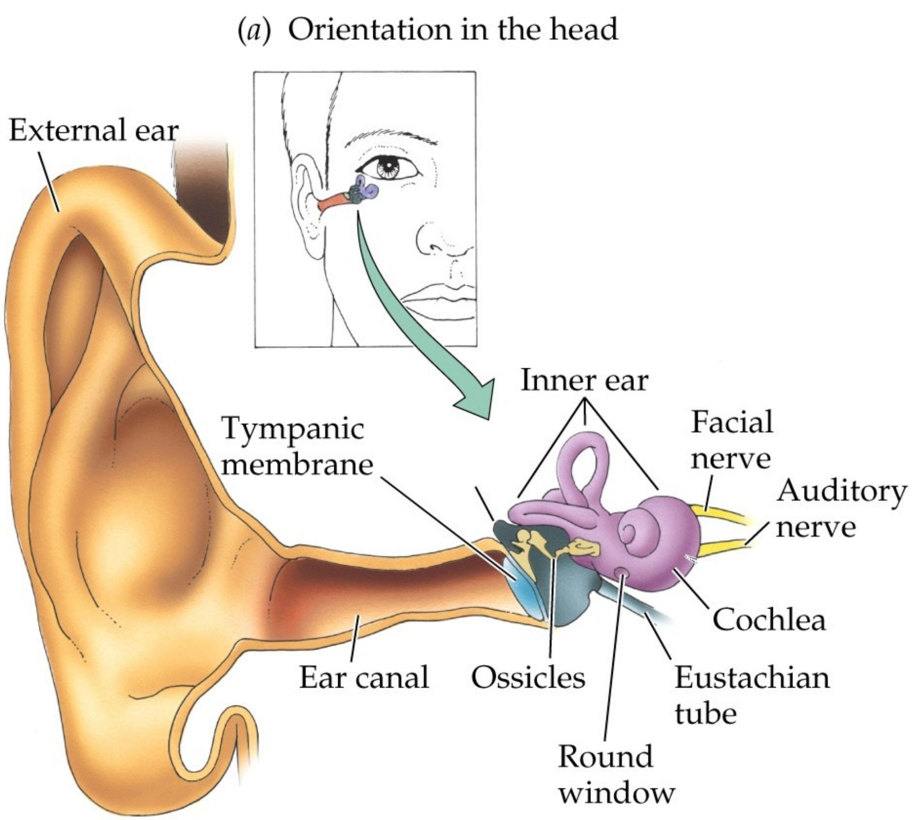
Neuron Signaling





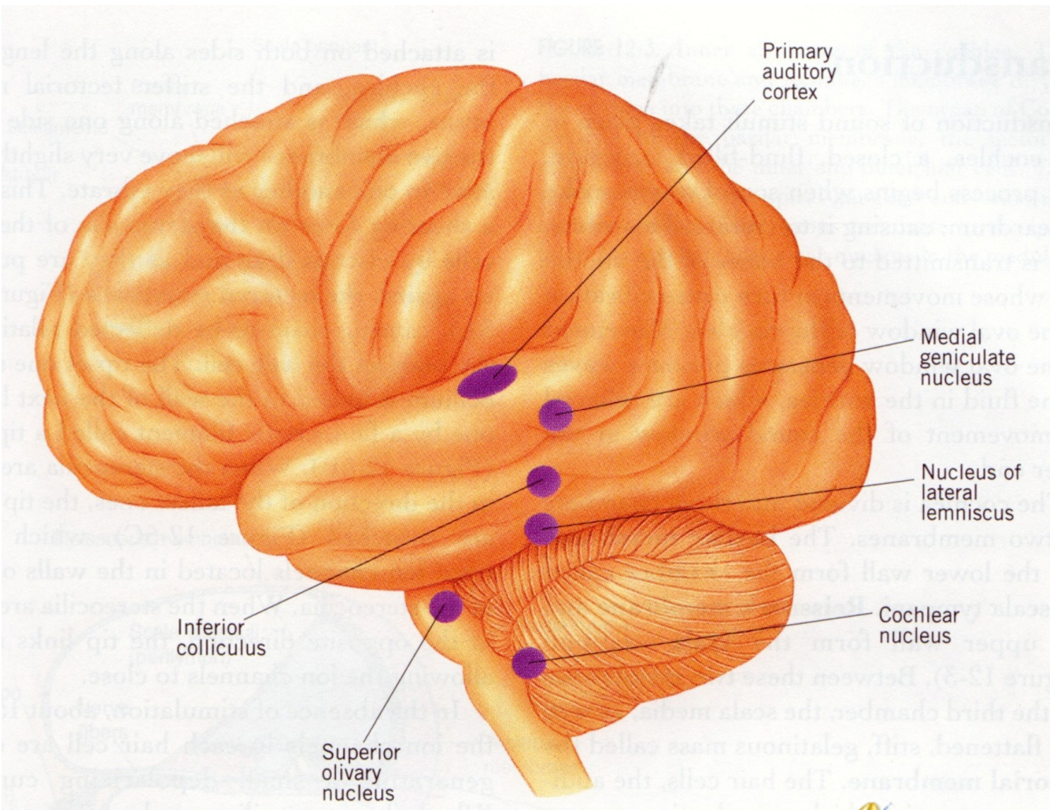
- Action Potential
- Release small packet of neurotransmitter to cause excite or inhibit next neuron
- Excitatory Postsynaptic Potential (EPSP)
- Inhibitory Postsynaptic Potential (IPSP)
- First must transduce physical signal

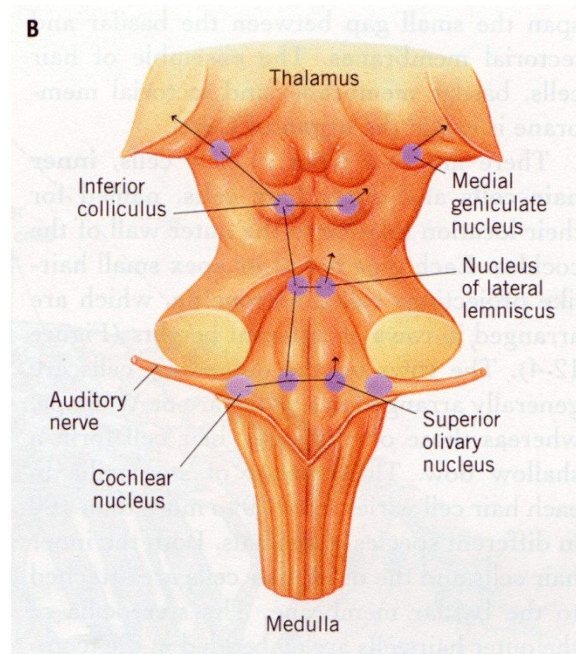
Peripheral Auditory System



- Pinna (external ear) amplifies sound
- Cochlea is where neurons transduce sound into neural signals. It is filled with fluid.
- Middle ear compensates for the loss of intensity as vibrations in air are changed to vibrations in fluid.
- Auditory nerve carries the signal to brain stem (medulla)

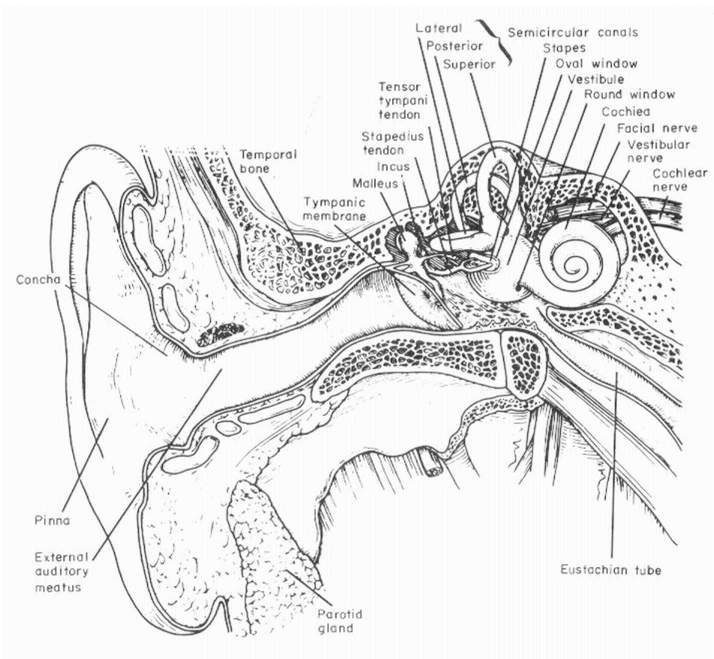
Auditory Pathway to Cortex

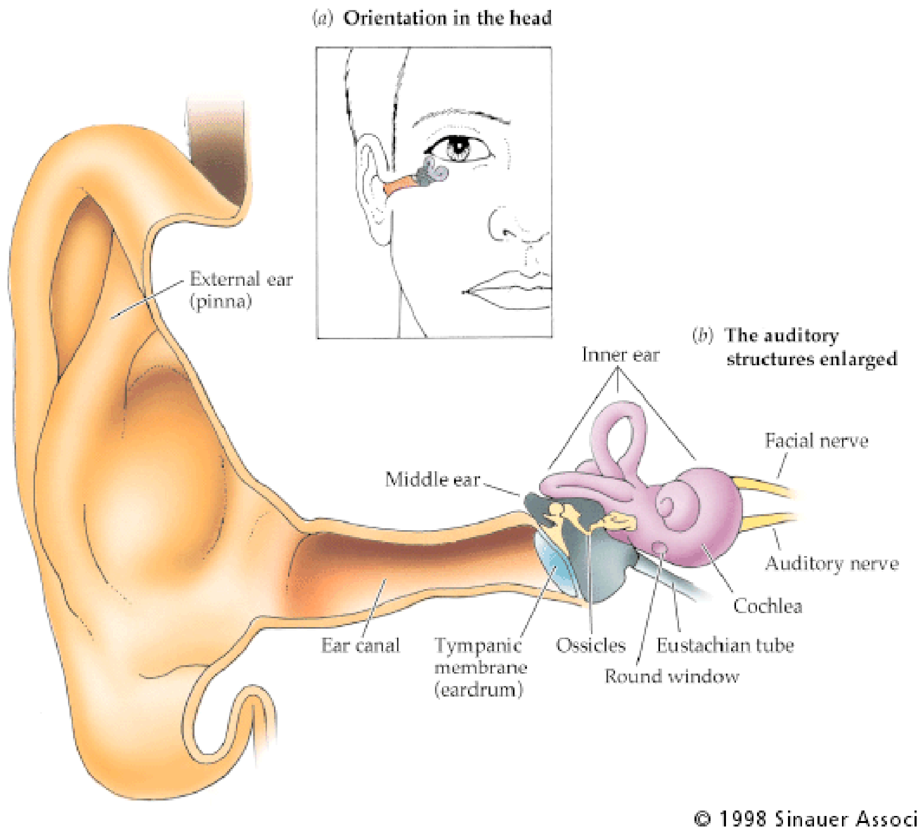


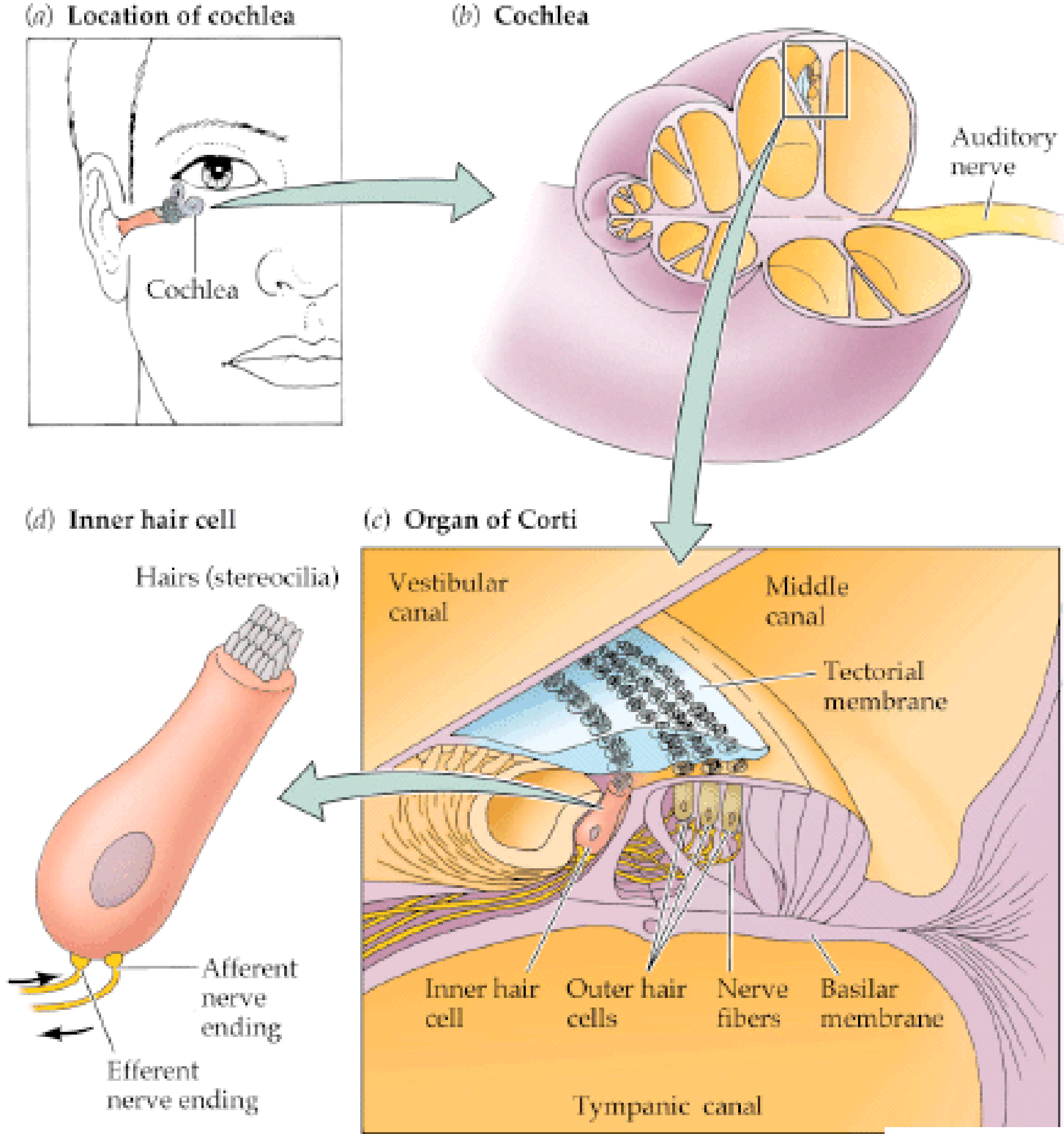


The Cochlea

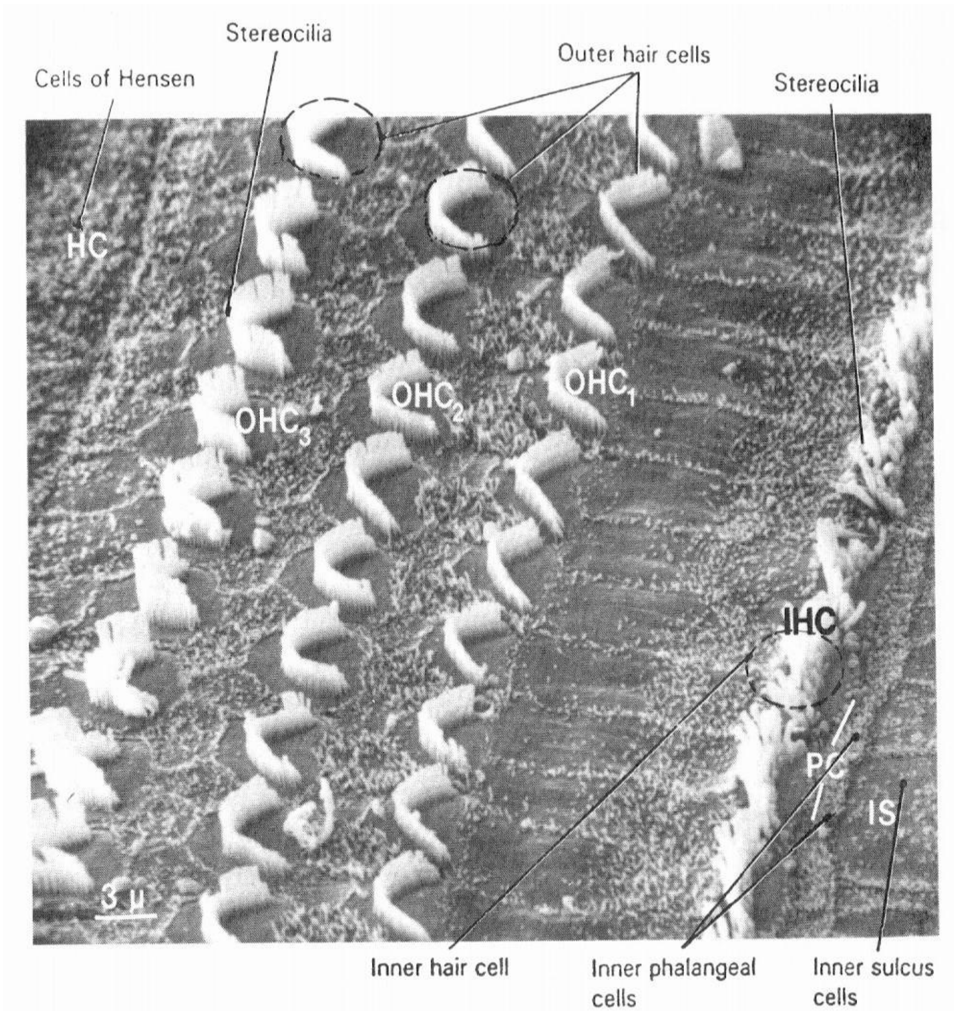
- Frequency analysis
- Transduction into neural impulses



