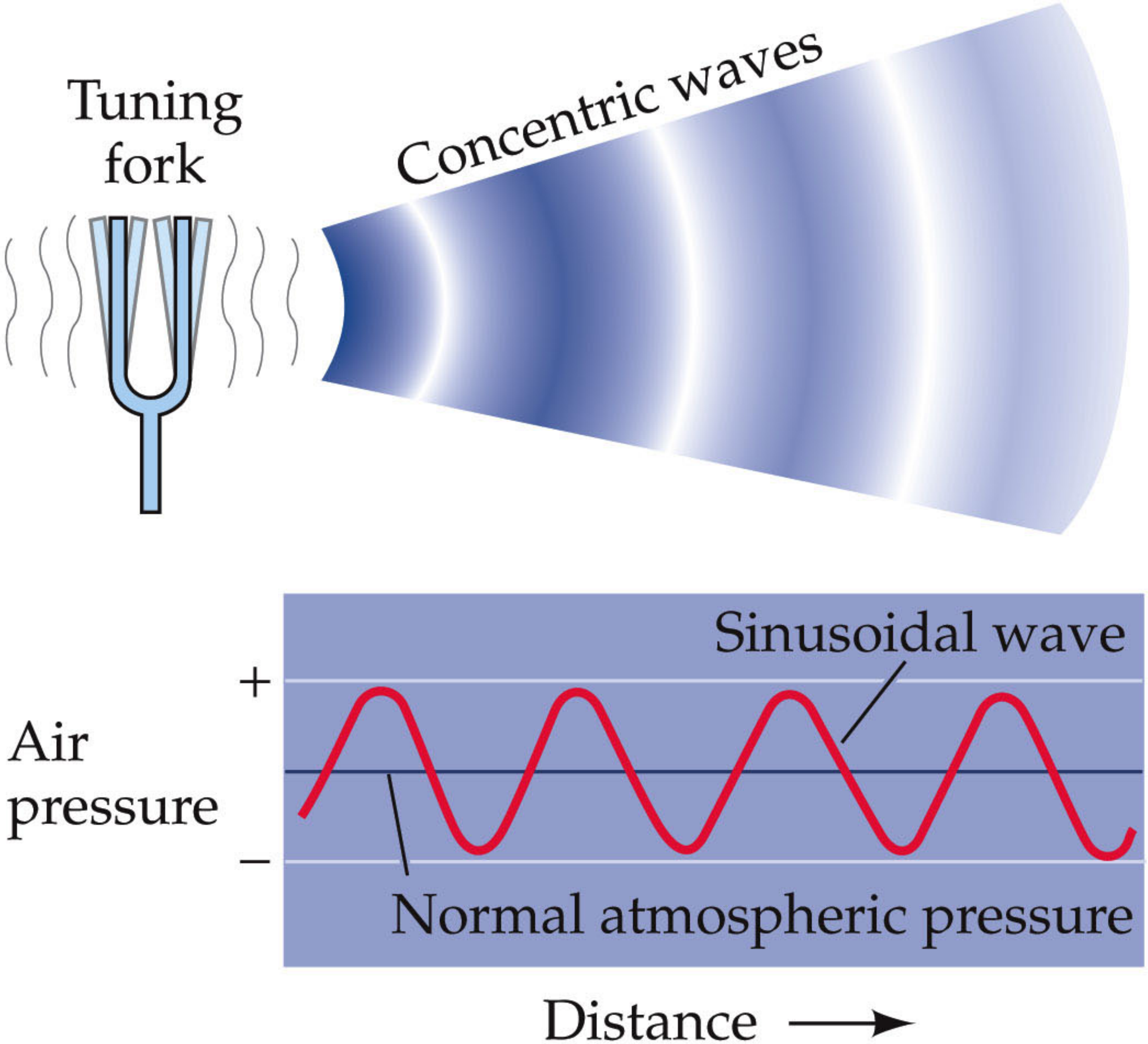
580.422

System Bioengineering II: Neurosciences

Periphery Auditory System

Prof. Xiaoqin Wang

Figure 13.1 The periodic condensation and rarefaction of air molecules produced by a tuning fork



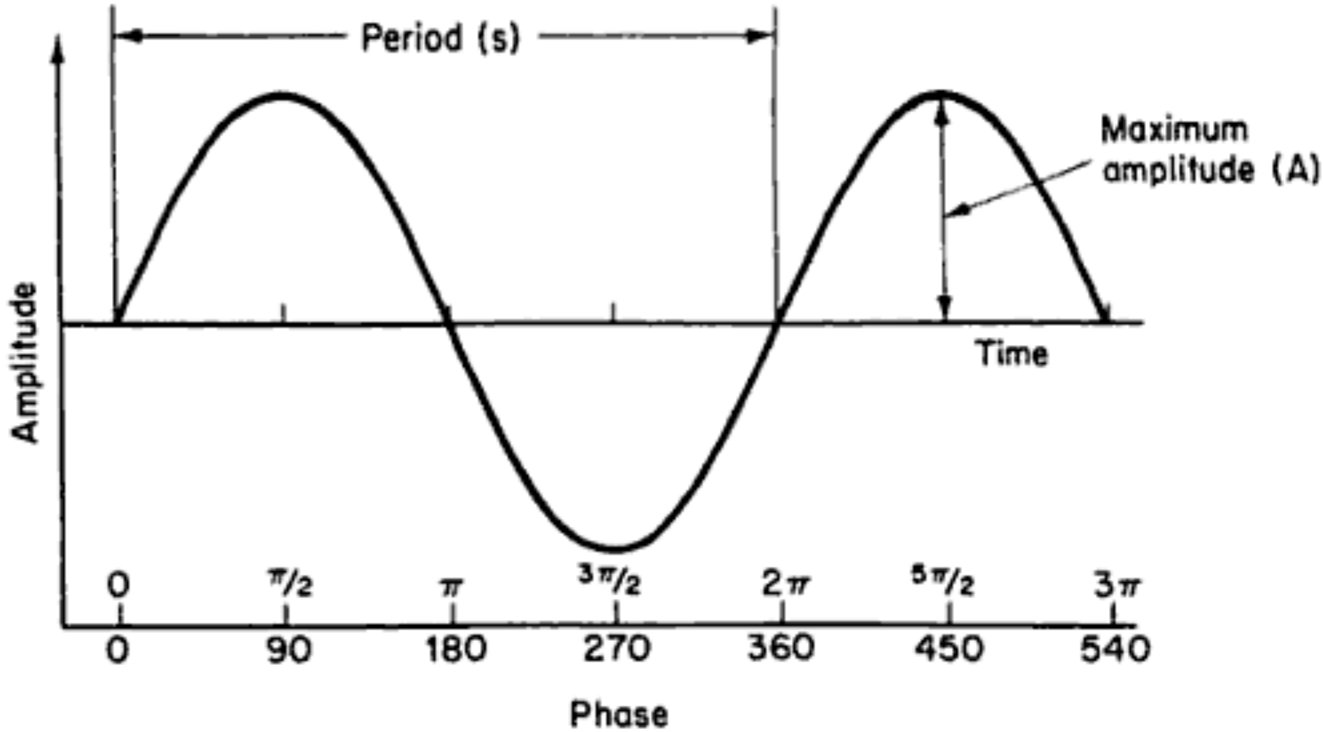


FIGURE 1.1 The waveform of a sine wave or sinusoidal vibration. Only 1.5 cycles are shown, although the waveform should be pictured as repeating indefinitely. The instantaneous amplitude is given by the expression $A \sin(2\pi ft)$, where t = time, f = frequency, and A = maximum amplitude. Phase is indicated along the bottom, using as a reference point the first zero-crossing of the wave. Phase may be measured in degrees or in radians. One complete cycle corresponds to 360° or 2π radians.

(From B.C. Moore “Introduction to Psychology of Hearing”)

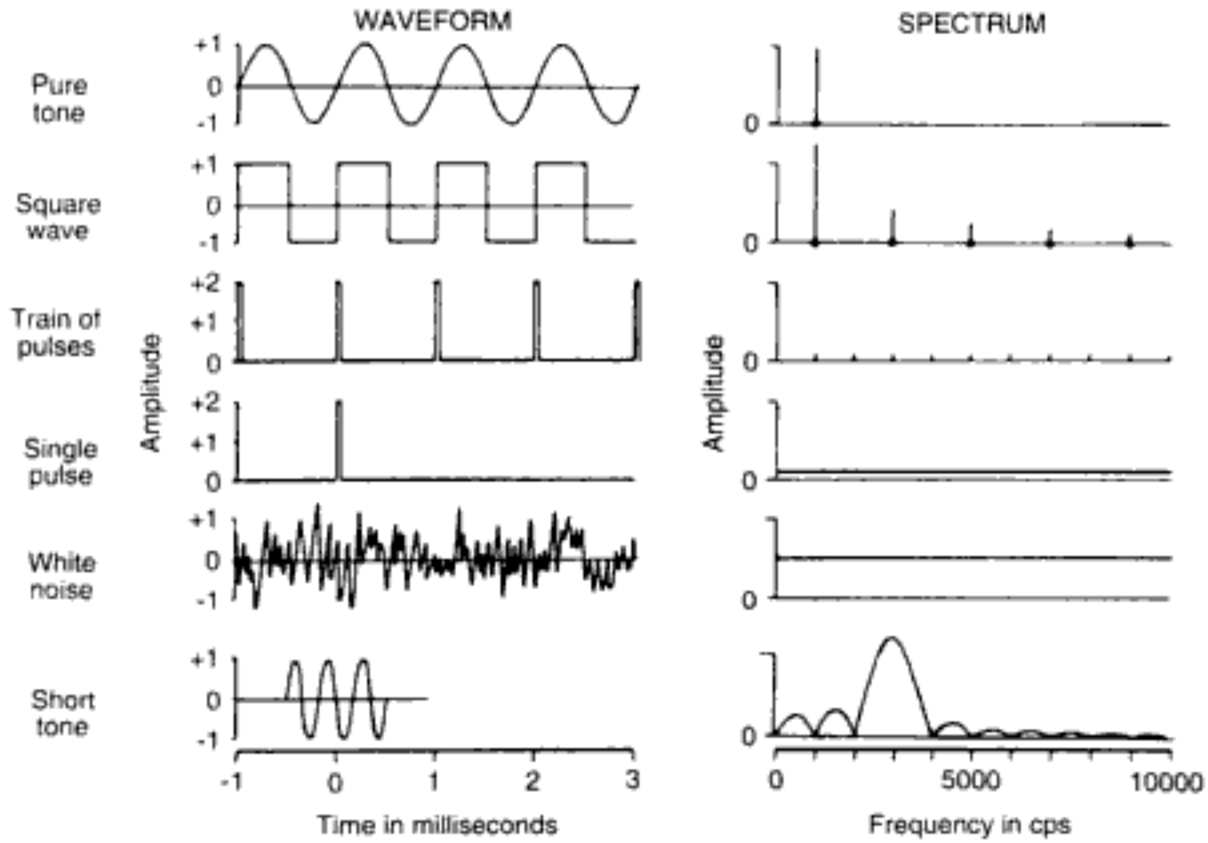


FIGURE 1.3 On the left are shown the waveforms of some common auditory stimuli, and on the right are the corresponding spectra. The periodic stimuli (pure tone, square wave, and train of pulses) have line spectra, while the nonperiodic stimuli (single pulse, white noise, and short tone burst) have continuous spectra.

(From B.C. Moore "Introduction to Psychology of Hearing")

TABLE 1.1 The relationship between decibels, intensity ratios and pressure ratios. Sound levels in dB SPL are expressed relative to a reference intensity I_0 of 10^{-12} W/m^2. This is equivalent to a pressure of 20μPa.

Sound level (dB SPL)	Intensity ratio (I/I_0)	Pressure ratio (P/P_0)	Typical example
140	10^{14}	10^{7}	Gunshot at close range
120	10^{12}	10^{6}	Loud rock group
100	10^{10}	10^{5}	Shouting at close range
80	10^{8}	10^{4}	Busy street
70	10^{7}	3160	Normal conversation
50	10^{5}	316	Quiet conversation
30	10^{3}	31.6	Soft whisper
20	10^{2}	10	Country area at night
6.5	4.5	2.1	Mean absolute threshold at 1 kHz
3	2	1.4	
0	1	1	Reference level
−10	0.1	0.316	

$$L_p = 10\ \log_{10}\left(\frac{p^2}{{p_{ref}}^2}\right) = 20\ \log_{10}\left(\frac{p}{p_{ref}}\right)\ \text{dB}$$

where p is the root-mean-square sound pressure and p_{ref} is a reference sound pressure. Commonly used reference sound pressures, defined in the standard ANSI S1.1-1994, are 20 μPa in air and 1 μPa in water. Without a specified reference sound pressure, a value expressed in decibels cannot represent a sound pressure level.

(From B.C. Moore “Introduction to Psychology of Hearing”)

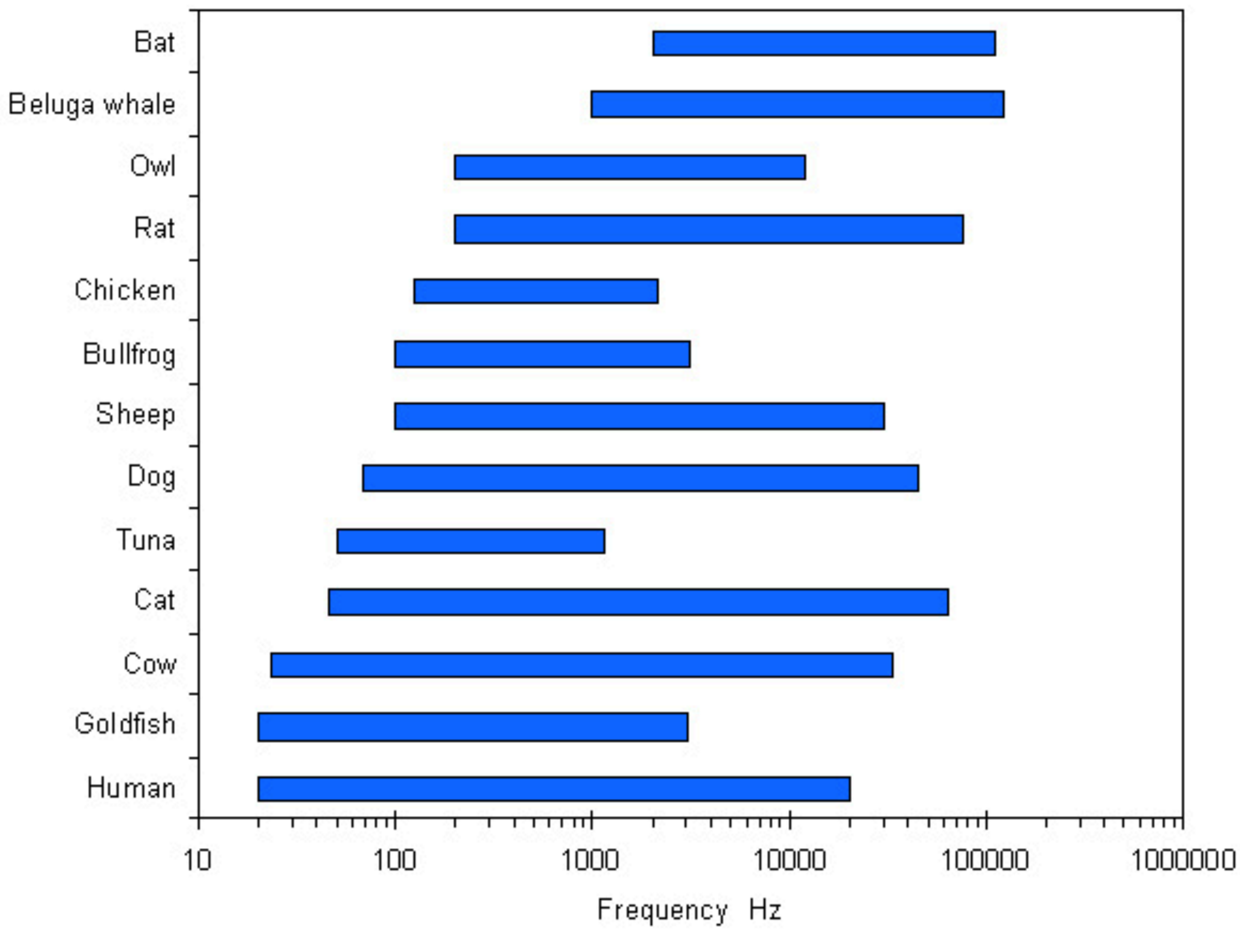
Frequencies and descriptions

[edit]

Frequency (Hz)	Octave	Description
16 to 32	1st	The human threshold of feeling, and the lowest pedal notes of a pipe organ.
32 to 512	2nd to 5th	Rhythm frequencies, where the lower and upper bass notes lie.
512 to 2048	6th to 7th	Defines human speech intelligibility, gives a horn-like or tinny quality to sound.
2048 to 8192	8th to 9th	Gives presence to speech, where labial and fricative sounds lie.
8192 to 16384	10th	Brilliance, the sounds of bells and the ringing of cymbals. In speech, the sound of the letter "S" (8000-11000 Hz)

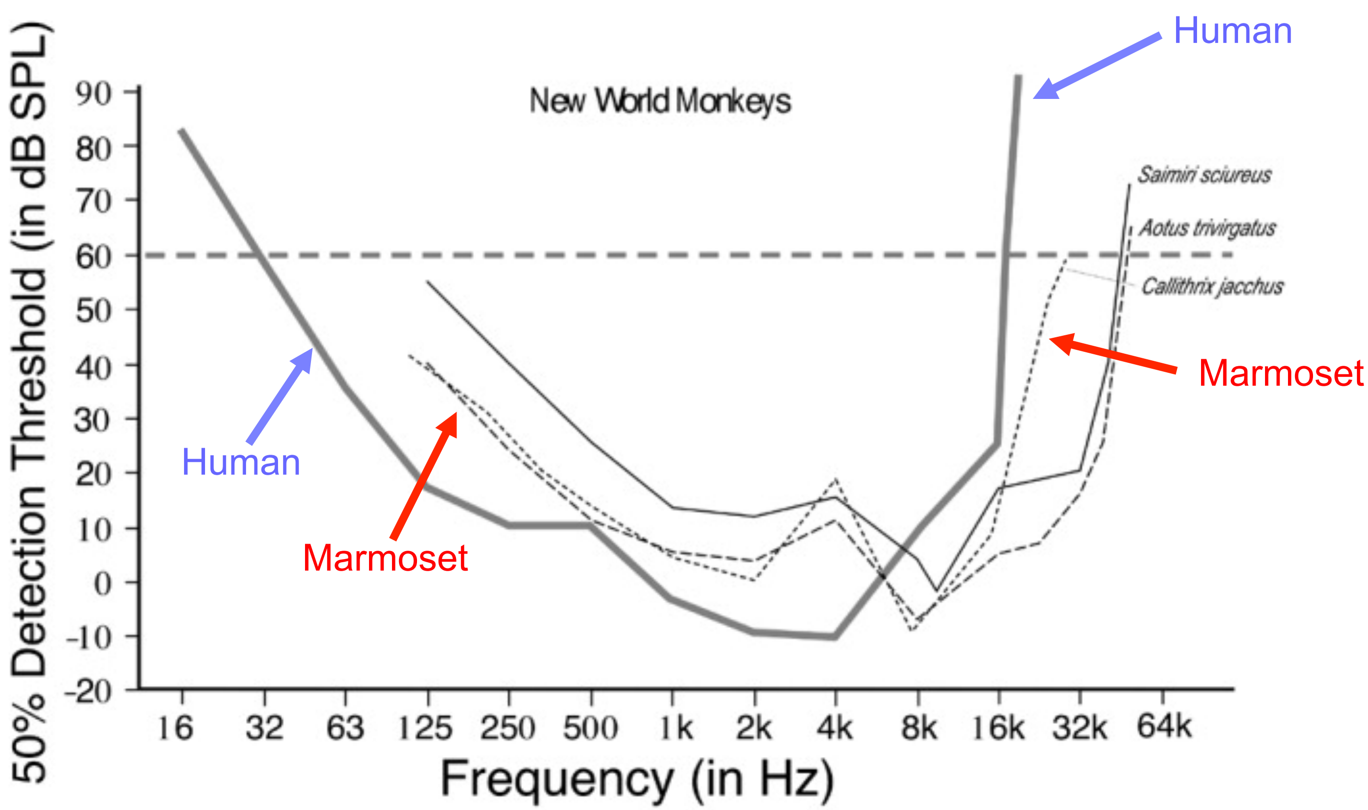
(From Wikipedia)