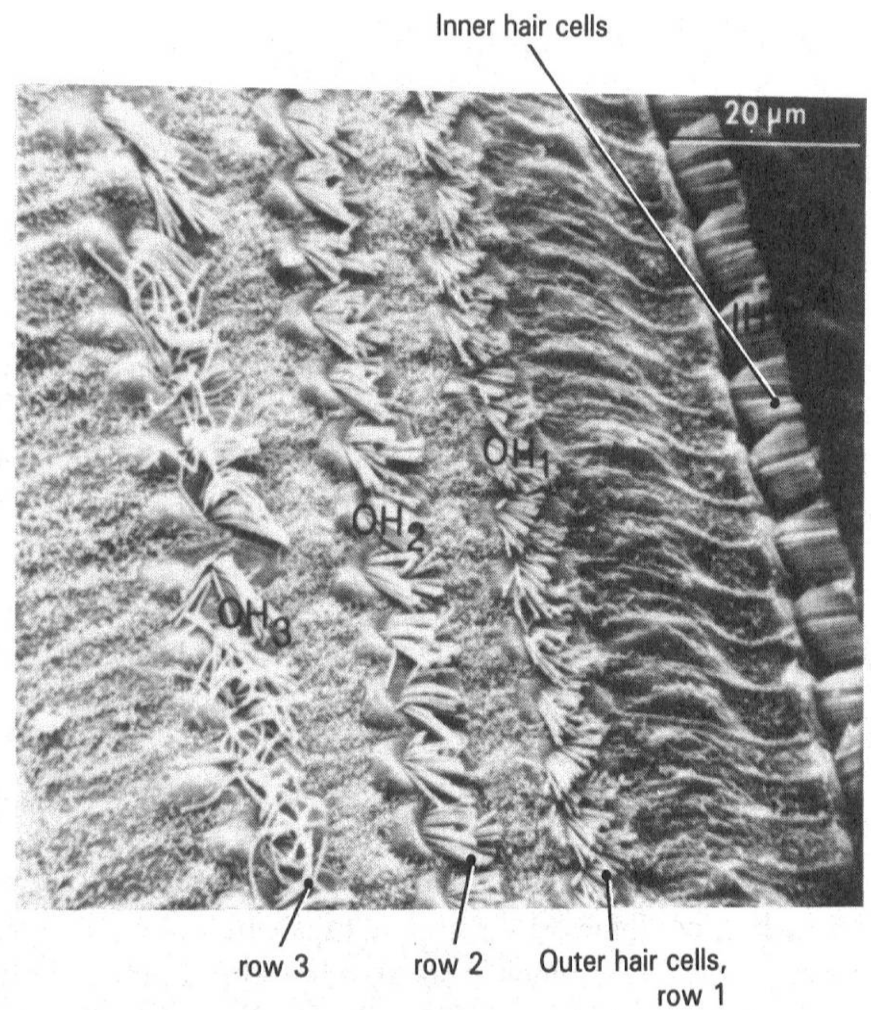



(a) Location of cochlea
Cochlea
(b) Cochlea
Auditory nerve
(c) Organ of Corti
Vestibular canal
Middle canal
Tectorial membrane
Inner hair cell
Outer hair cells
Nerve fibers
Basilar membrane
Tympanic canal
(d) Inner hair cell
Hairs (stereocilia)
Afferent nerve ending
Efferent nerve ending

These Are Your Stereocilia



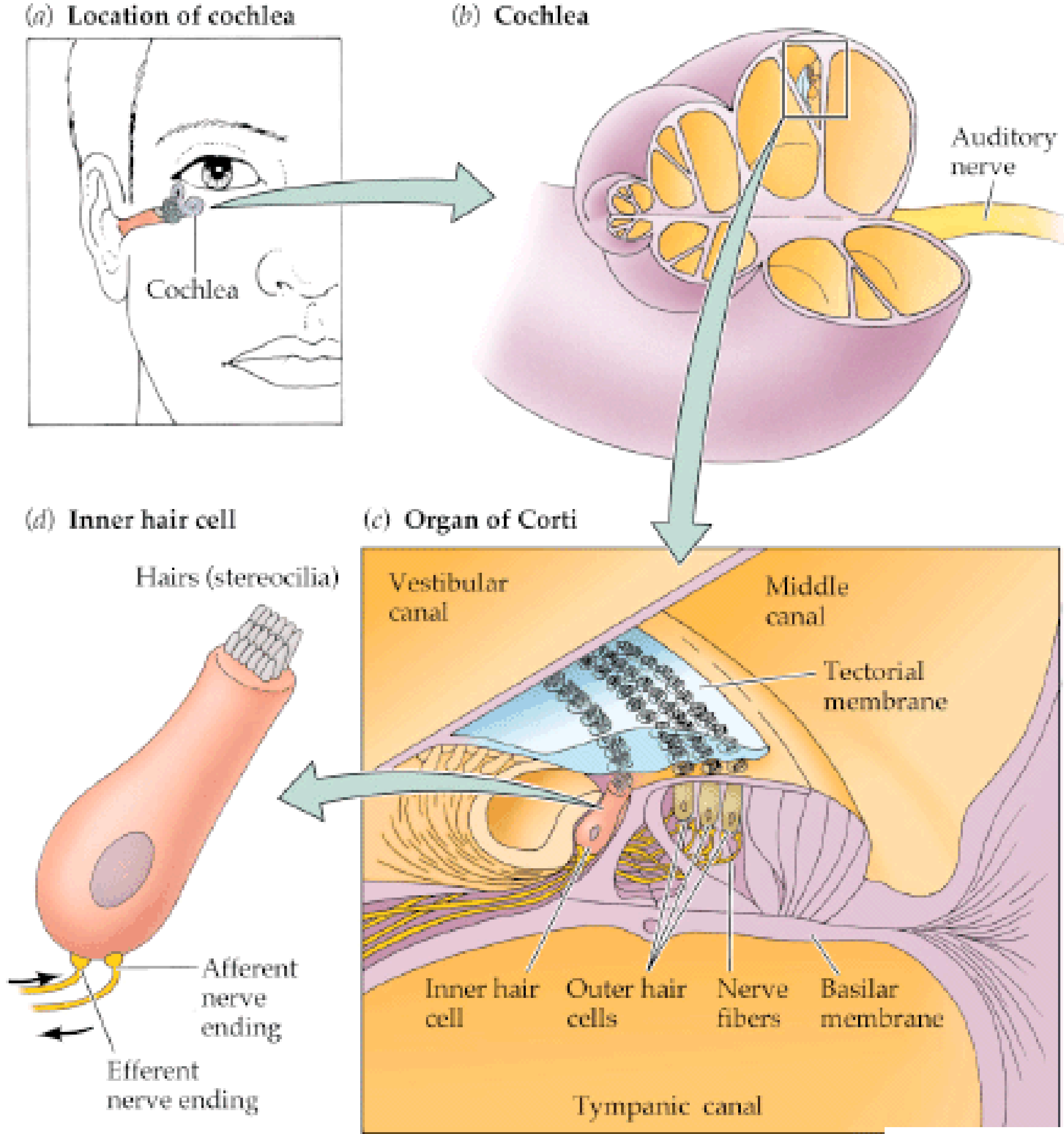
These Are Your Stereocilia On Loud Sounds



TURN

IT

DOWN!


(a) Location of cochlea
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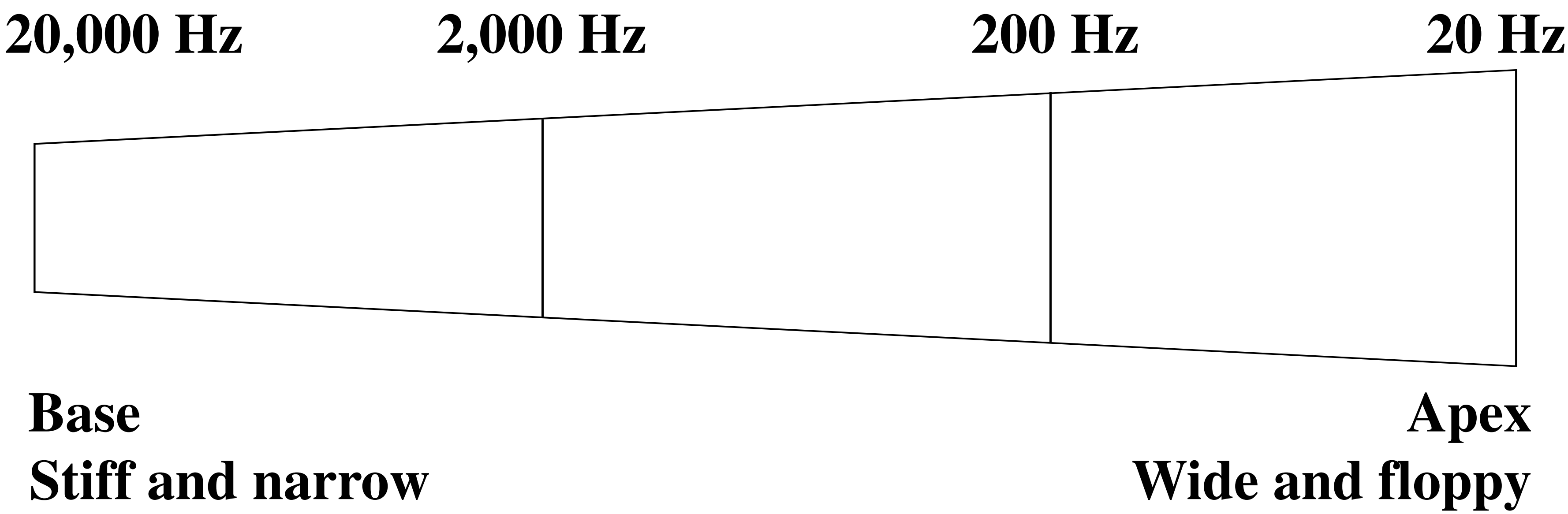
(d) Inner hair cell
Hairs (stereocilia)
Afferent nerve ending
Efferent nerve ending

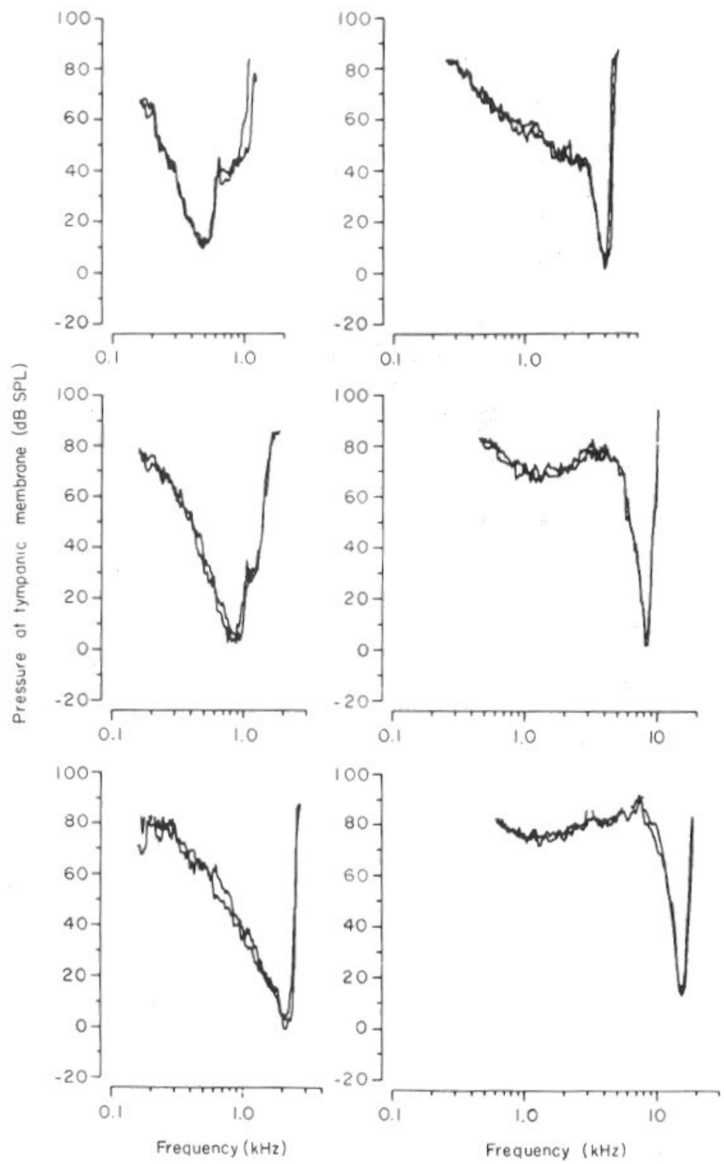
Frequency-to-Place (Tonotopic) Map

- Approximately logarithmic arrangement of frequency along basilar membrane
  - High frequencies near base
  - Low frequencies near apex



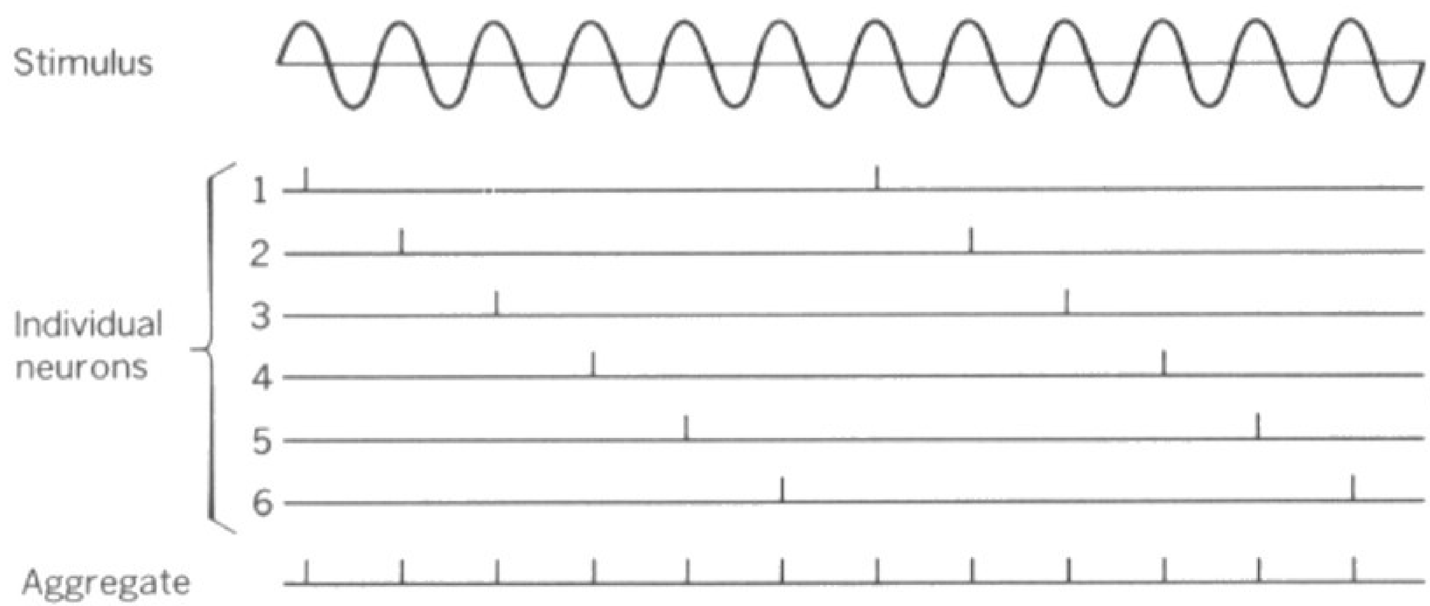
Tuning

- Frequency response is usually plotted as a tuning curve – at how loud does a tone at a specific frequency have to be to excite an auditory nerve fiber
- Auditory nerve fibers are narrowly tuned at high frequencies and broadly tuned at low frequencies
- Tonotopic map in cochlea – high frequenies at base and frequency decreases as go to apex
- Place theory of pitch perception



Volley Theory of Pitch Perception

The number of action potentials every second along with the time interval between action potentials determines the frequency (pitch) of the sound we are listening to.