Hearing Range in Animals



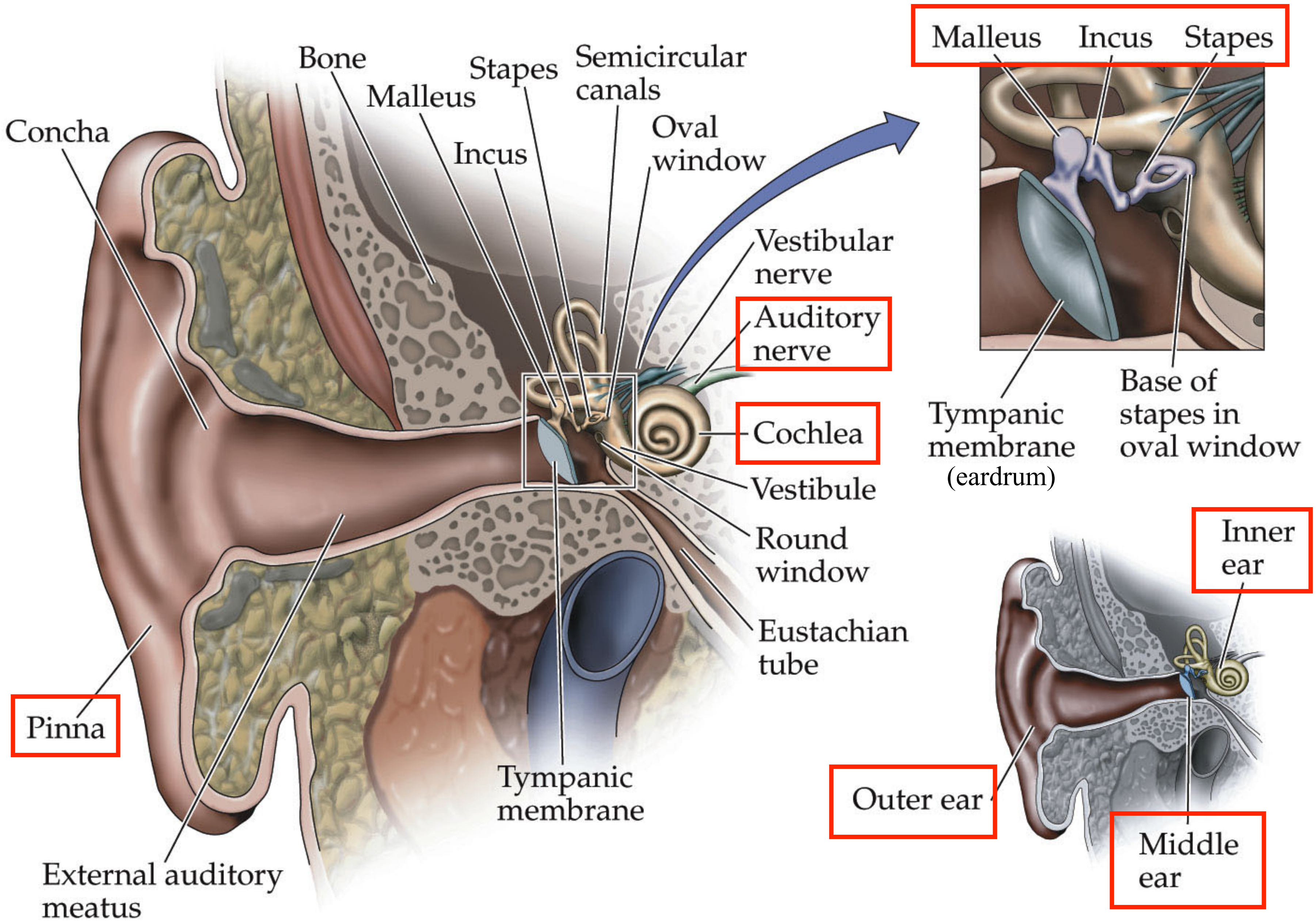
(From www.diracdelta.co.uk)

Audiograms of Humans and Monkeys



Heffner (*Anat. Rec.* 2004)

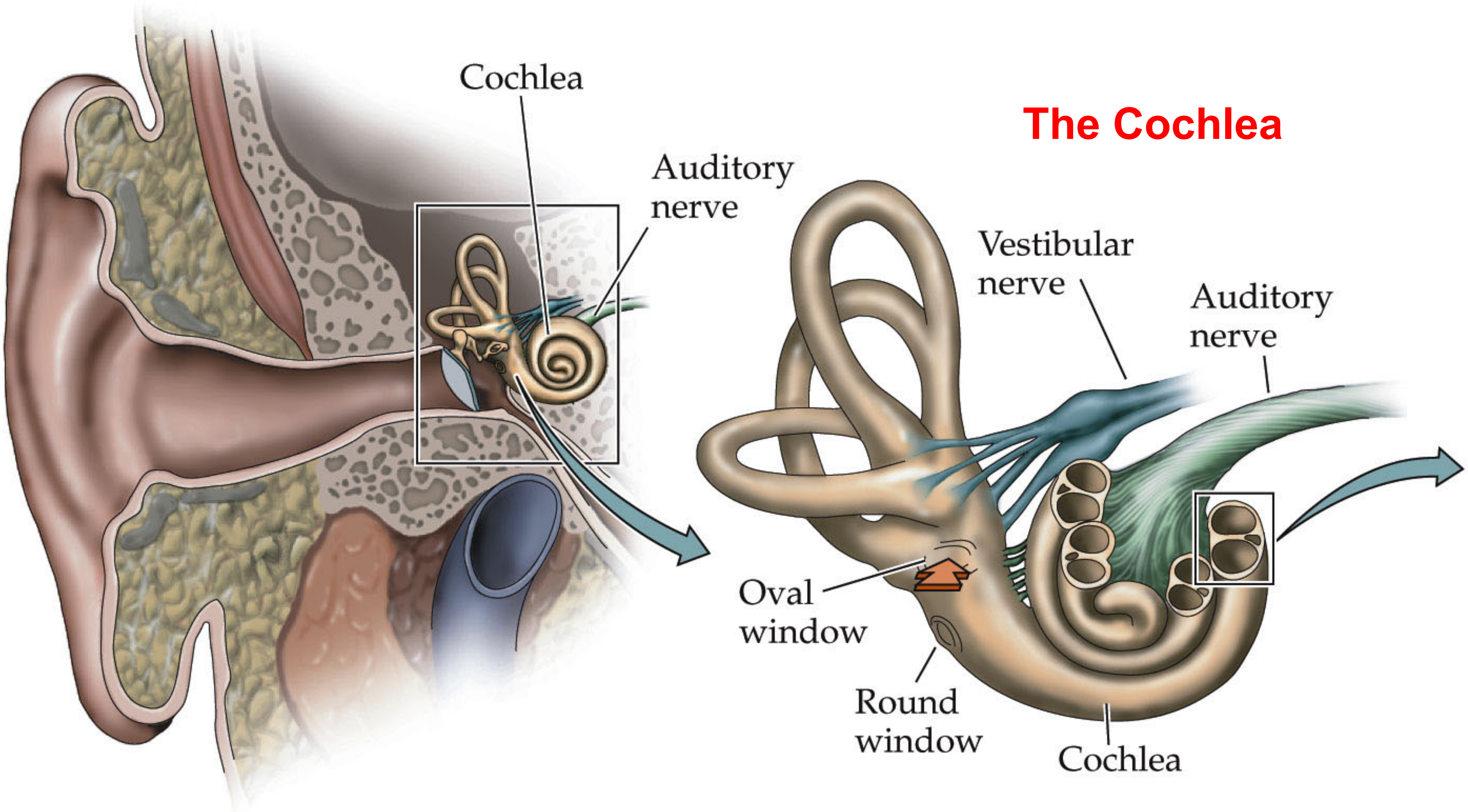
Figure 13.3 The human ear



NEUROSCIENCE, Fourth Edition, Figure 13.3

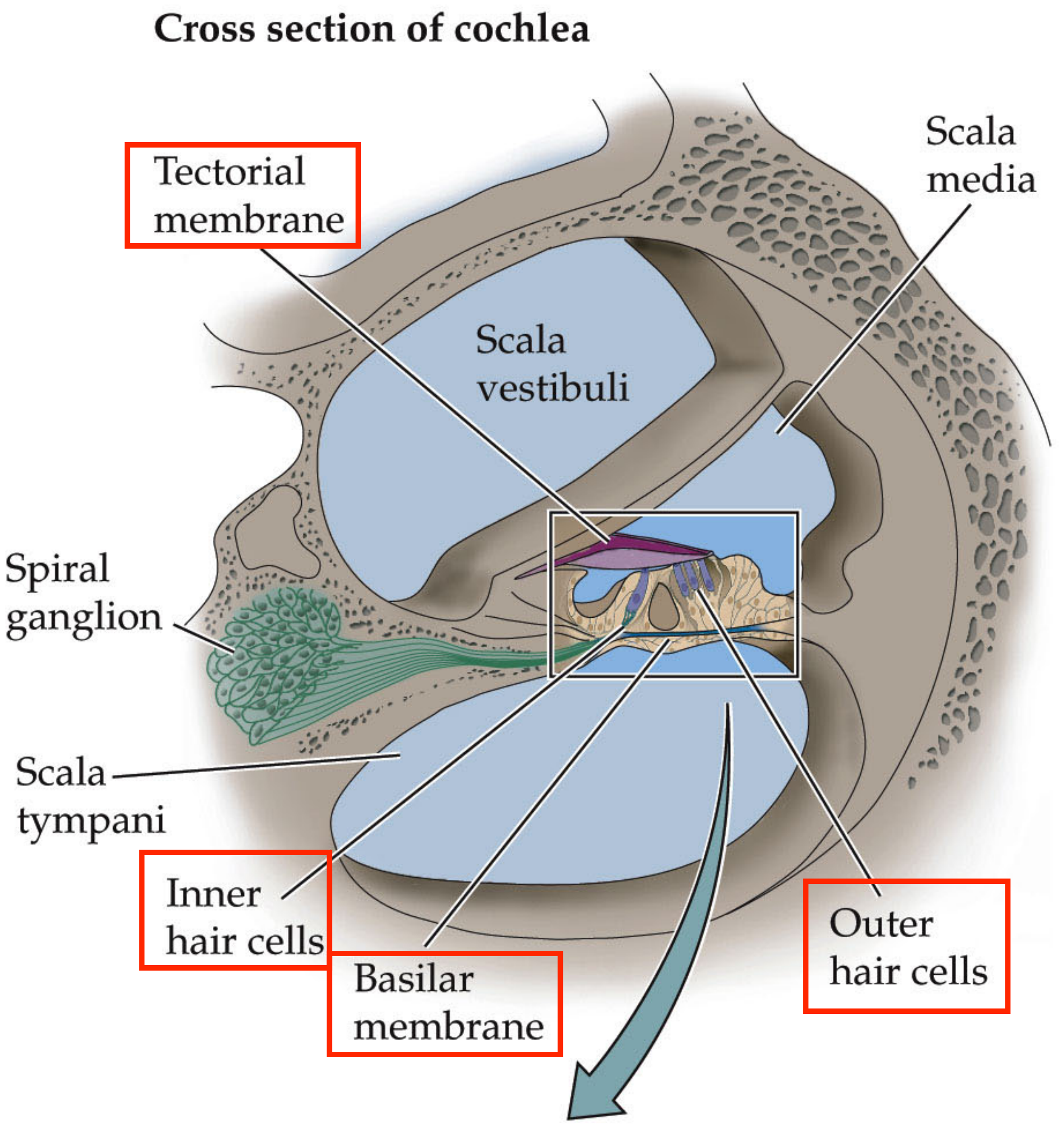
Figure 13.4 The cochlea (Part 1)