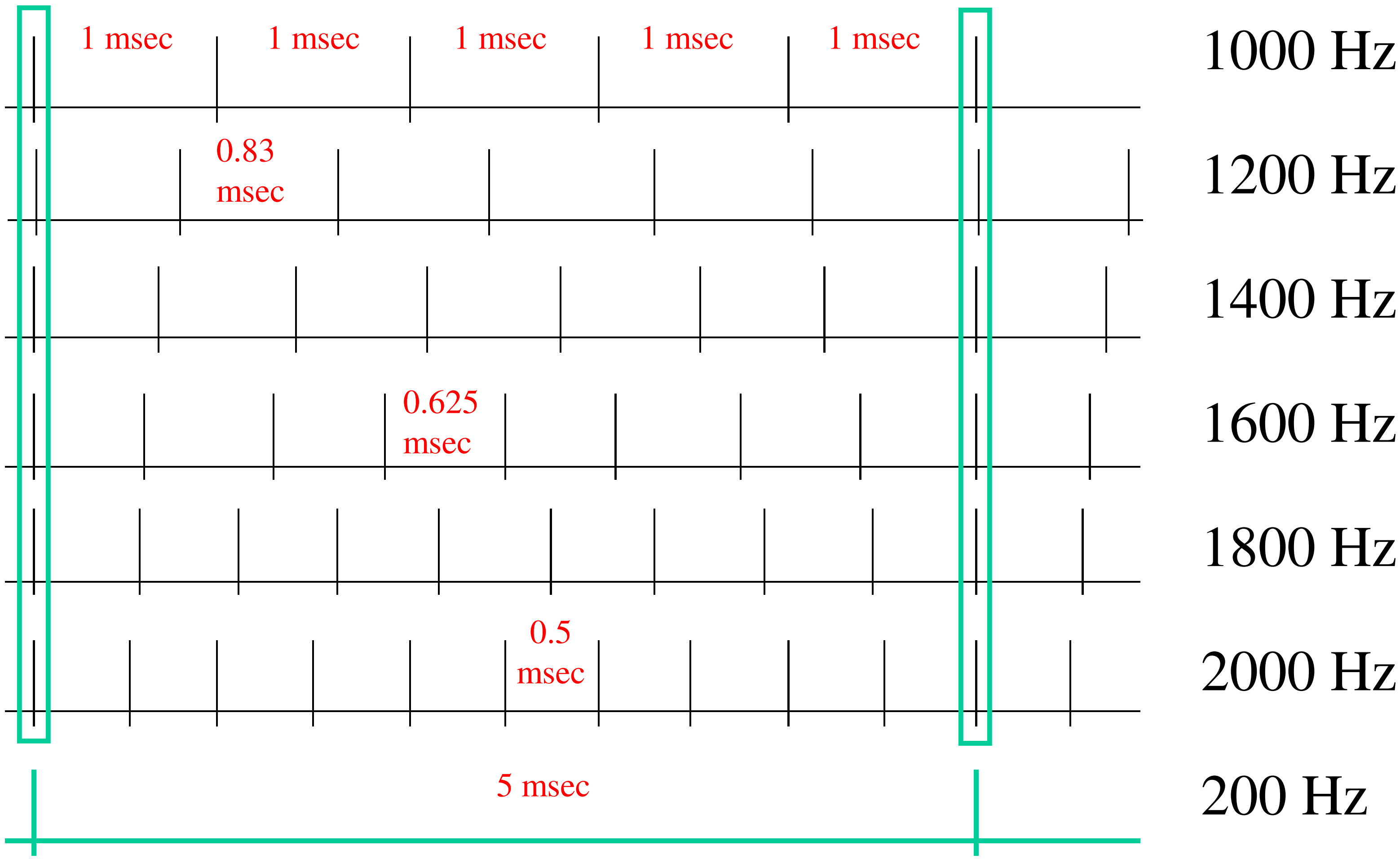


Virtual Pitch

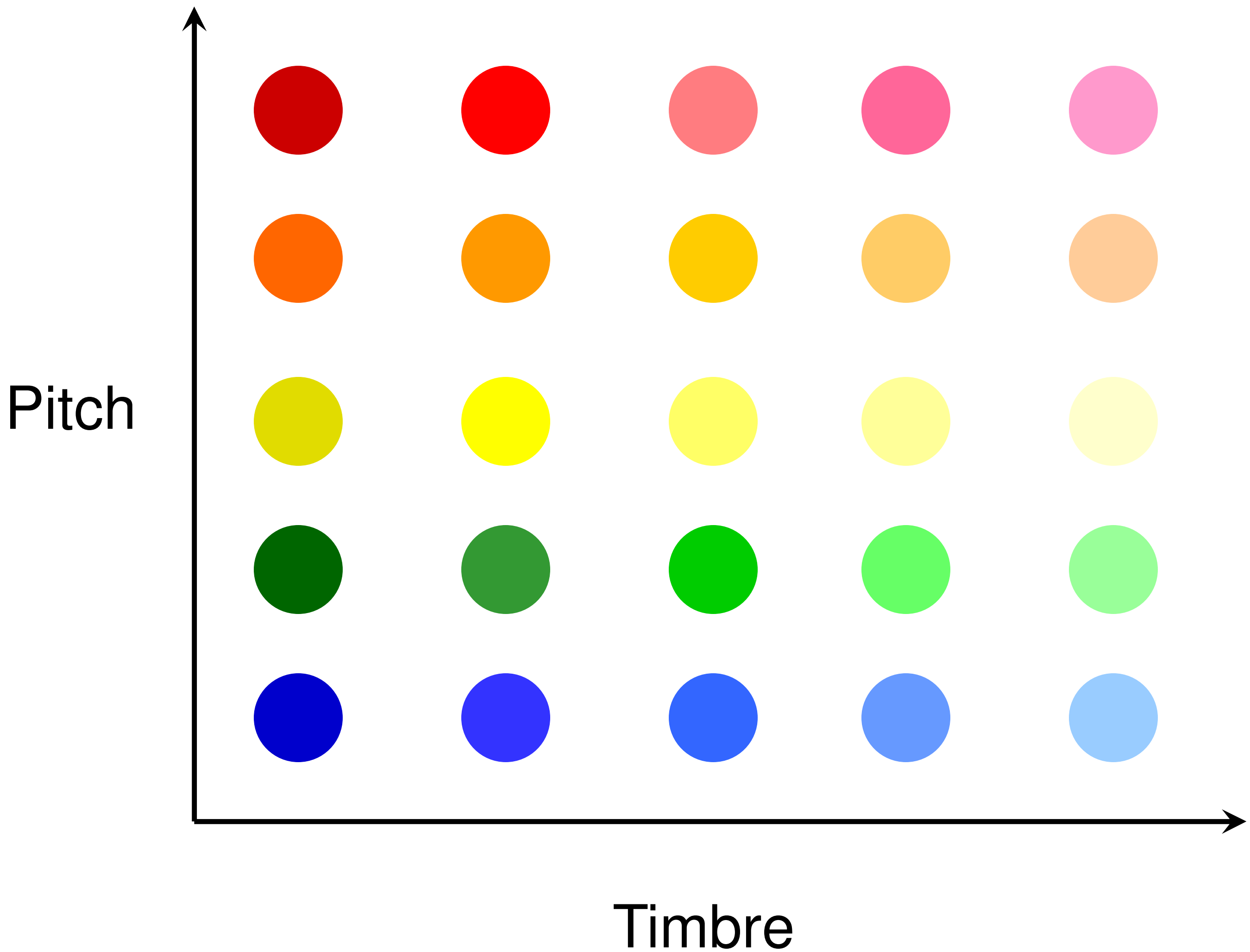
- Pitch of the missing fundamental

1400	1400	1400	1400
1200	1200	1200	1200
1000	1000	1000	1000
800	800	800	800
600	600	600	
400	400		
200			

Pitch of a Complex Sound

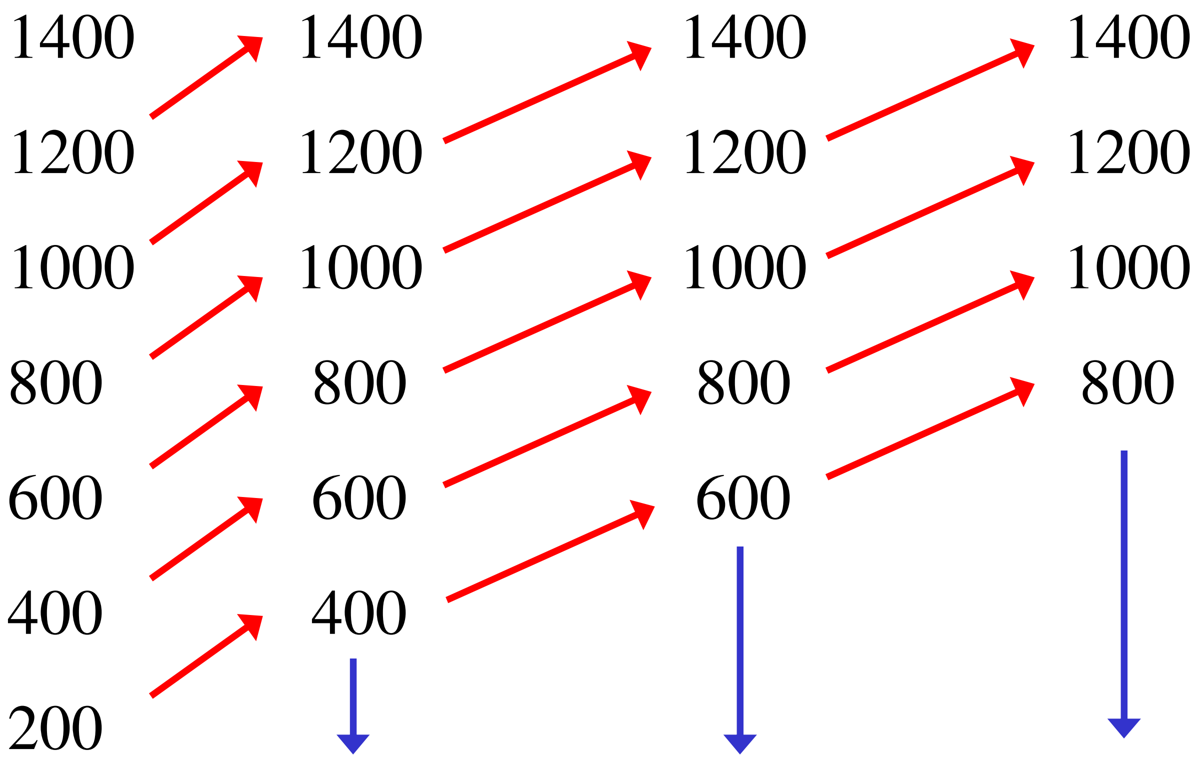


Pitch vs Timbre

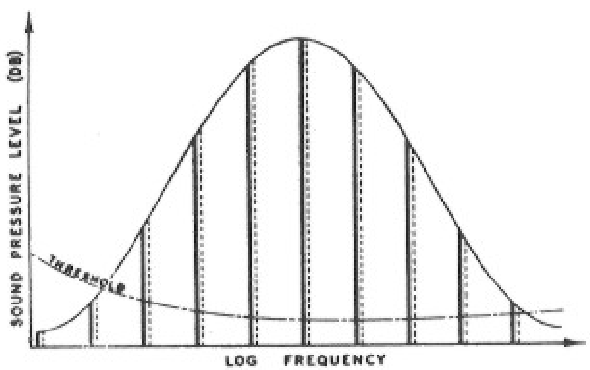


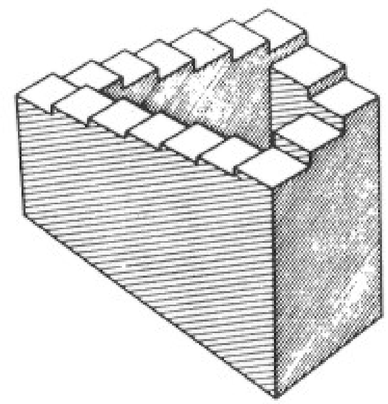
Circular Pitch

- Increase frequency and return to the same pitch



Circular Pitch



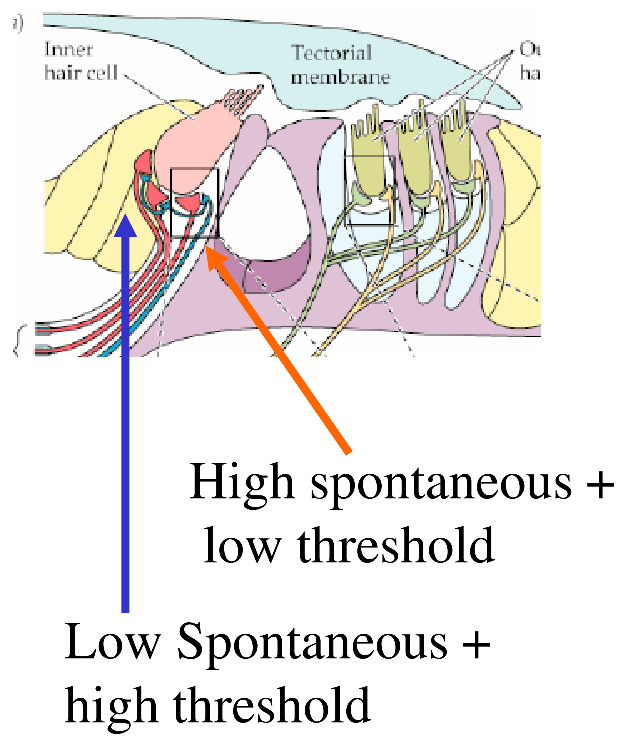


- This demonstration uses a cyclic set of complex tones, each composed of 10 partials separated by octave intervals. The frequencies of the partials are shifted upward in steps corresponding to a musical semitone (~6%).

"Two examples of scales that illustrate circularity in pitch judgements are presented. The first is a discrete scale of Roger N. Sheppard, the second a continuous scale of Jean Claude Risset".

Hair cells and auditory nerve fibers

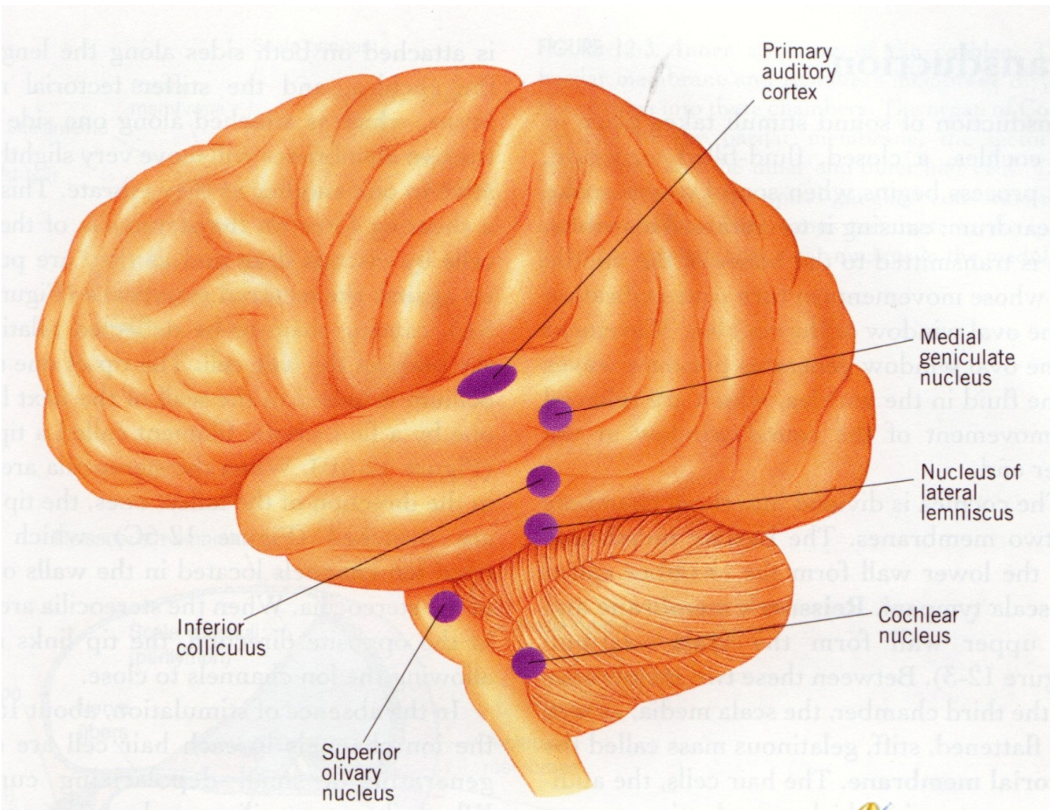
- The thresholds of auditory nerve fibers vary regularly with low threshold fibers on the pillar side of the inner hair cell and high threshold fibers on the modiolar side.
- The low threshold fibers have high spontaneous activity rates, while the high threshold fibers have low spontaneous activity rates.

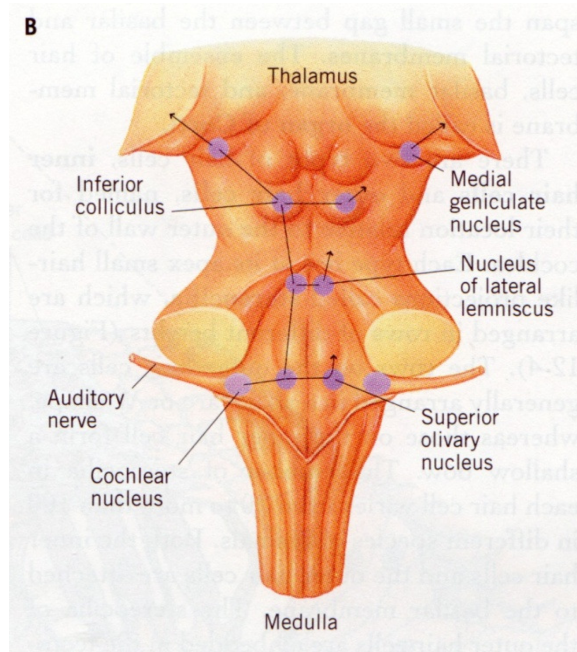


Inferences about auditory nerve fibers

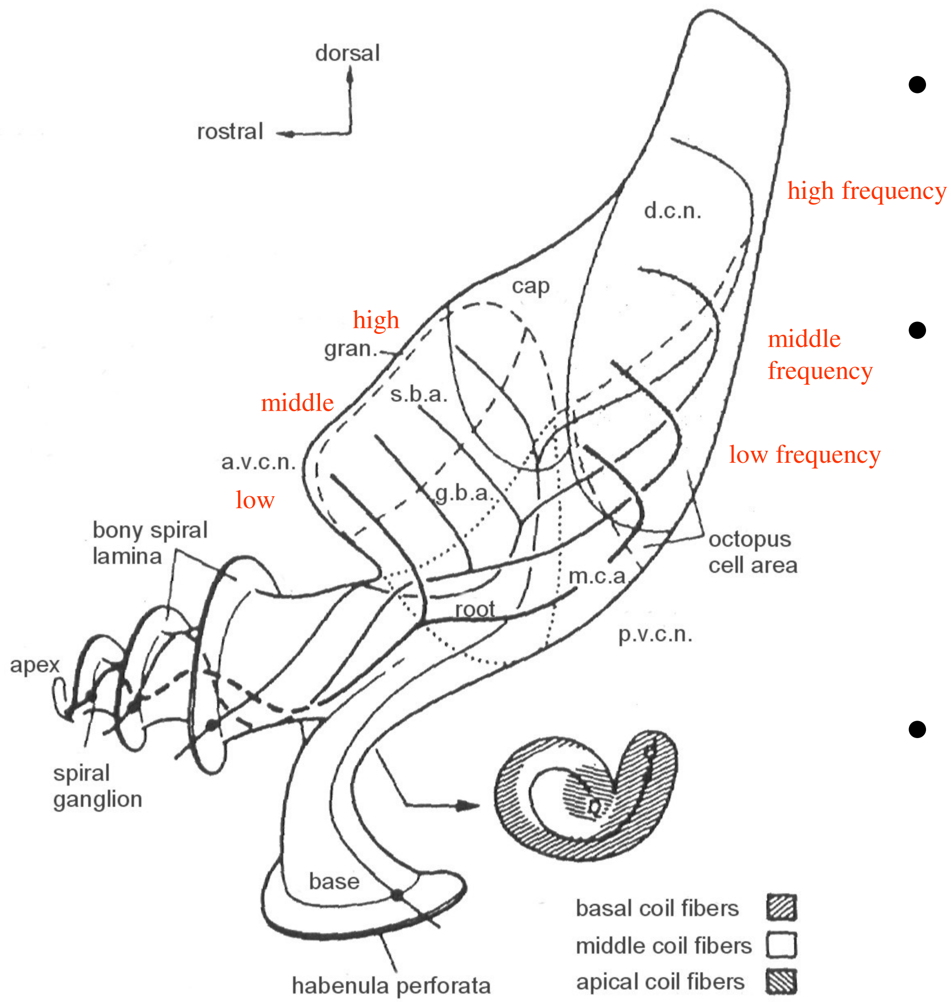
- Tuning: an auditory nerve fiber responds to a limited frequency range with fibers from the base tuned to high frequencies and fibers from the apex tuned to low frequencies (place theory of pitch perception).
- Timing: auditory nerve fibers preserve temporal information at low frequencies (<4000 Hz) for pitch perception (volley theory) and for sound localization.
- Threshold: auditory nerve fibers have different thresholds so that we can hear over a large intensity range while preserving timing information

Auditory Pathway to Cortex



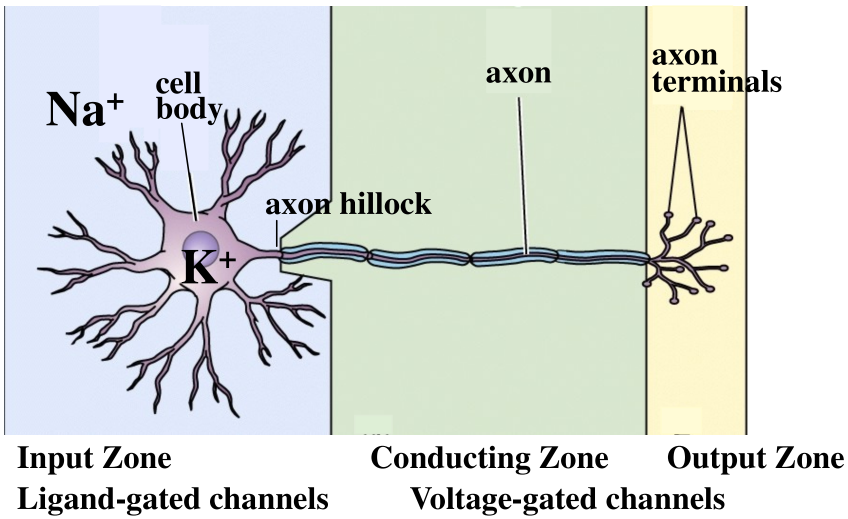


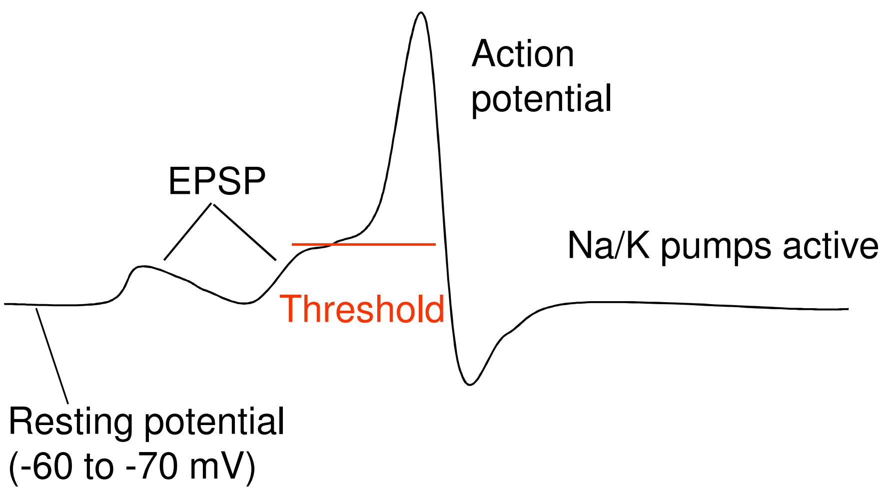
Parts of the cochlear nucleus



- The cochlear nucleus is divided into dorsal (DCN) and ventral (VCN) parts
- The ventral cochlear nucleus is divided by the auditory nerve into anterior (AVCN) and posterior (PVCN) divisions.
- There is a tonotopic map in each subdivision.

Neuron Signaling



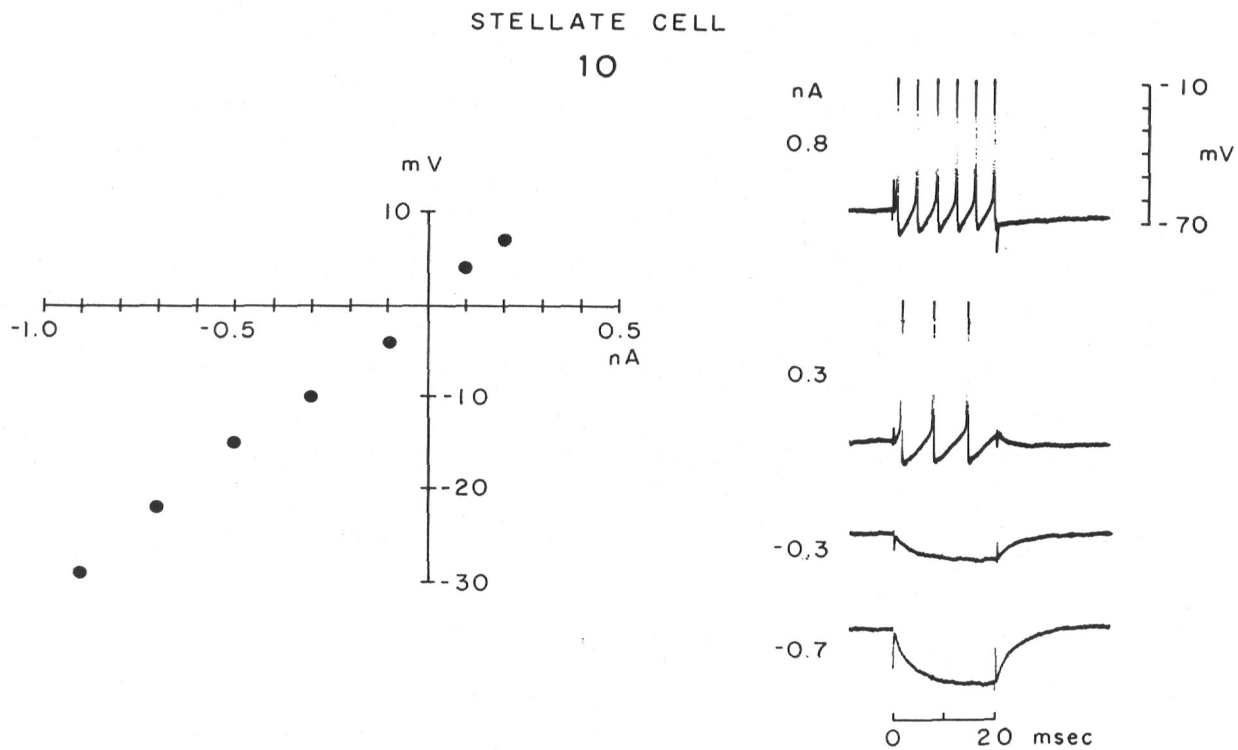


- Action Potential
- Release small packet of neurotransmitter to cause excite or inhibit next neuron
- Excitatory Postsynaptic Potential (EPSP)
- Inhibitory Postsynaptic Potential (IPSP)
- First must transduce physical signal

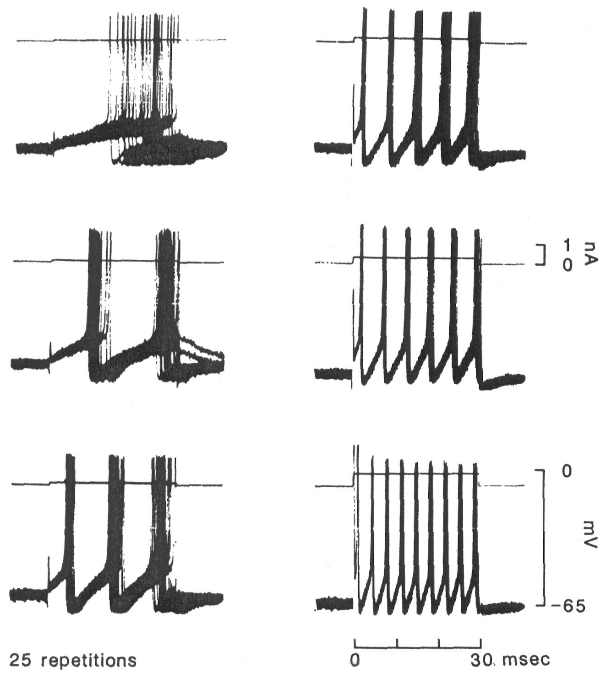
Stellate Cells

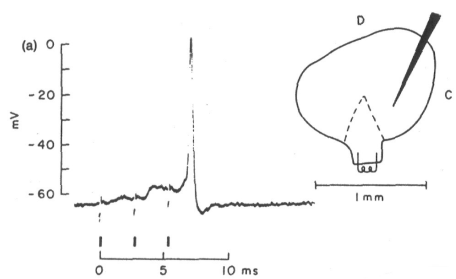
- Stellate cells have dendrites that run parallel to the path of auditory nerve fibers
- Each stellate cell receives many inputs from only a few nerve fibers
- A stellate cell responds only to a narrow band of frequencies

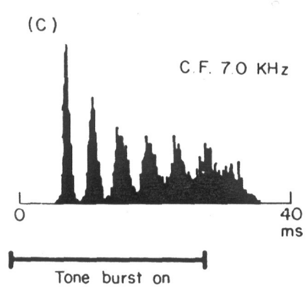
Stellate cells are linear



- Stellate cells respond linearly to depolarizations and hyperpolarizations.
- In response to depolarizing current, they produce a train of action potentials.