The Cochlea



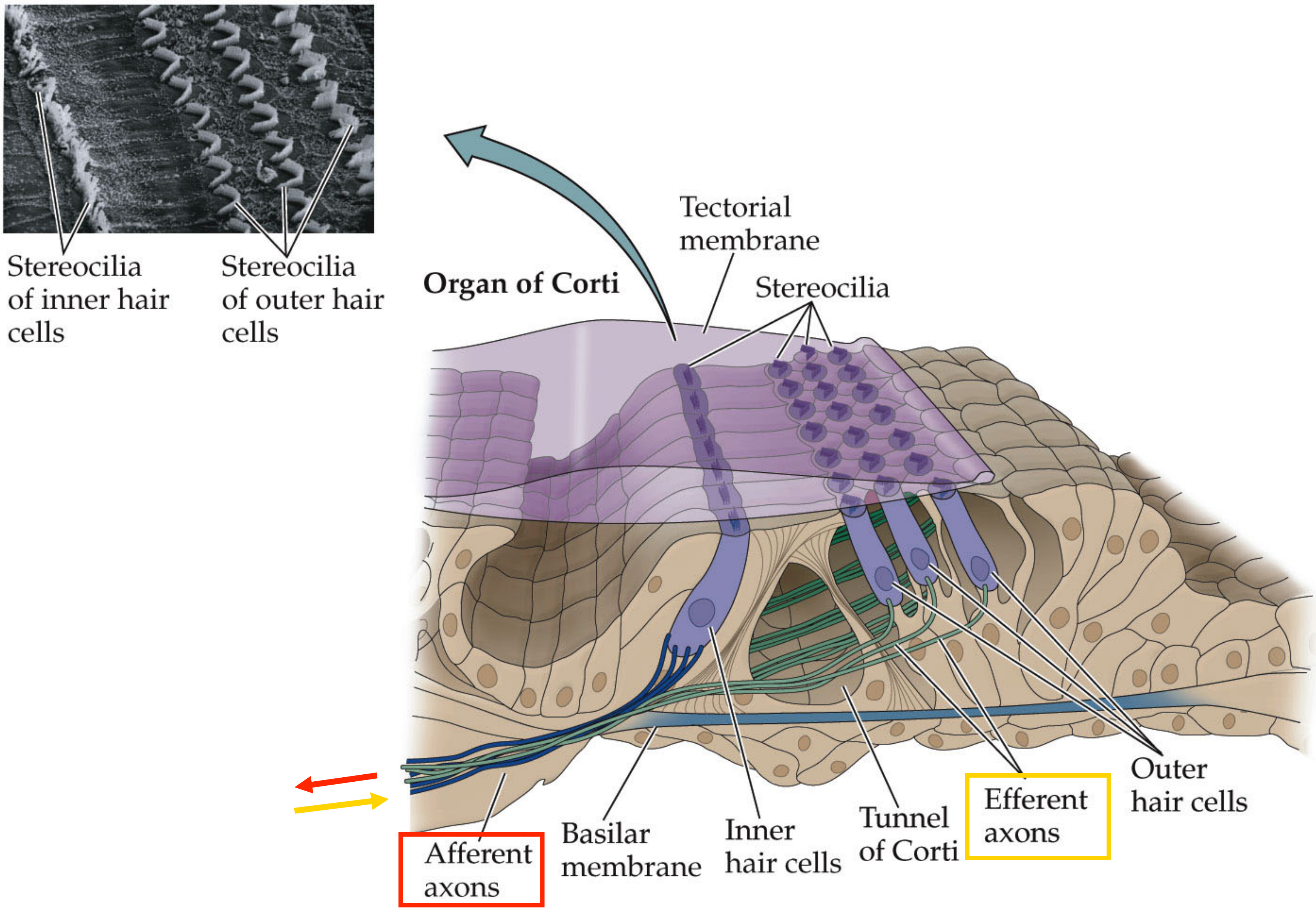
NEUROSCIENCE, Fourth Edition, Figure 13.4 (Part 1)

Figure 13.4 The cochlea (Part 2)



NEUROSCIENCE, Fourth Edition, Figure 13.4 (Part 2)

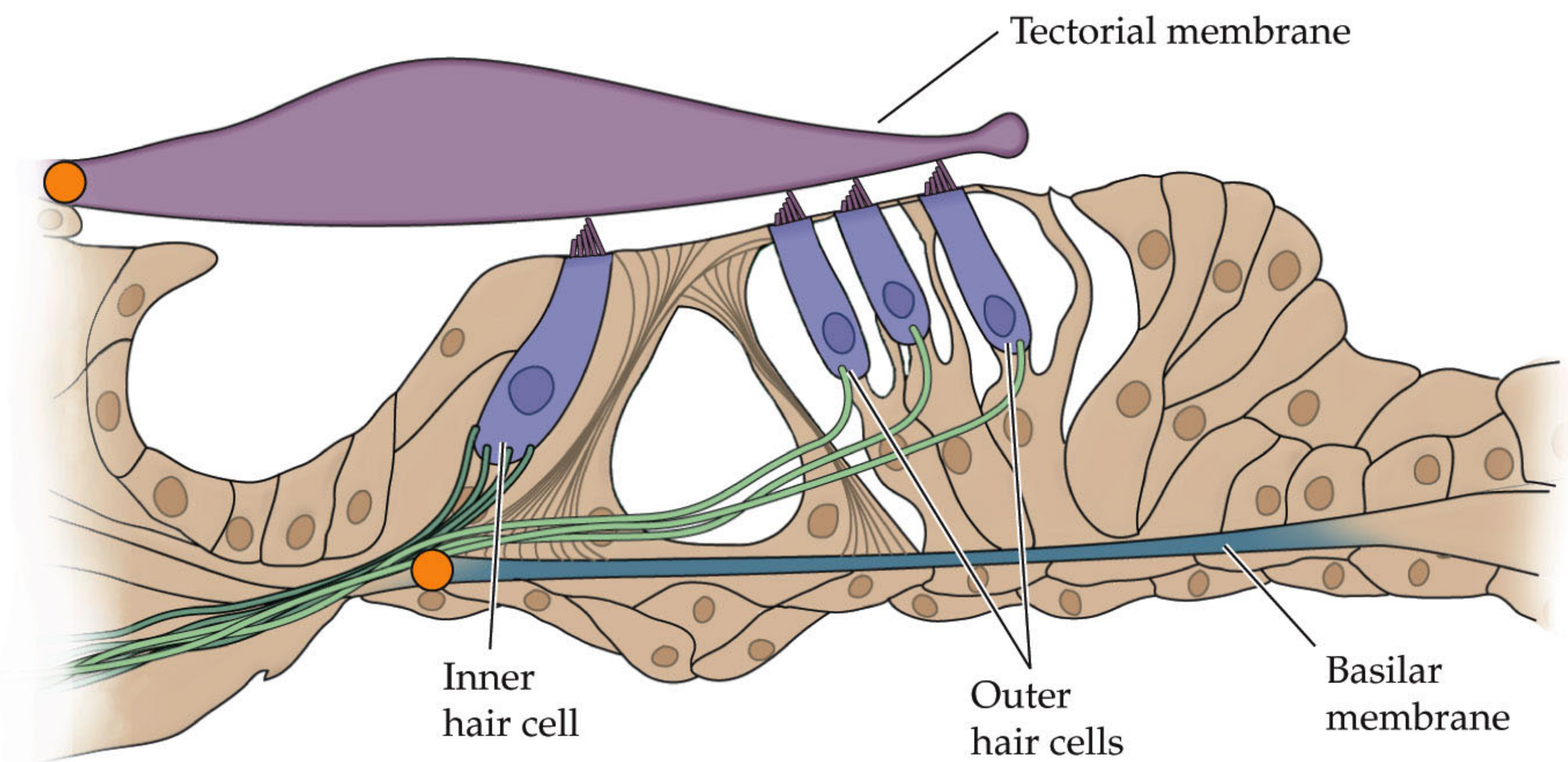
Figure 13.4 The cochlea (Part 3)



NEUROSCIENCE, Fourth Edition, Figure 13.4 (Part 3)

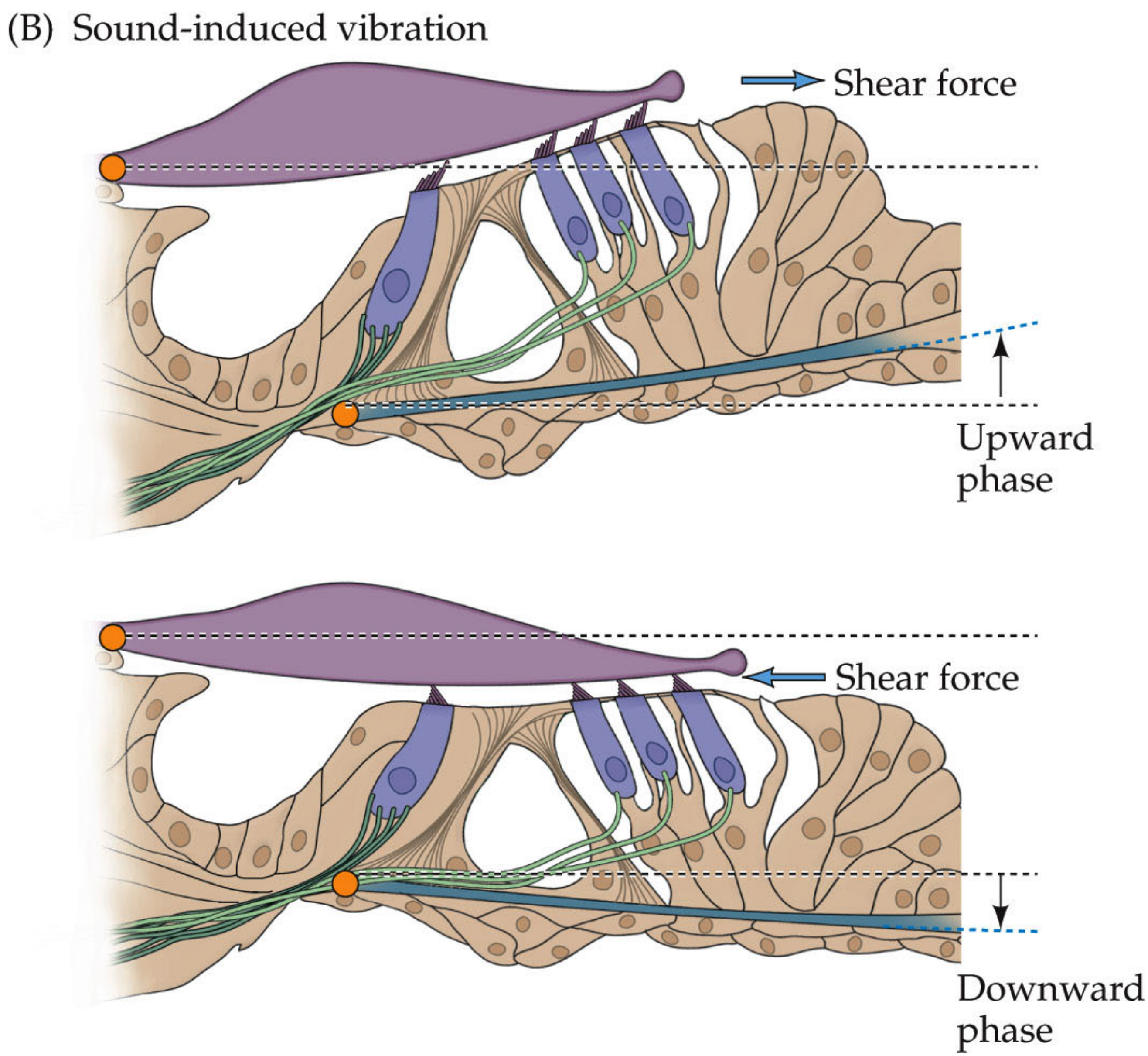
Figure 13.6 Vertical movement of the basilar membrane bends the stereocilia of hair cells (Part 1)