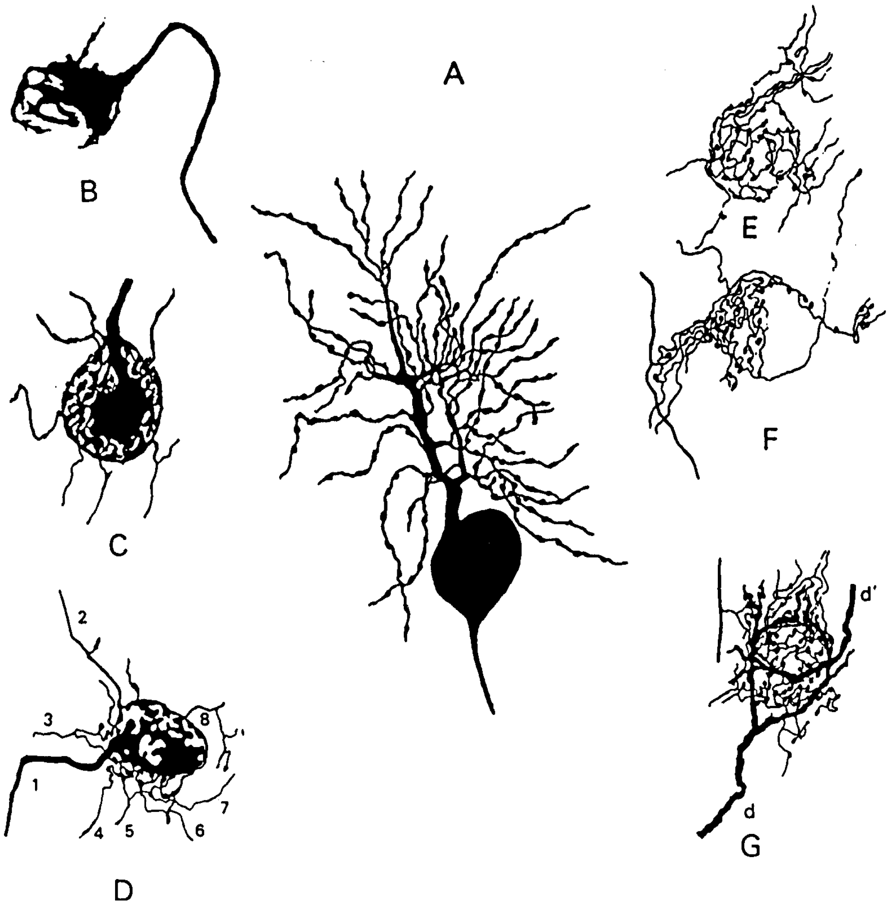




Stellate cells fire regularly in response to tones

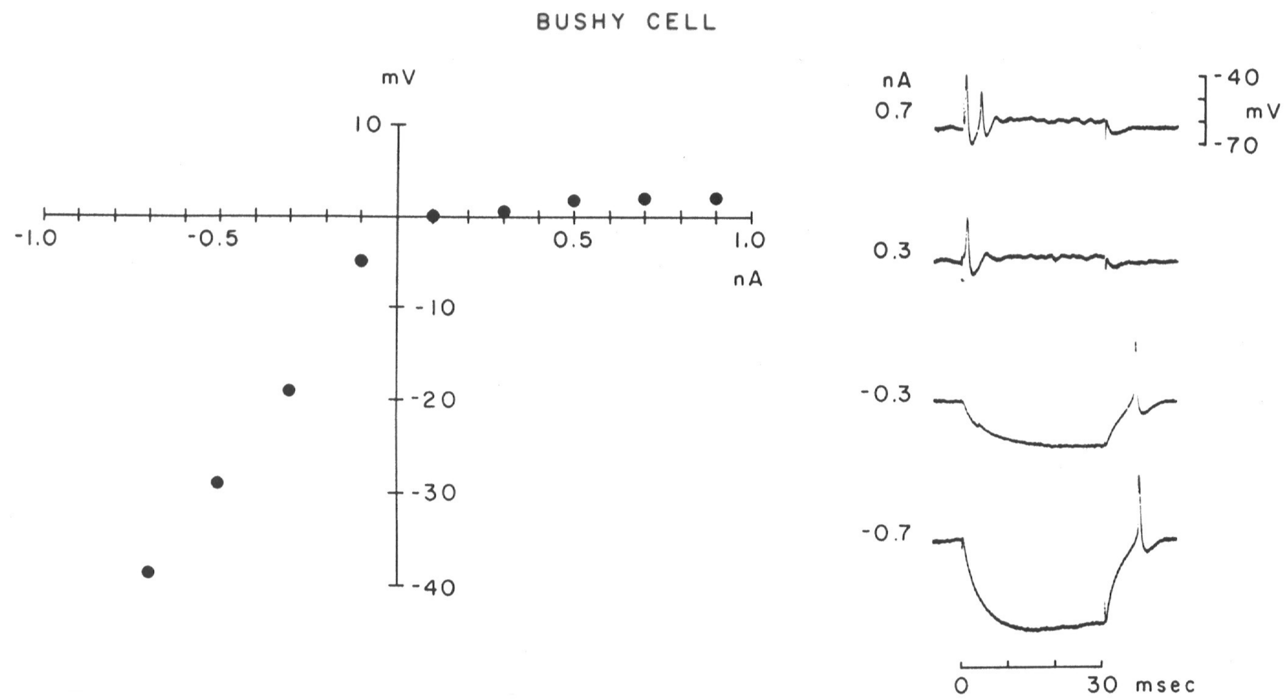
- The train of action potentials is very regular.
- Stellate cells integrate information temporally (sum EPSPs) but not over a wide frequency range.
- Stellate cells respond to tones with a “chopper” PST that reflects their regular firing pattern.

Bushy Cells



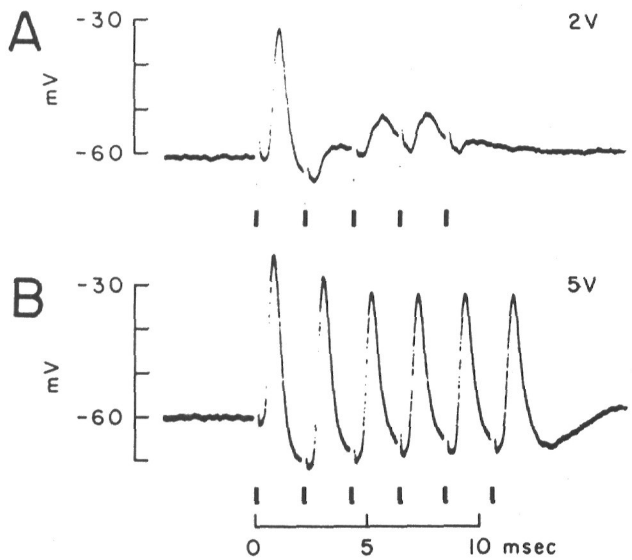
- Spherical bushy cells (A) in anterior AVCN receive endbulbs of Held from only a couple of auditory nerve fibers (B,C,D).
- Globular bushy cells in posterior AVCN receive multiple inputs from just a few auditory nerve fibers (E,F,G).
- Each bushy cell responds only to a narrow band of frequencies

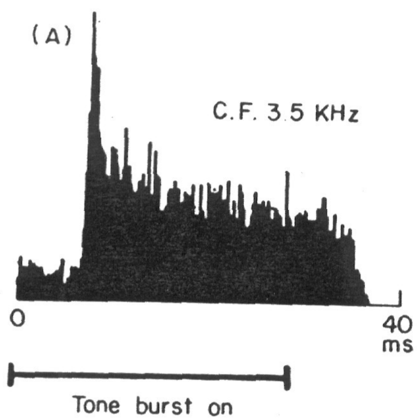
Bushy cells are nonlinear



- Bushy cells are hard to depolarize. For long depolarizations they produce one or two action potentials.
- Bushy cells are linear when hyperpolarized.

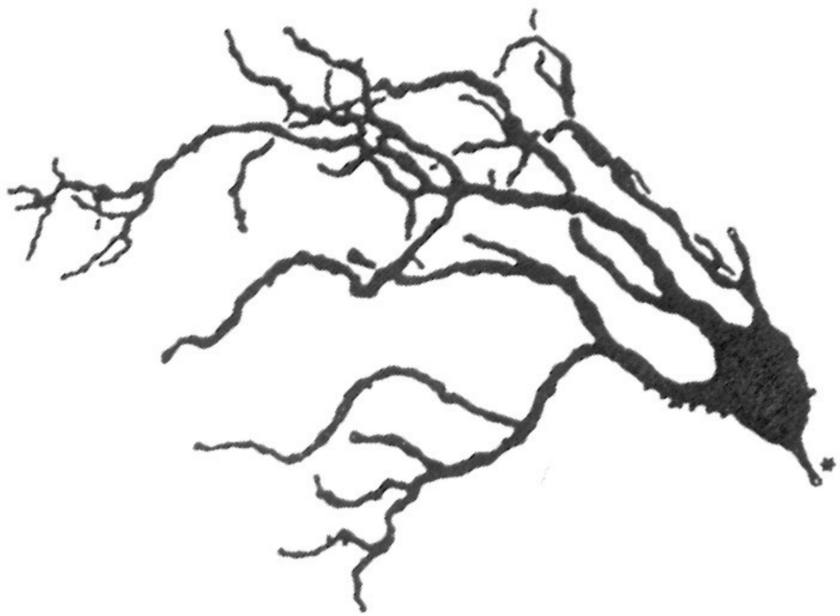
Bushy cells preserve temporal information





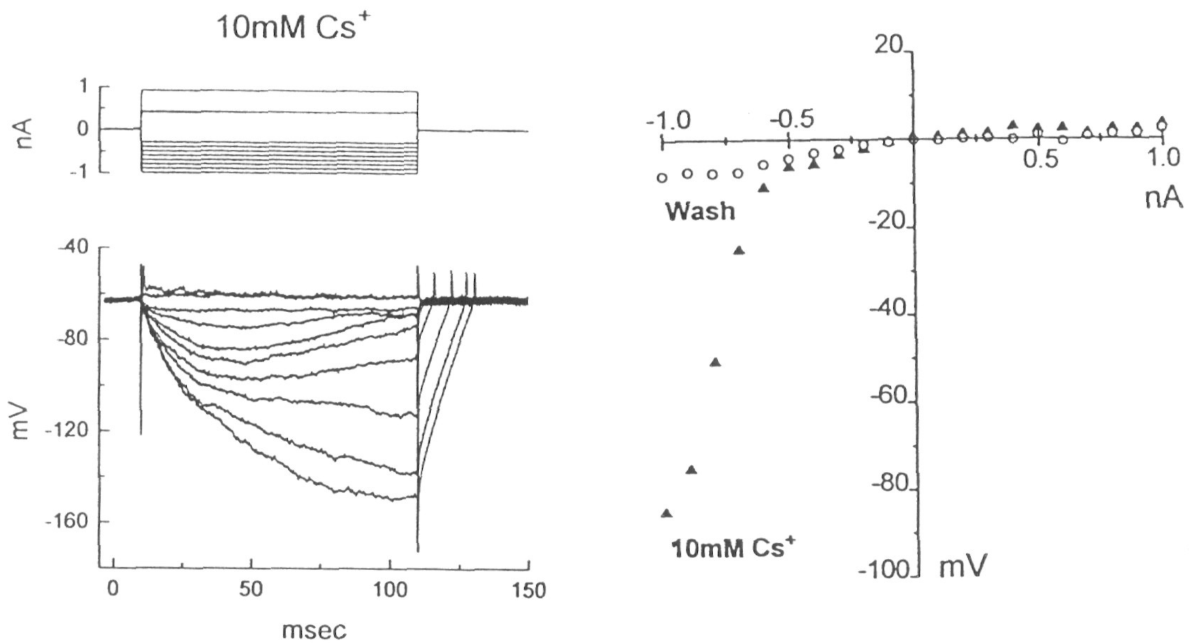
- They do not integrate over time. Each auditory nerve input (at |) produces an EPSP, A&B, but there is no summation.
- Bushy cells preserve the temporal characteristics of the auditory nerve input. Their peristimulus time (PST) histograms look like those of auditory nerve fibers, and are called Primary-like.
- Temporal information needed for sound localization.

Octopus Cells in PVCN

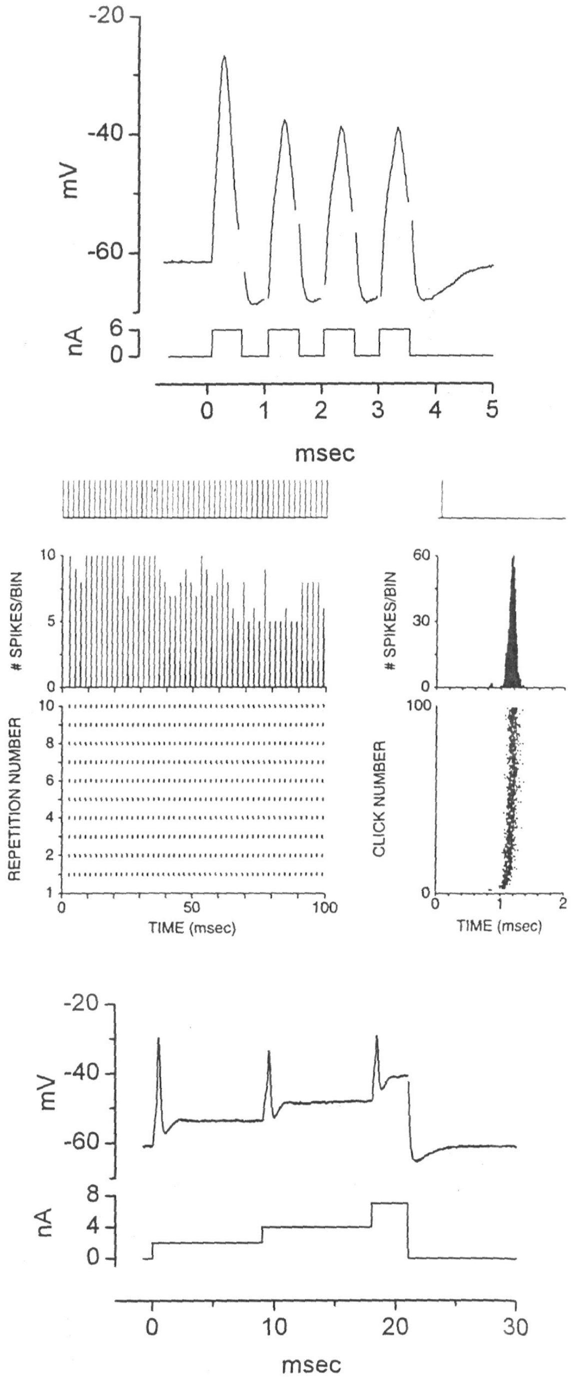


- Octopus cells have two or three large dendrites that extend perpendicularly across the paths of many auditory nerve fibers.
- Octopus cells are ideally situated to integrate information across frequency.

Octopus cells are nonlinear



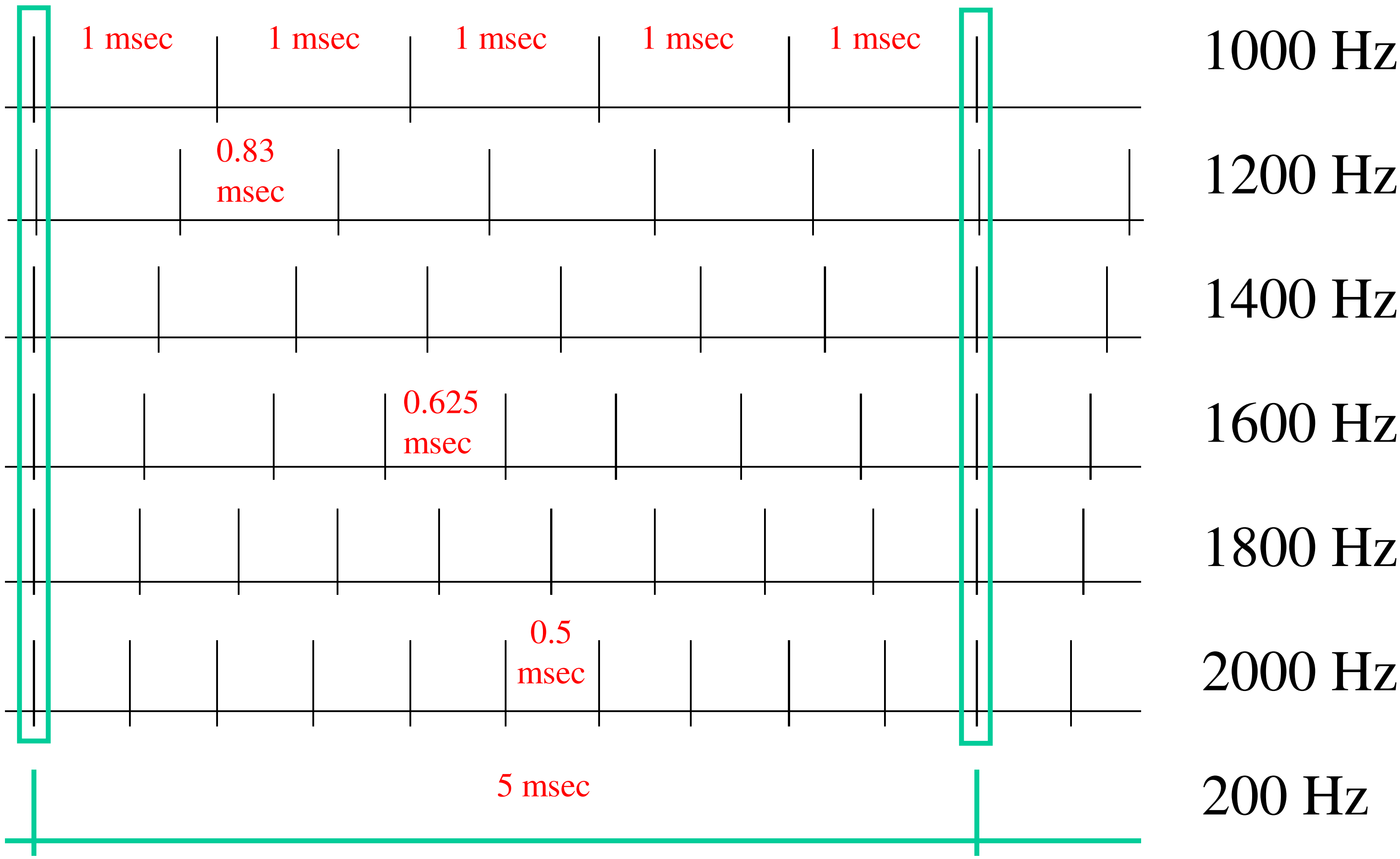
- Like bushy cells octopus cells are hard to depolarize and produce only a single action potential.
- Octopus cells are also hard to hyperpolarize



Octopus cells detect synchrony

- Octopus cells respond to a tone with an "onset" PST histogram
- Octopus cells are capable of firing very rapidly (1000 action potentials/second)
- Octopus cells are activated by synchronous activity of many auditory nerve fibers generated by such stimuli as clicks.

Pitch of a Complex Sound



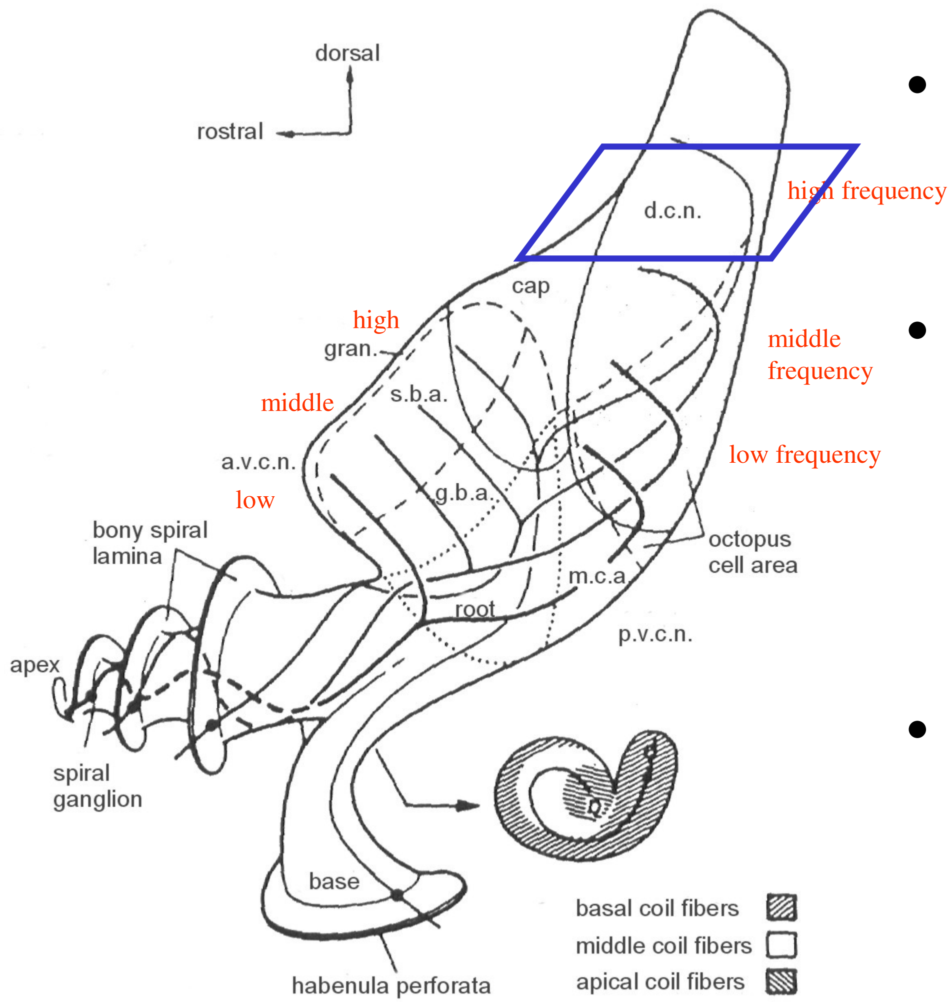
Multipolar Cells

- Multipolar cells have dendrites that extend across a large number of auditory nerve fibers.
- Multipolar cells project to the DCN, the AVCN and to the cochlear nucleus on the other side of the brainstem.

Characteristics of Ventral Cochlear Nucleus Neurons

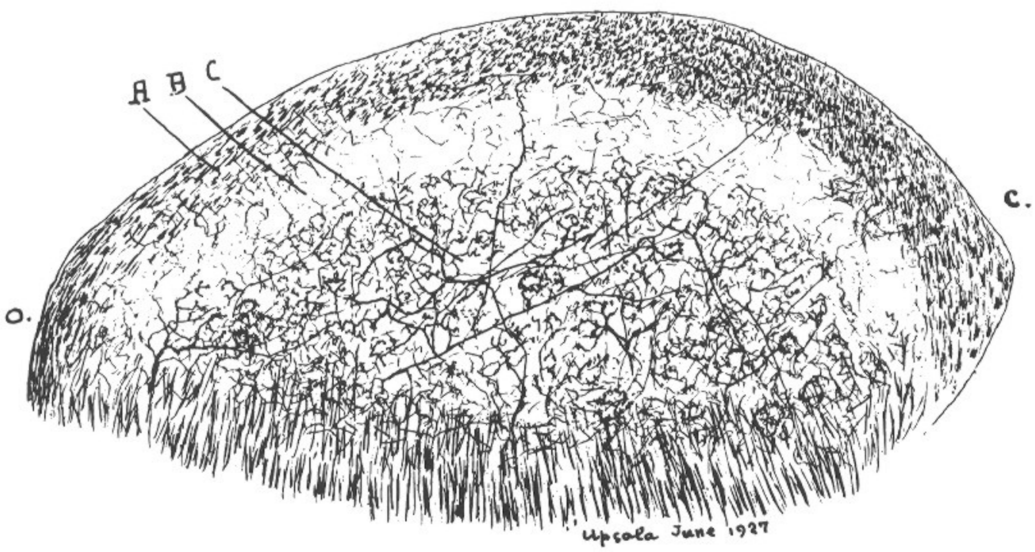
	Spherical Bushy cells	Globular Bushy cells	Stellate cells	Multipolar cells	Octopus cells
Tuning	Narrow	Narrow	Narrow	Broad	Broad
Intrinsic Membrane Properties	Nonlinear	Nonlinear	Linear	Linear	Nonlinear
PST Histogram	Primary-like	Primary-like with notch	Chopper	Onset - Chopper	Onset
Function	Preserve timing information	Preserve timing information	Loudness - integrate in critical band	Loudness – overall (AGC?)	Synchrony – integrate across freq.
Project to - send info	Superior Olivary Complex	Superior Olivary Complex *	Inferior Colliculus	Cochlear nucleus on other side	Lateral Lemniscus

Parts of the cochlear nucleus



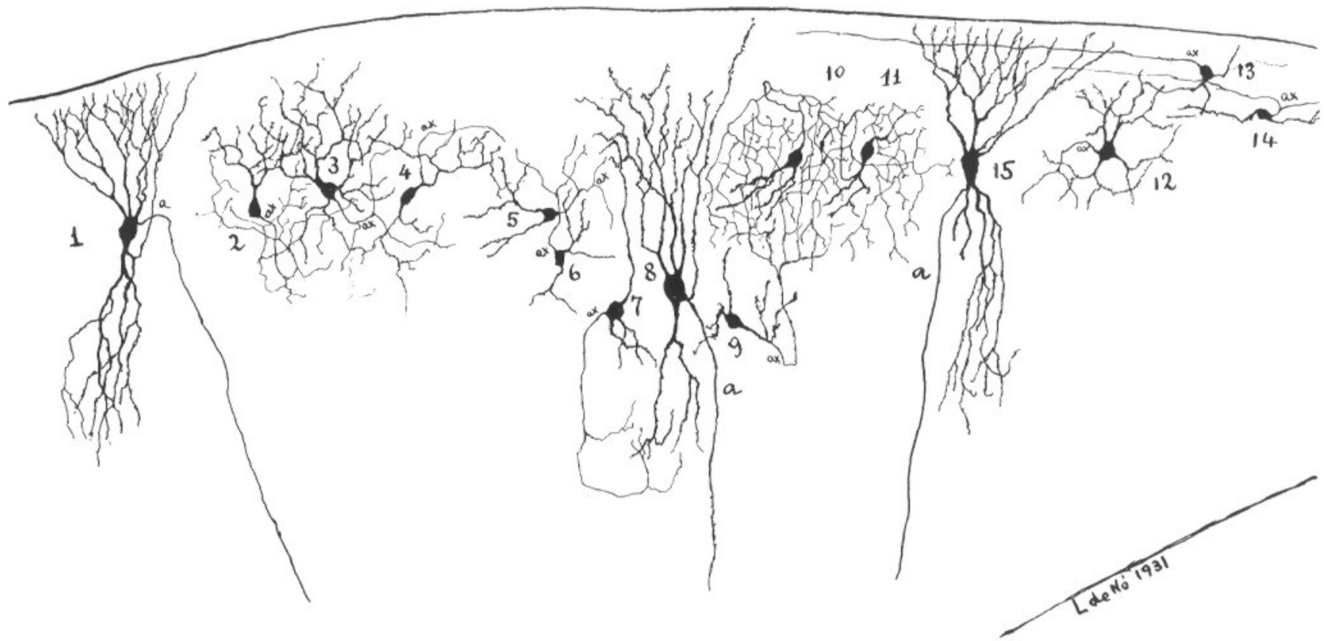
- The cochlear nucleus is divided into dorsal (DCN) and ventral (VCN) parts
- The ventral cochlear nucleus is divided by the auditory nerve into anterior (AVCN) and posterior (PVCN) divisions.
- There is a tonotopic map in each subdivision.

Dorsal Cochlear Nucleus



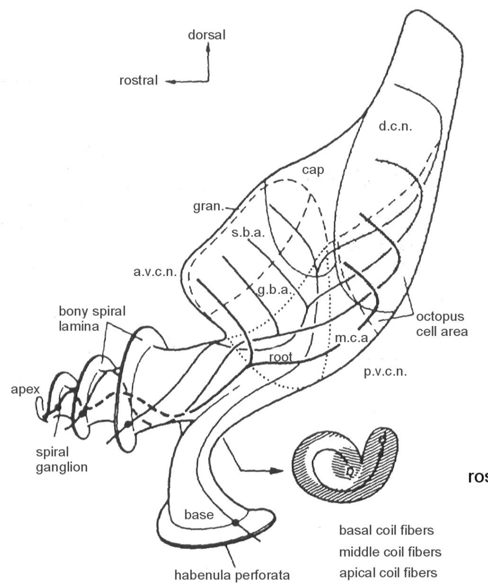
- The dorsal cochlear nucleus is a layered structure.
- Outer layer is the molecular layer and contains axons of granule cells
- Large fusiform cell layer
- Deep DCN – contains auditory nerve axons and neurons

Molecular and Fusiform cell layers

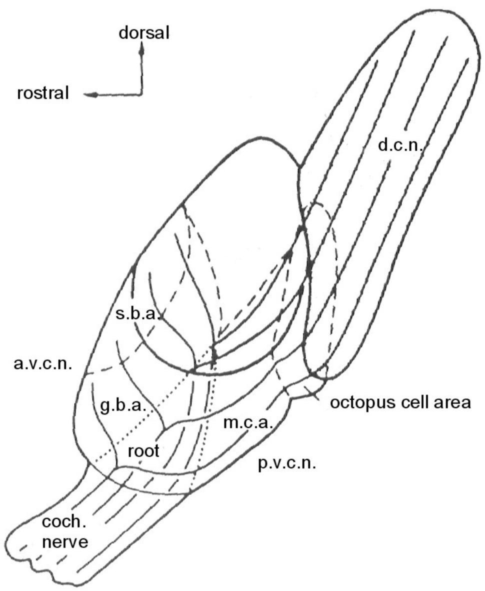


- Fusiform cells have two sets of dendrites – one set extends into the molecular layer perpendicular to the paths of granule cell axons, and the other set extends into the deep DCN to make contact with the axons of auditory nerve fibers.
- Structure is similar to the cerebellum

Role of cells in fusiform and molecular layers



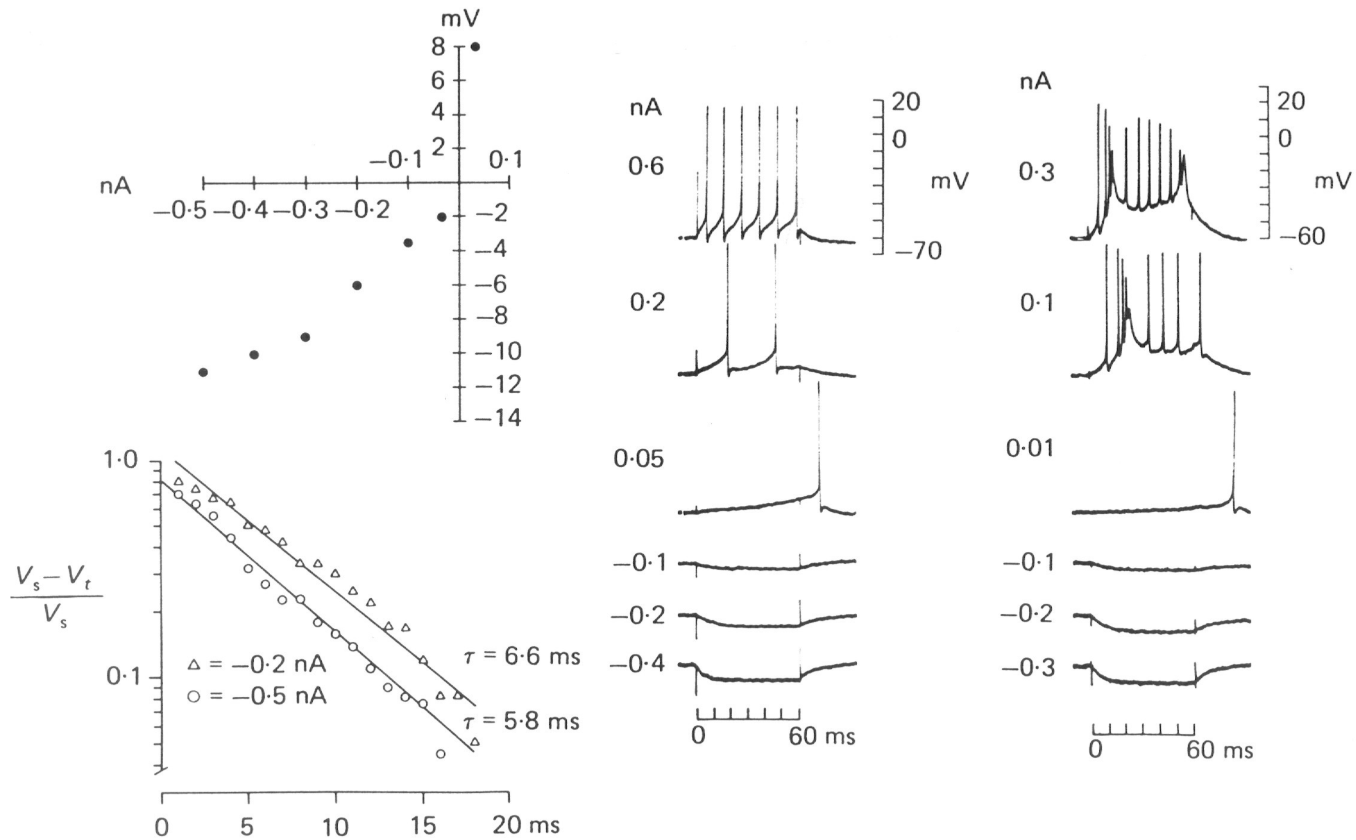
cat



human

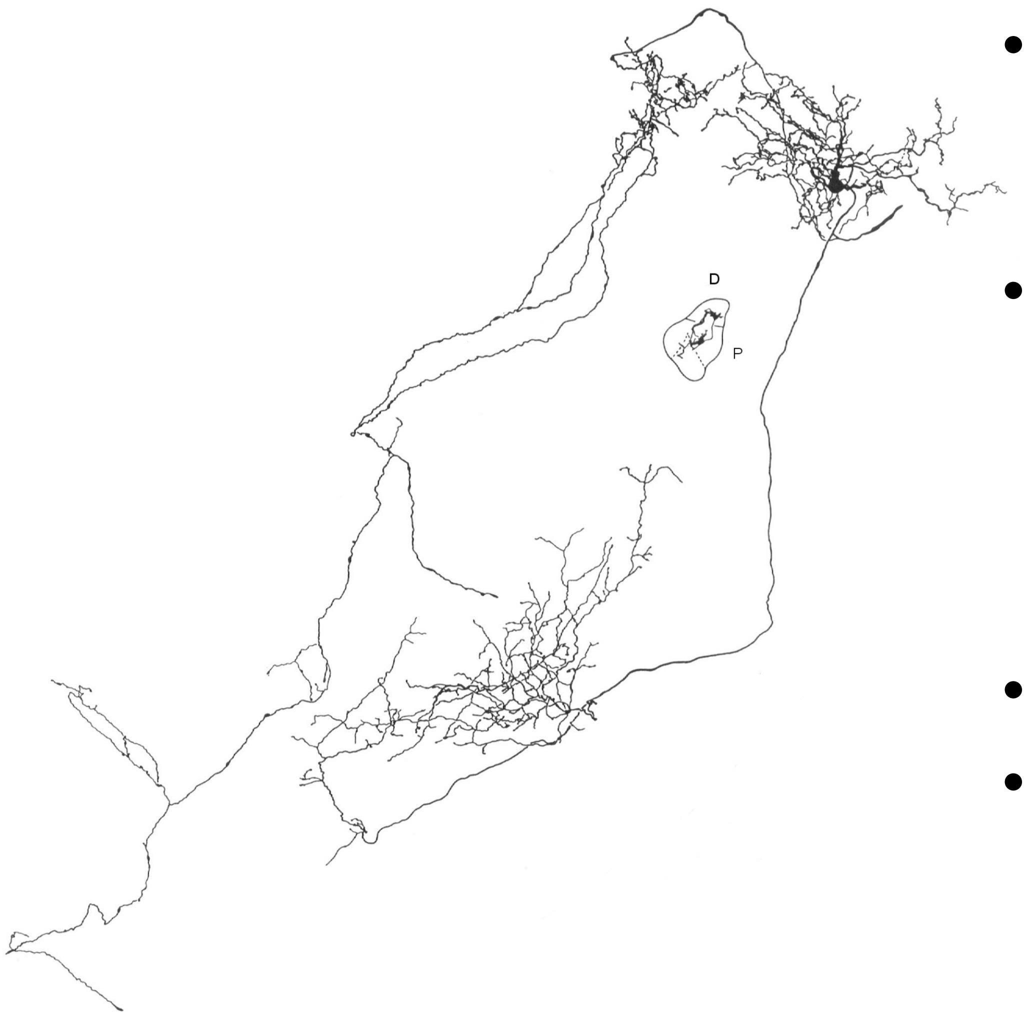
- Layers only found in animals that can move their ears
- Humans lack these layers
- Granule cells receive inputs from somatosensory nuclei in the brainstem
- Perpendicular arrangement of granule cell axon and fusiform cell dendrites cross-correlates ear position with auditory input