(A) Resting position



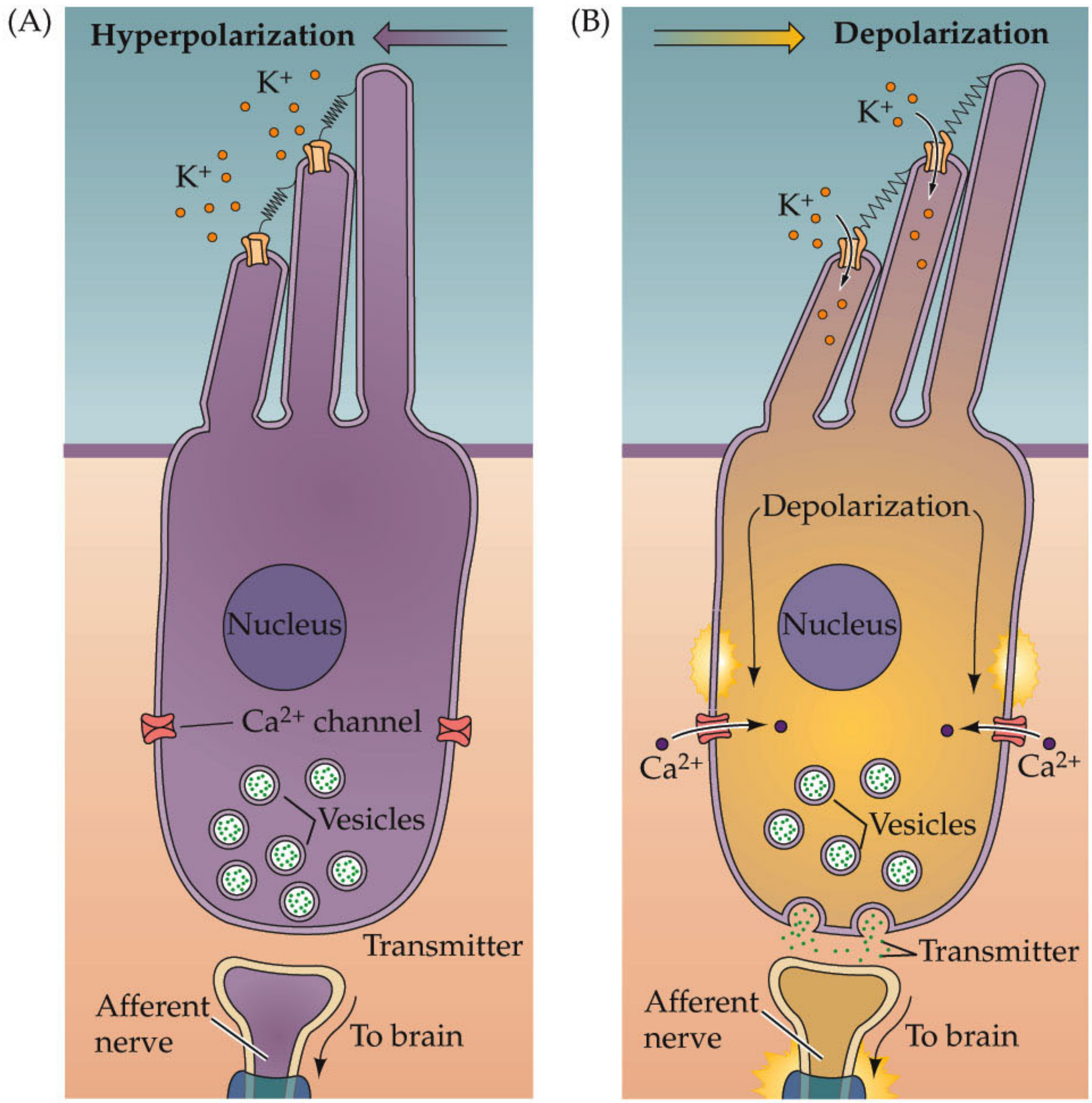
NEUROSCIENCE, Fourth Edition, Figure 13.6 (Part 1)

Figure 13.6 Vertical movement of the basilar membrane bends the stereocilia of hair cells (Part 2)



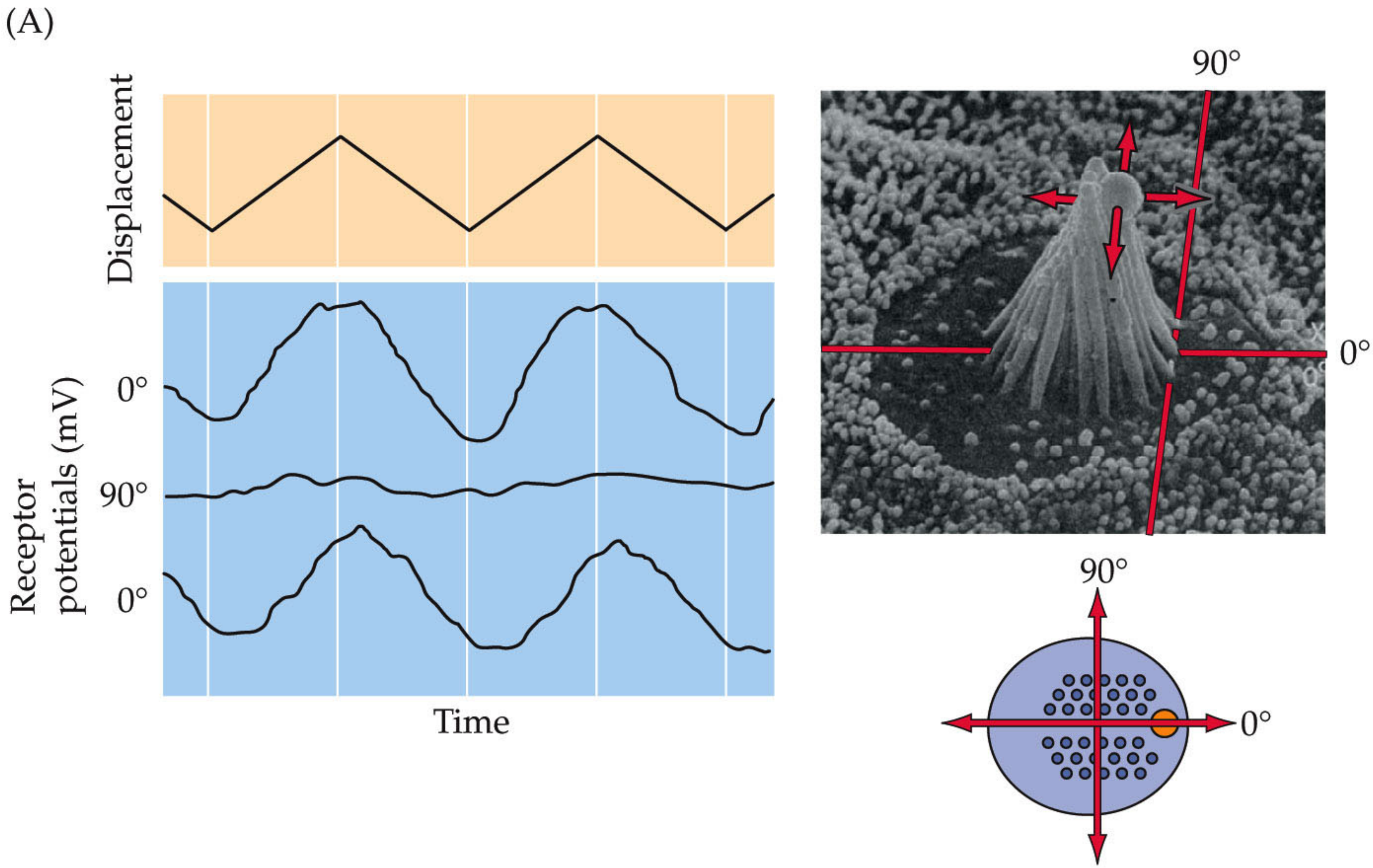
NEUROSCIENCE, Fourth Edition, Figure 13.6 (Part 2)

Figure 13.8 Mechanoelectrical transduction mediated by hair cells



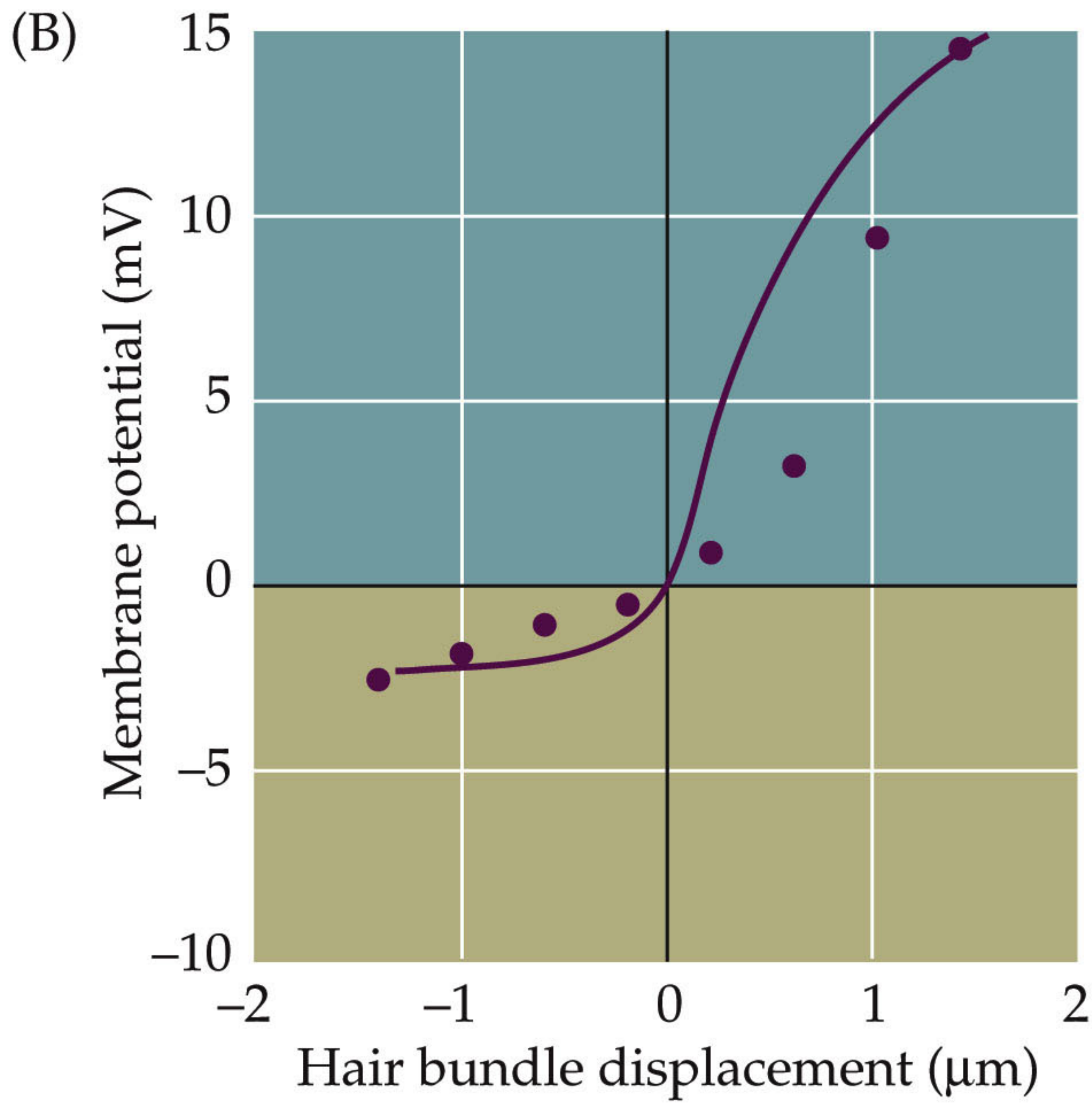
***NEUROSCIENCE*, *Fourth Edition*, Figure 13.8**

Figure 13.9 Mechanoelectrical transduction mediated by vestibular hair cells (Part 1)



NEUROSCIENCE, Fourth Edition, Figure 13.9 (Part 1)

Figure 13.9 Mechanoelectrical transduction mediated by vestibular hair cells (Part 2)



NEUROSCIENCE, Fourth Edition, Figure 13.9 (Part 2)

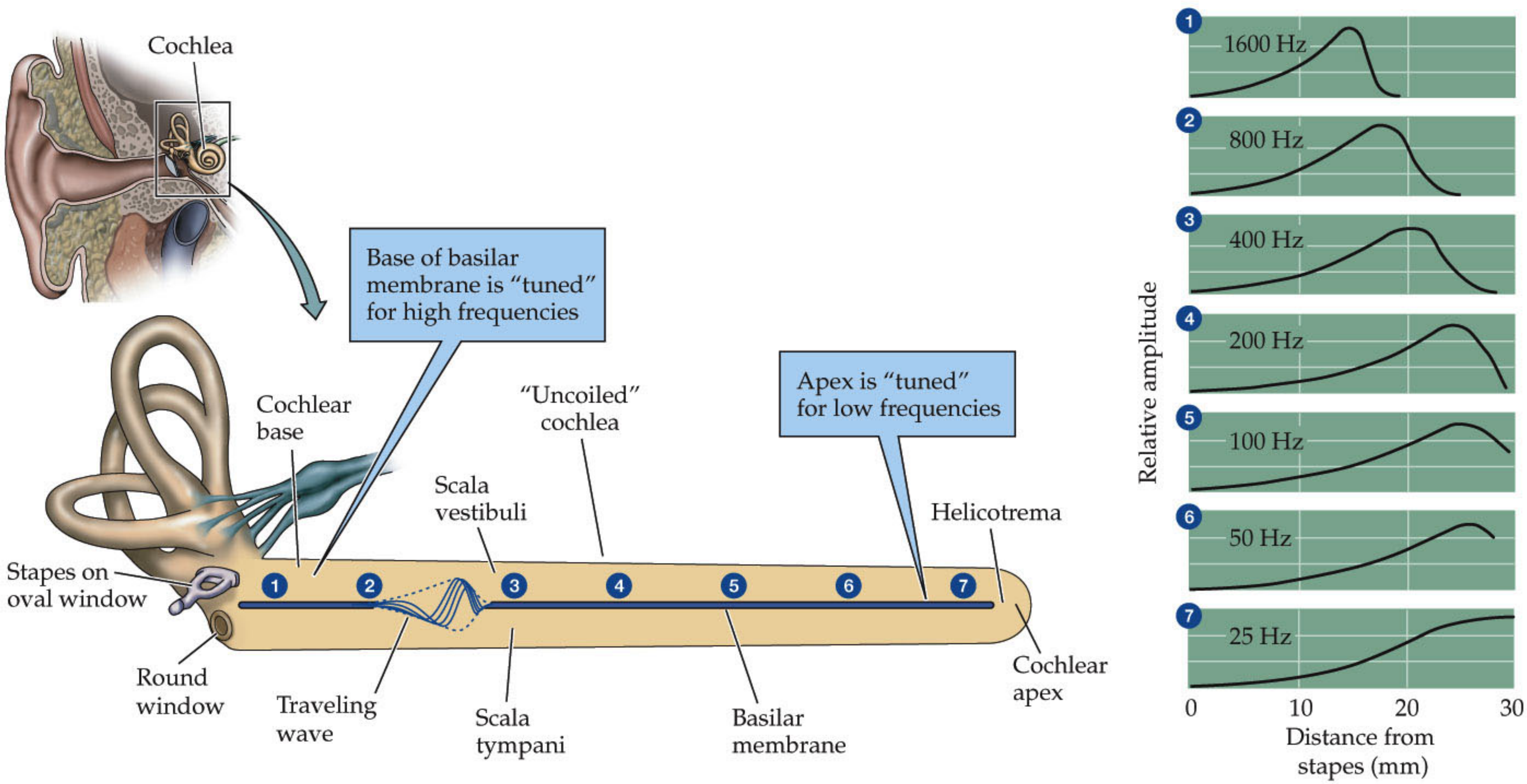
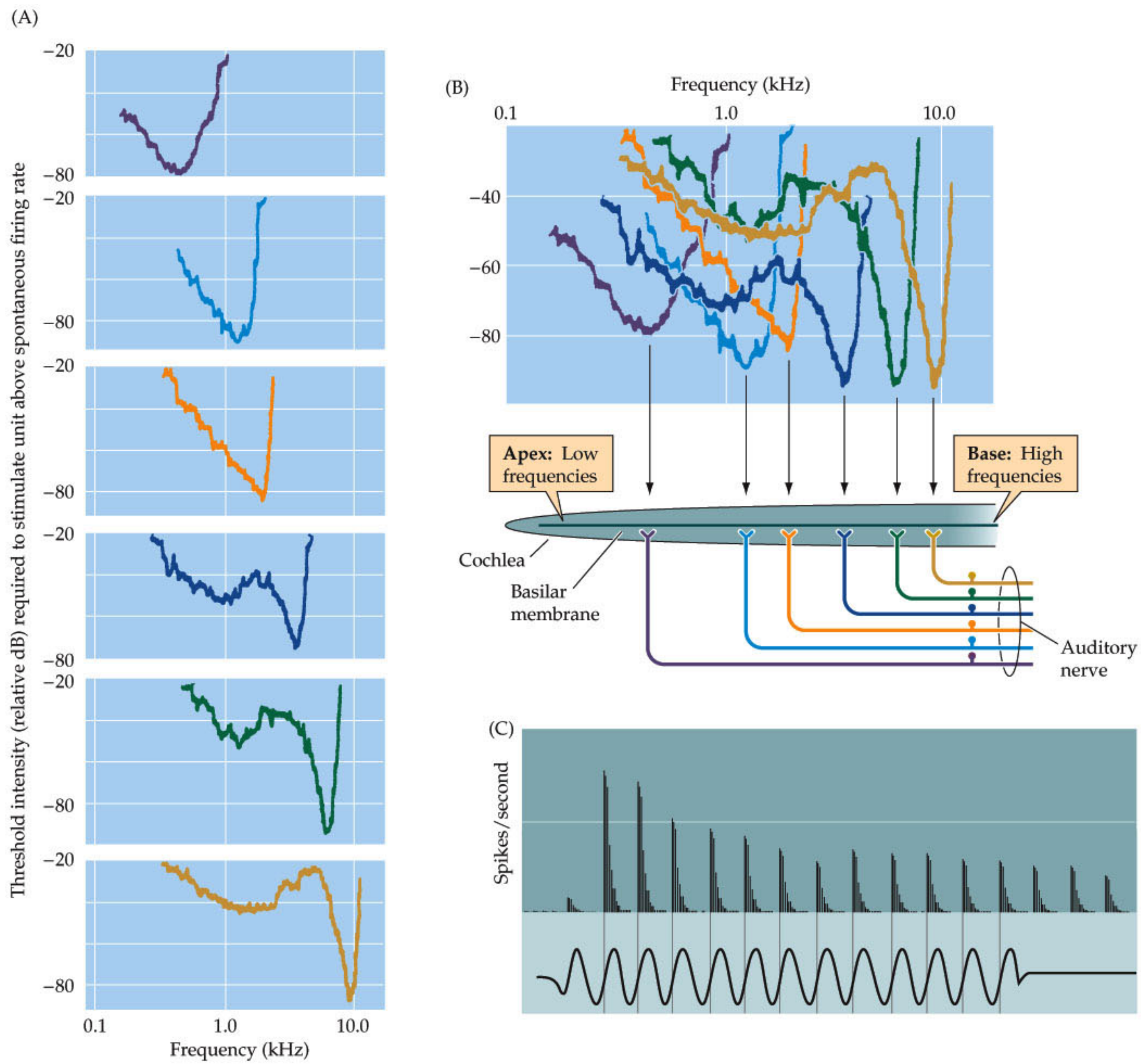

Cochlea
Base of basilar membrane is "tuned" for high frequencies
Cochlear base
"Uncoiled" cochlea
Apex is "tuned" for low frequencies
Scala vestibuli
Helicotrema
Stapes on oval window
1
2
3
4
5
6
7
Round window
Traveling wave
Scala tympani
Basilar membrane
Cochlear apex
1600 Hz
800 Hz
400 Hz
200 Hz
100 Hz
50 Hz
25 Hz
Relative amplitude
0
10
20
30
Distance from stapes (mm)