Fusiform cells are nonlinear



- Fusiform cells have complex, nonlinear characteristics similar to Purkinje cell in the cerebellum

Tuberculoventral neurons



- Tuberculoventral neurons in the deep layer of the DCN project to the VCN
- They inhibit cells that receive inputs from the same auditory nerve fibers that innervate them – it is a frequency-specific inhibition
- The inhibition is delayed
- A delayed, frequency-specific inhibition can suppress echoes

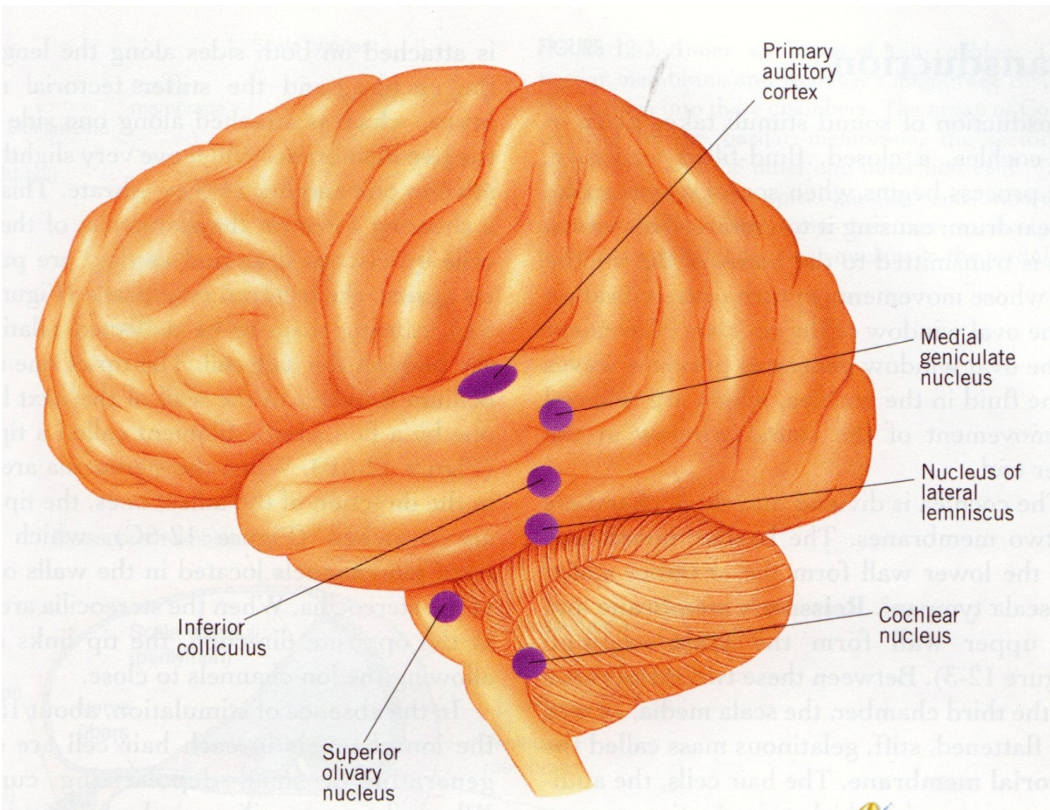
Characteristics of Dorsal Cochlear Nucleus Neurons

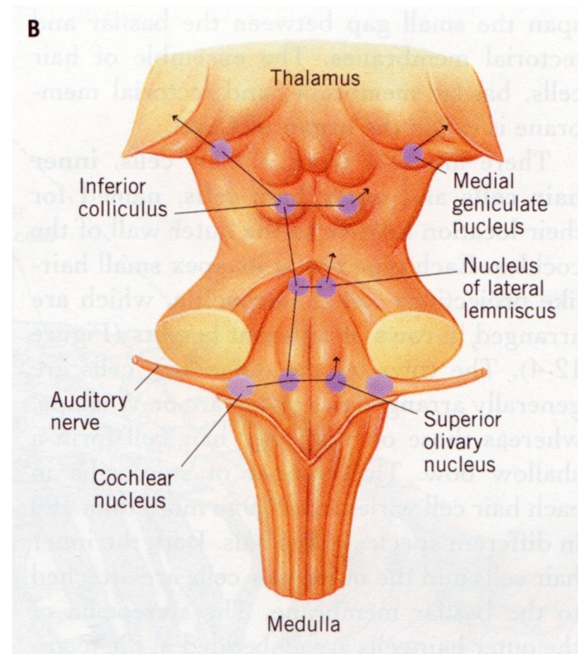
	Fusiform cells	Granule cells	Tuberculoventral neurons
Tuning	Narrow/broad sidebands	?	Narrow
Intrinsic Membrane Properties	Nonlinear	?	Nonlinear
PST Histogram	Pauser - Buildup		Many different shapes
Function	Compensate for motion of pinna	Convey info about position of pinna	Suppress echoes
Project to - send info	Inferior Colliculus	Molecular layer of DCN	Ventral cochlear nucleus

Role of the cochlear nucleus

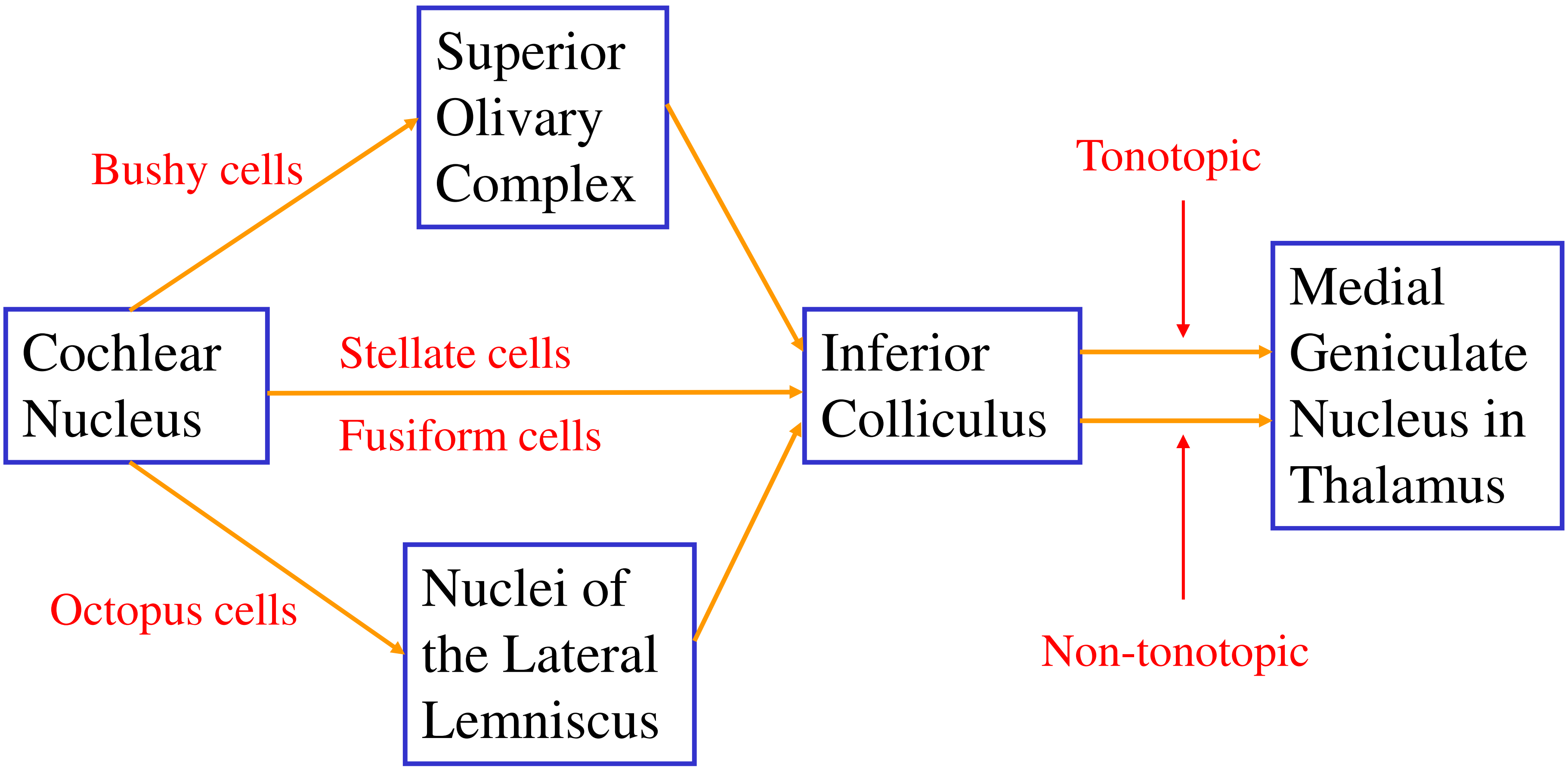
- Spread information from an auditory nerve fiber onto multiple parallel ascending pathways
- Extract specific features of the stimulus
  - Intensity in a critical band
  - Overall intensity
  - Synchrony across frequency
- Process information to make subsequent analysis possible
  - Echo suppression
- Compensate for position of external ear (if necessary)

Auditory Pathway to Cortex

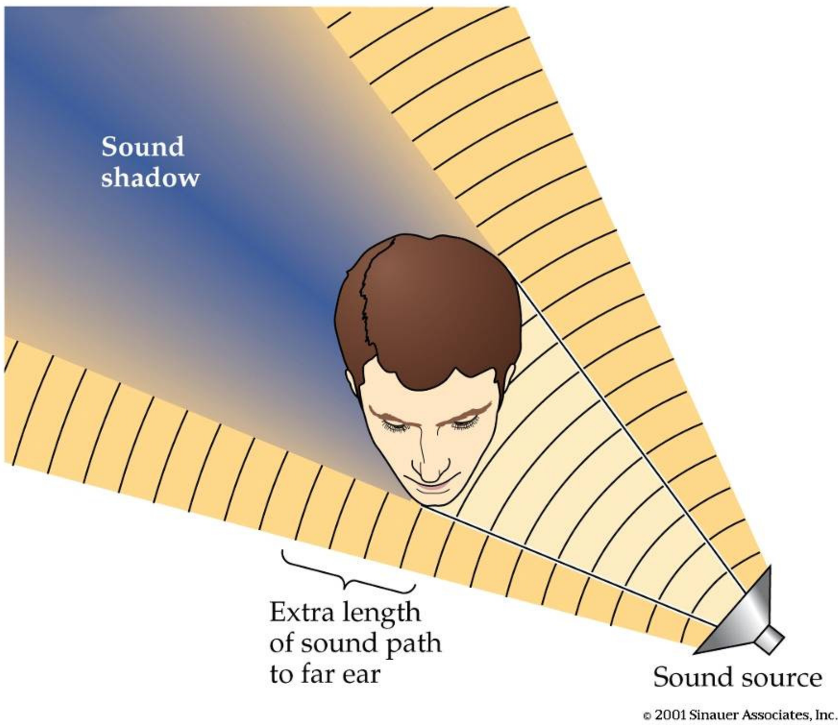




Projections from the cochlear nucleus

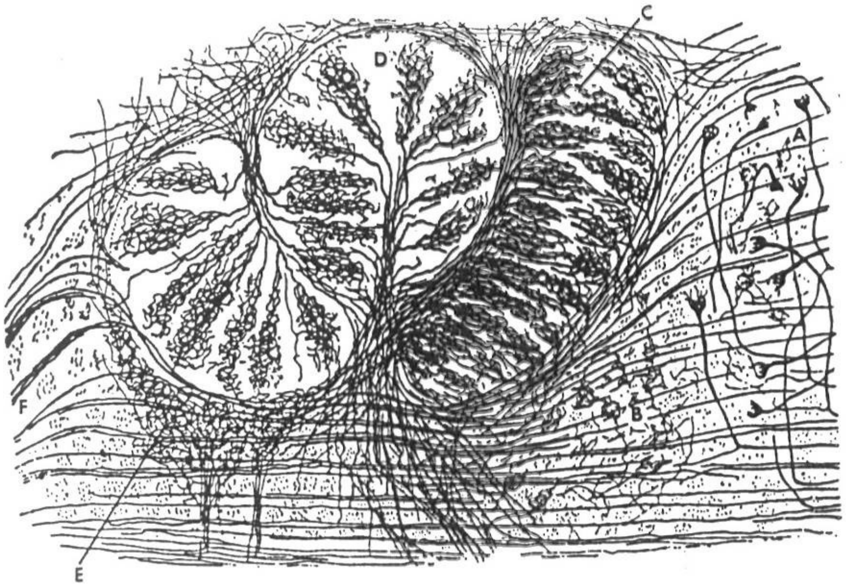


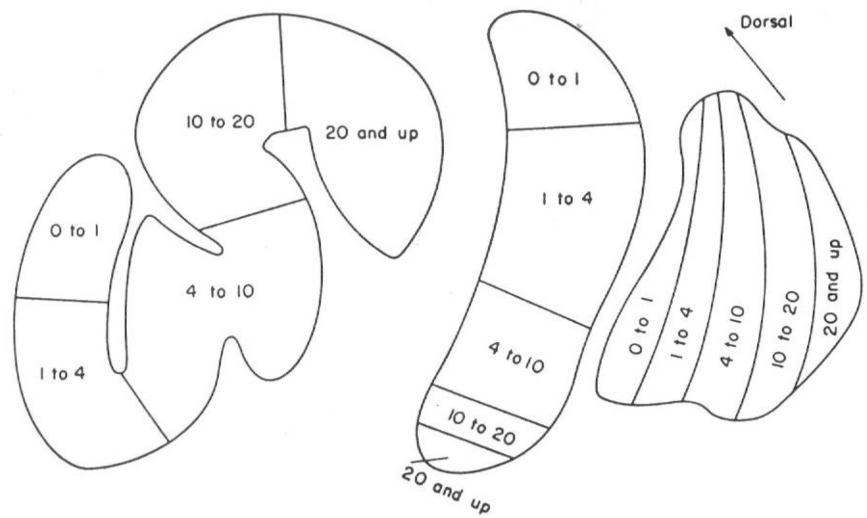
Sound Localization in Superior Olive

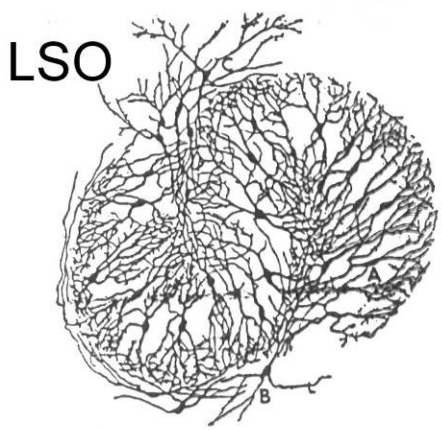


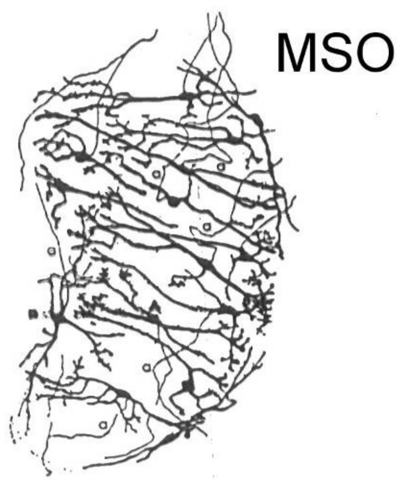
- Location of a sound must be computed by auditory system
- Two cues
  - Difference in the arrival time of the sound at each ear
  - Intensity difference between the two ears caused by the head
- Medial superior olive computes time difference
- Lateral superior olive computes intensity difference