Figure 13.11 Response properties of auditory nerve fibers



Box 13C Sensorineural Hearing Loss and Cochlear Implants

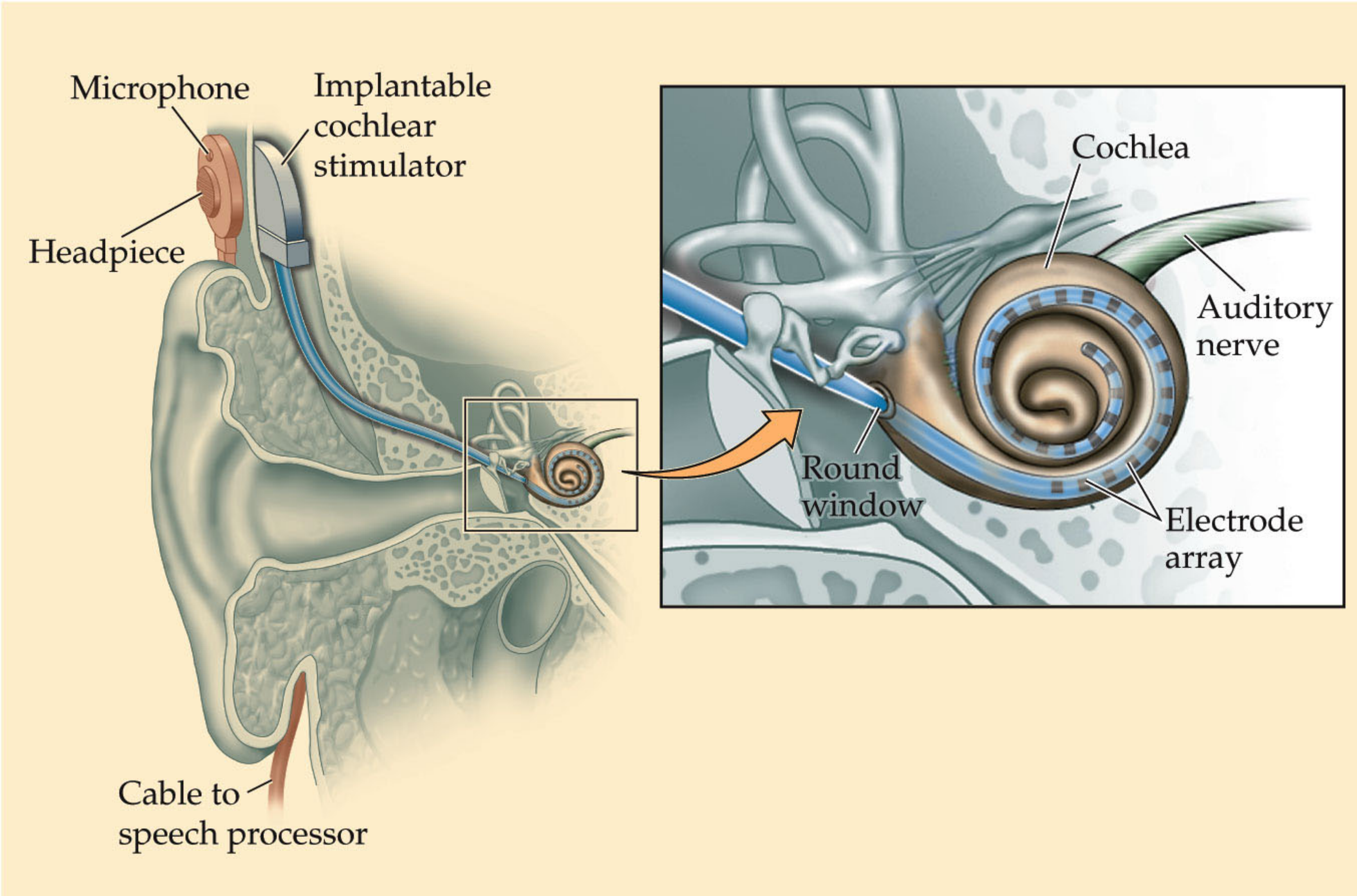
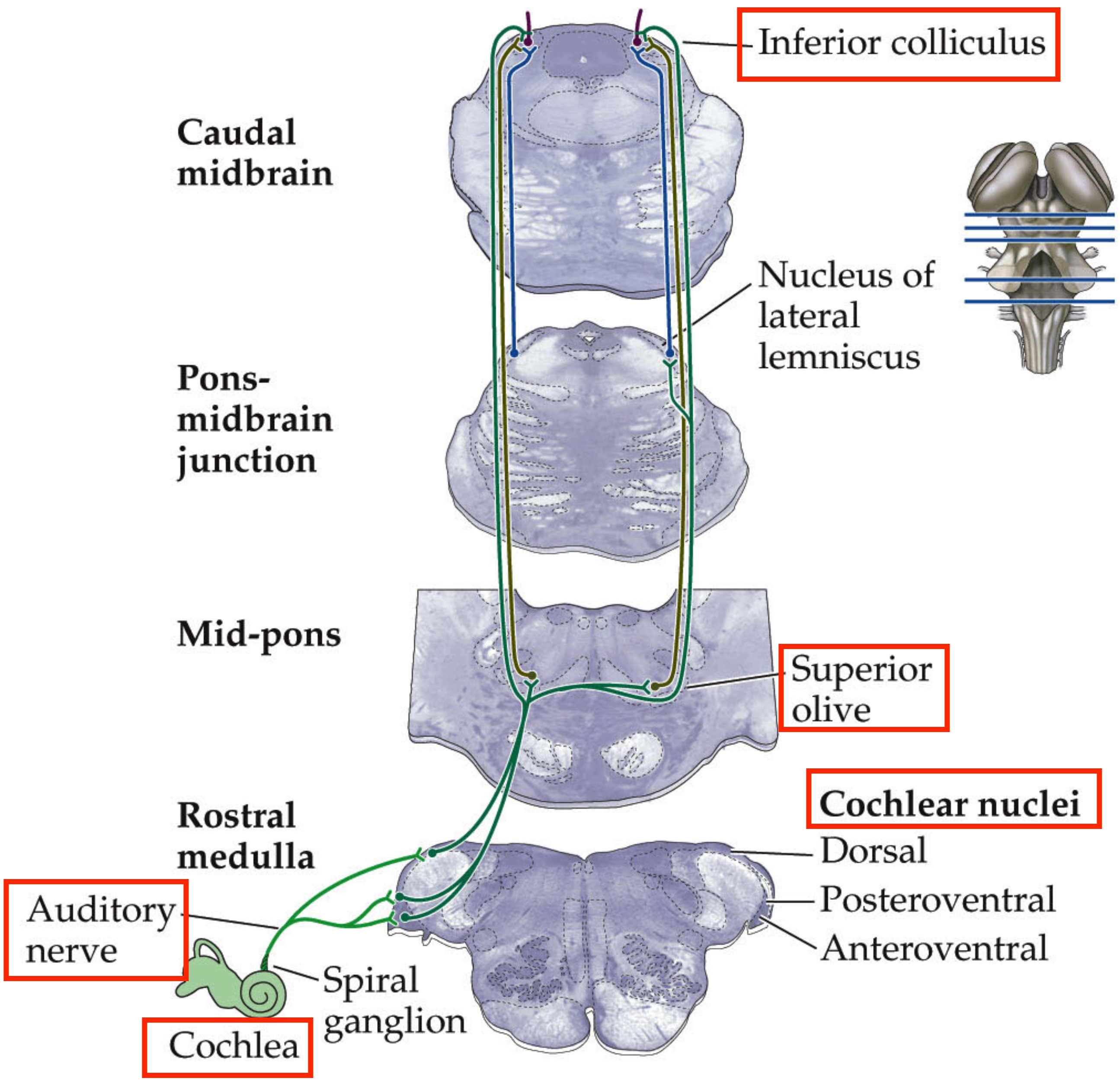
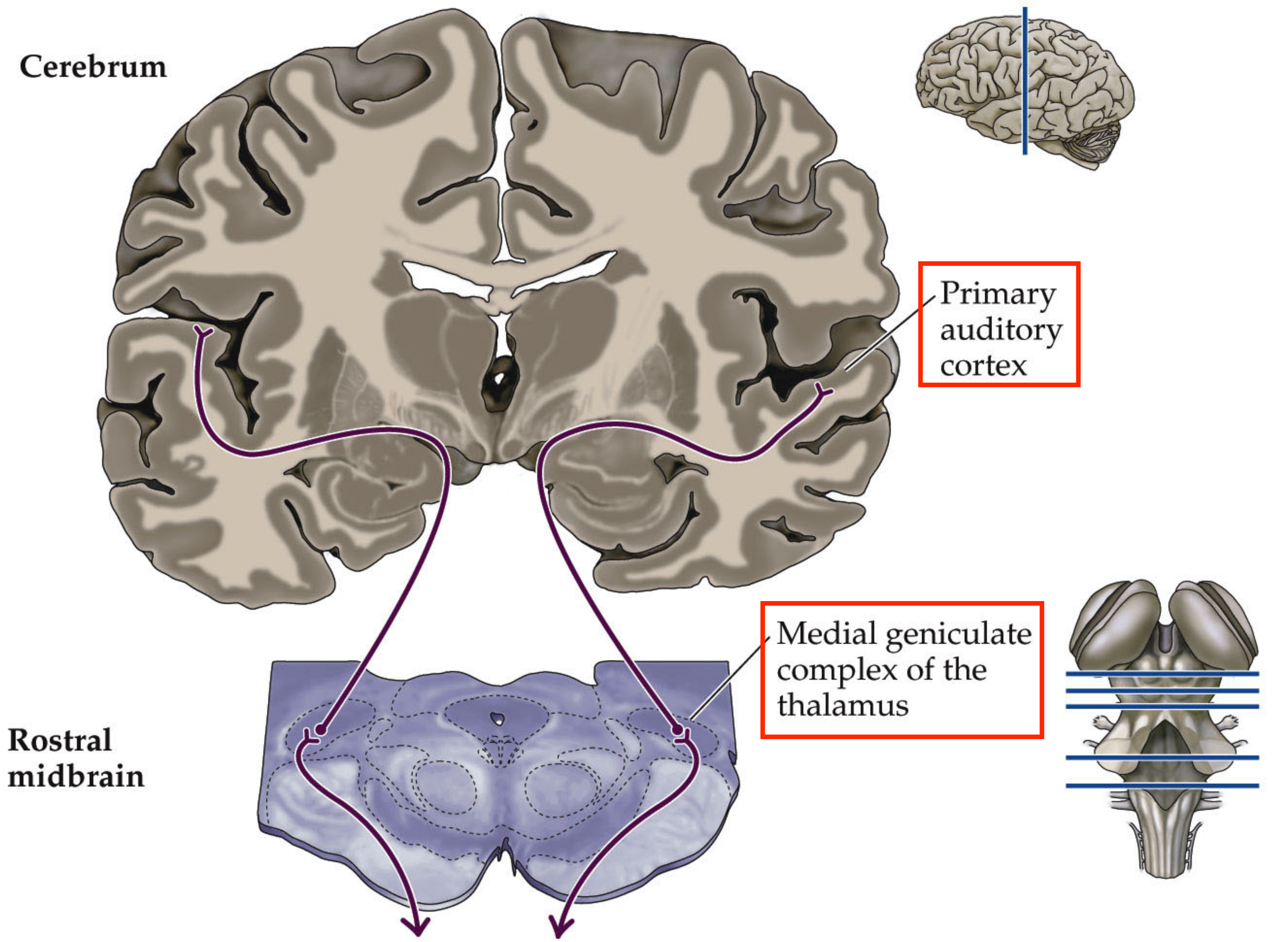


Figure 13.12 The major auditory pathways (Part 2)



NEUROSCIENCE, Fourth Edition, Figure 13.12 (Part 2)

Figure 13.12 The major auditory pathways (Part 1)



NEUROSCIENCE, Fourth Edition, Figure 13.12 (Part 1)

Figure 13.15 The human auditory cortex (Part 1)