Structure of the LSO and MSO



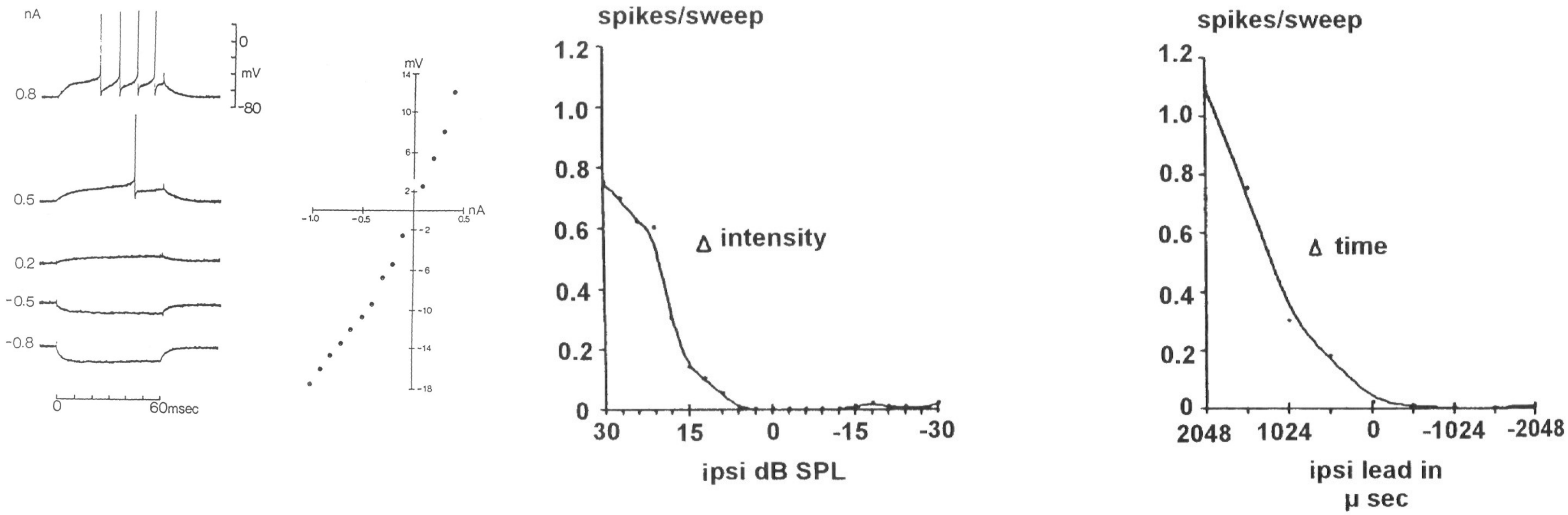






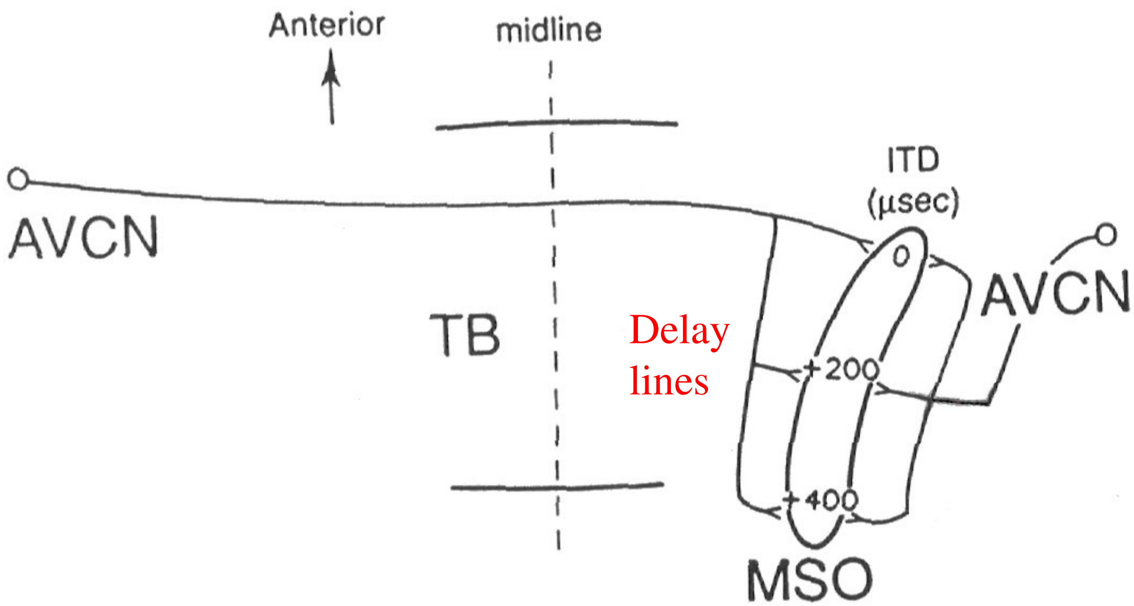
- LSO neurons respond to intensity differences between the ears
- MSO neurons respond to the timing differences between the ears

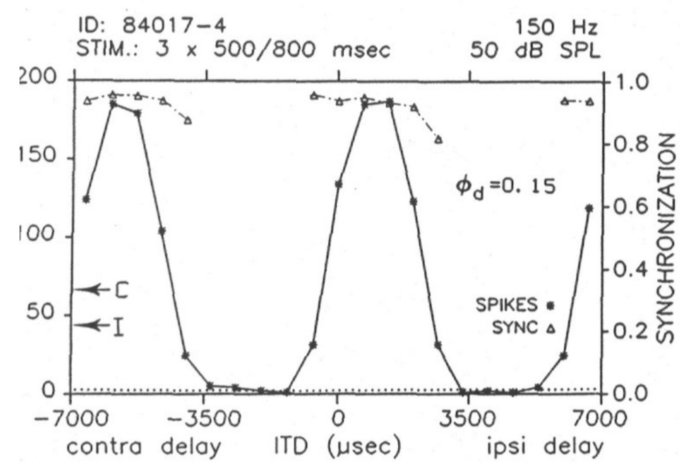
LSO processes intensity differences



- LSO neurons respond mostly to high frequencies
- Excited by sound at the ipsilateral ear (from spherical bushy cells)
- Inhibited by sound at the contralateral ear (from globular bushy cells via MNTB)

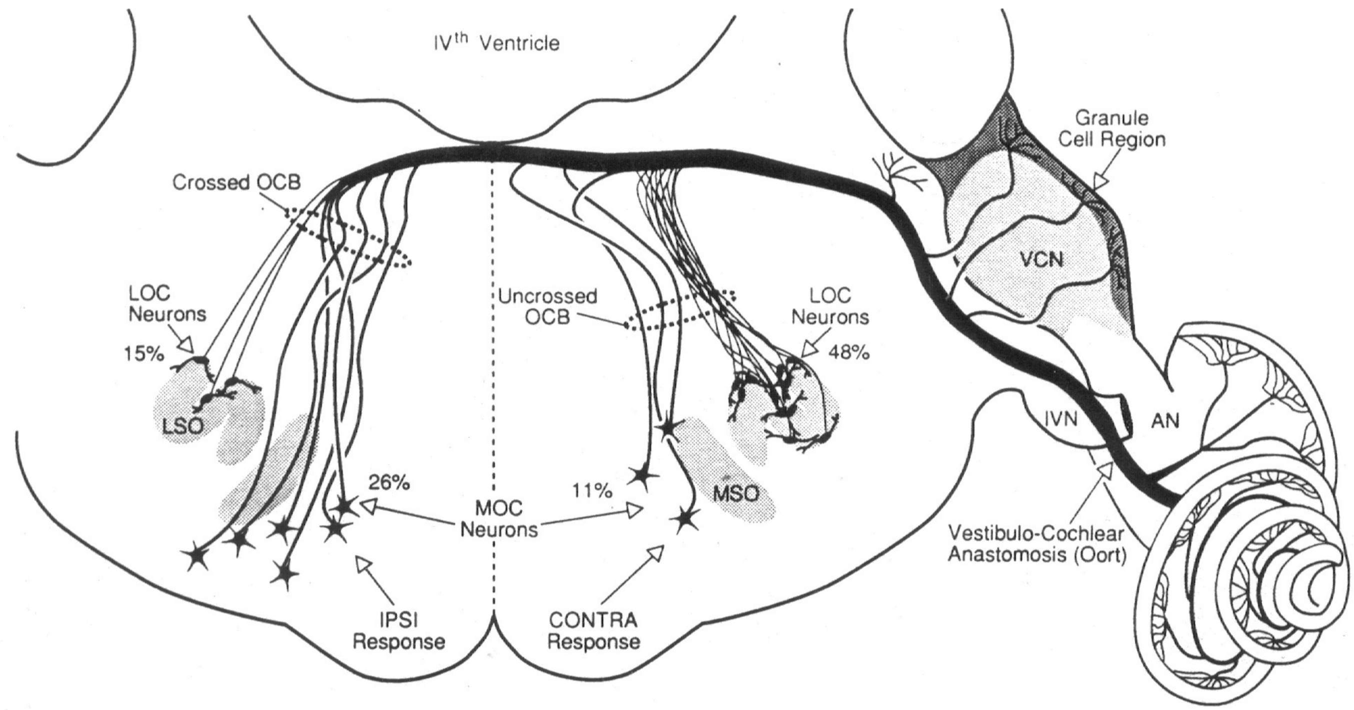
MSO processes timing differences





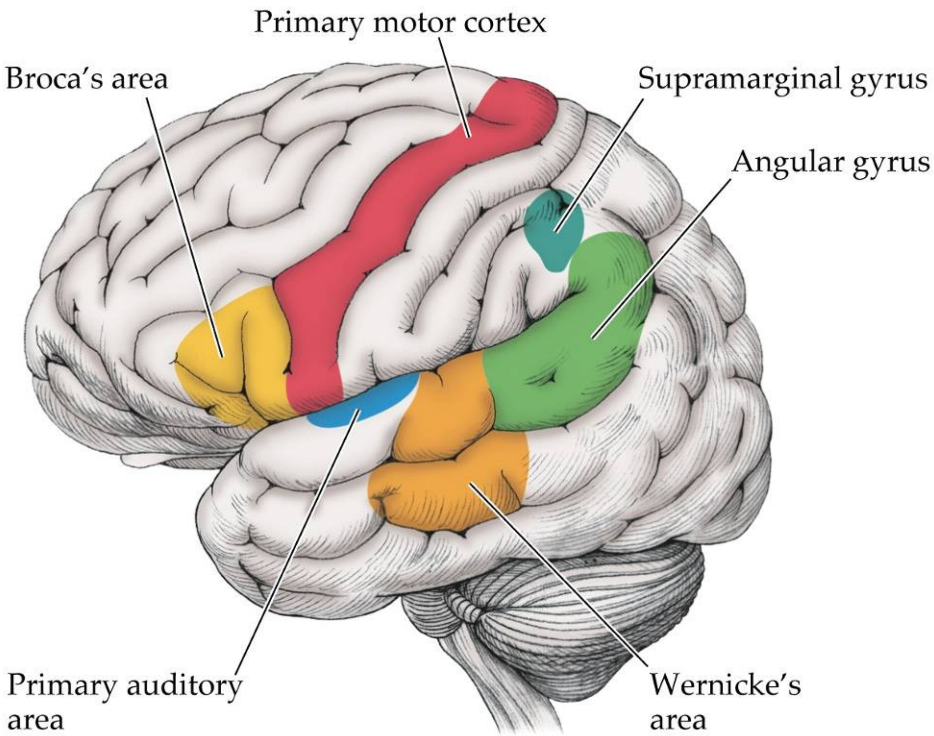
- MSO responds mostly to low frequency sounds
- Cells in the MSO are coincidence detectors
- Input from the opposite side is delayed
- MSO cells respond at specific interaural time difference (ITD)
- Center to ear encoded from front to back in MSO

Descending pathway (efferents)

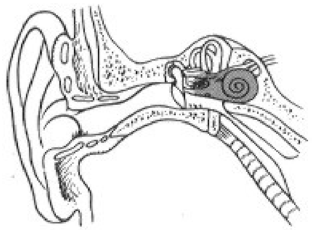


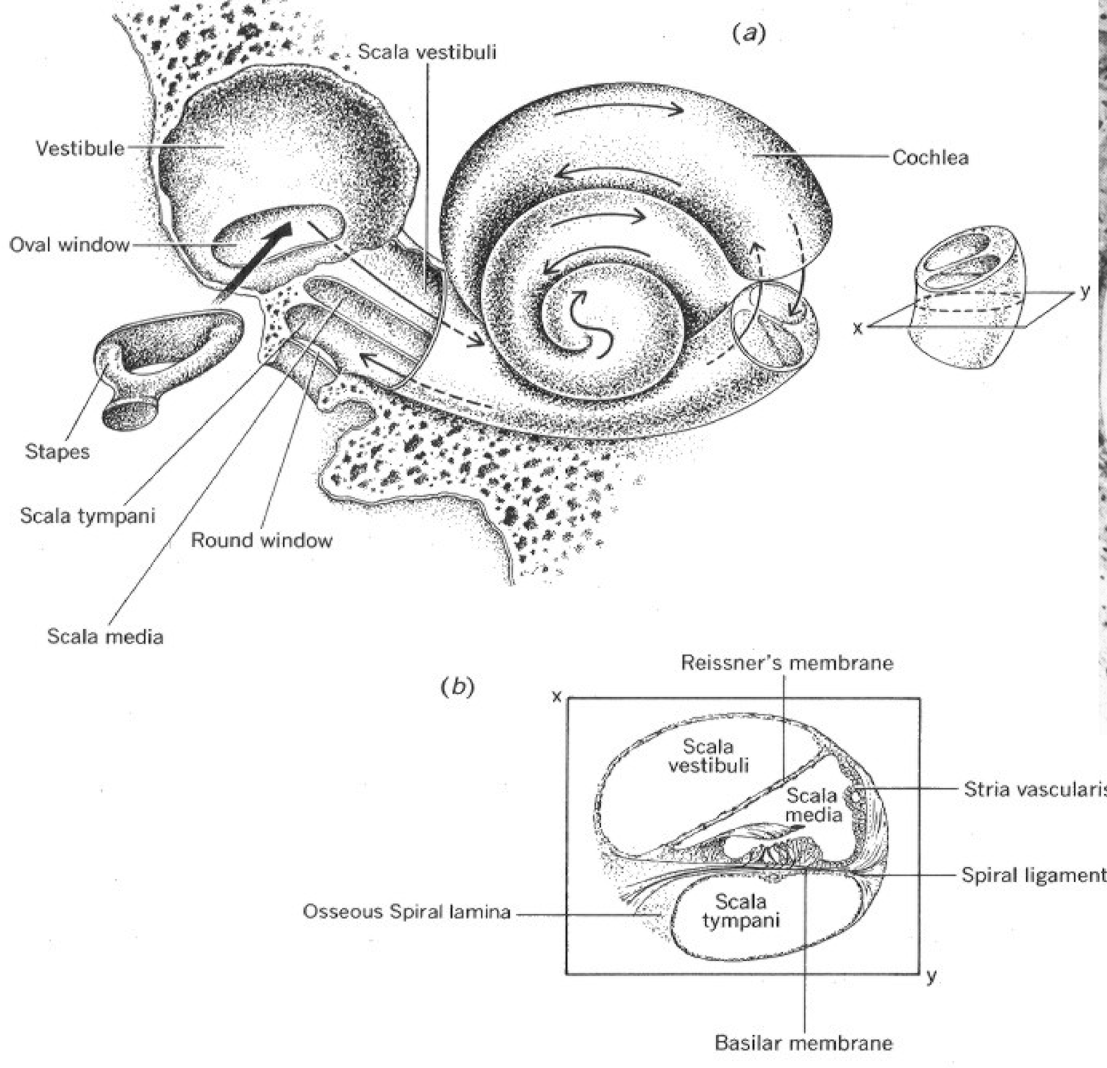
- Two pathways project from the SOC to the cochlea
  - Medial system (around MSO) – large, myelinated fibers
  - Lateral system (around LSO) – thin, unmyelinated fibers

Auditory Areas in Neocortex



- Primary auditory cortex is in the temporal lobe on the bank of the Sylvian fissure
- Wernicke's area involved in speech analysis (Broca's area is for speech production).
- All components of speech identified and combined before the information reaches this level.




(a)
Scala vestibuli
Vestibule
Cochlea
Oval window
Stapes
Scala tympani
Round window
Scala media
x
y
(b)
Reissner's membrane
Scala vestibuli
Scala media
Stria vascularis
Spiral ligament
Osseous Spiral lamina
Scala tympani
Basilar membrane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