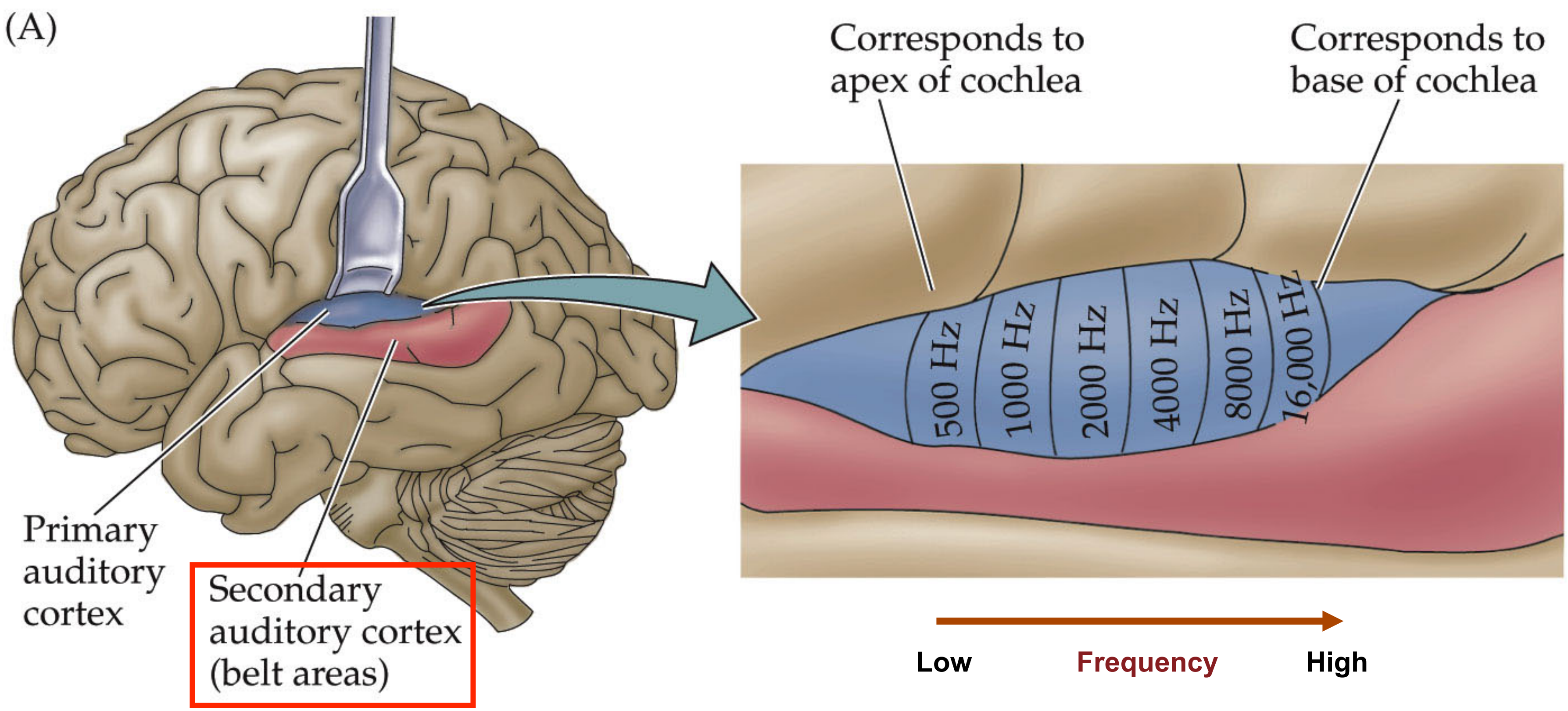
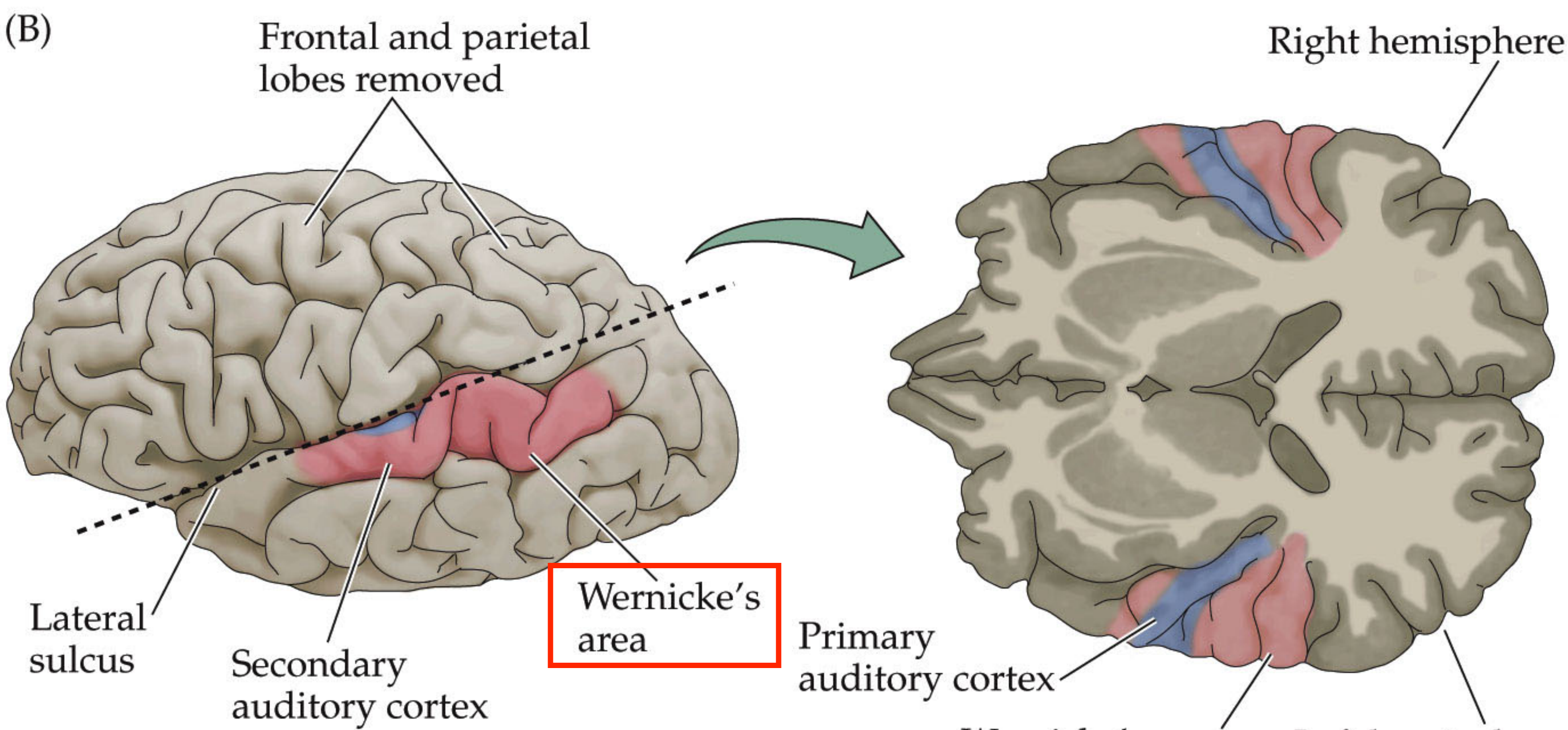
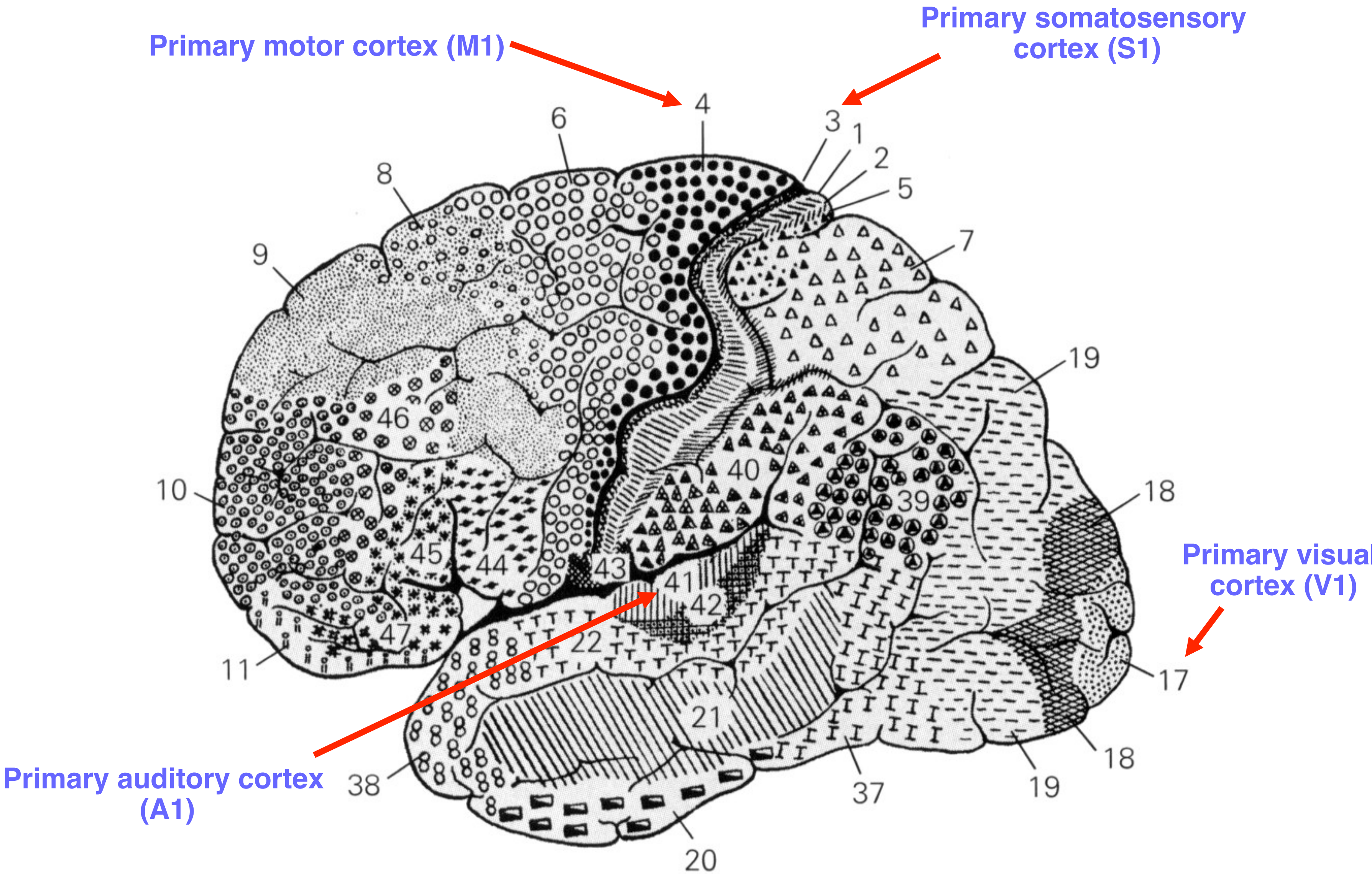


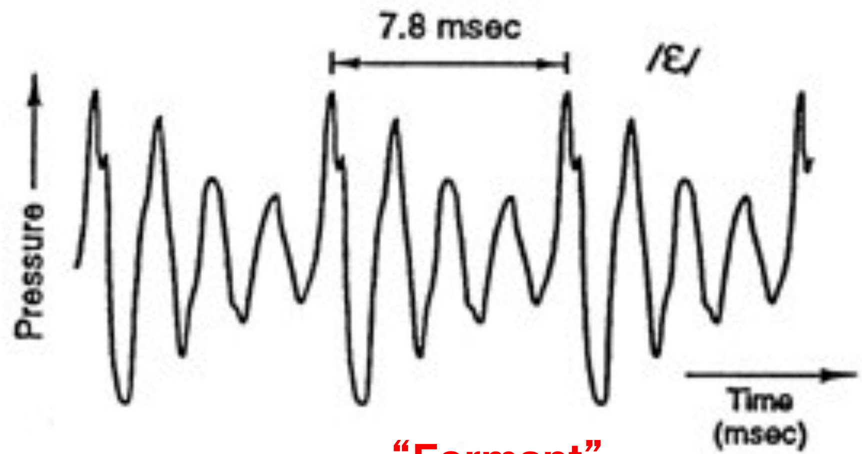
Figure 13.15 The human auditory cortex (Part 2)



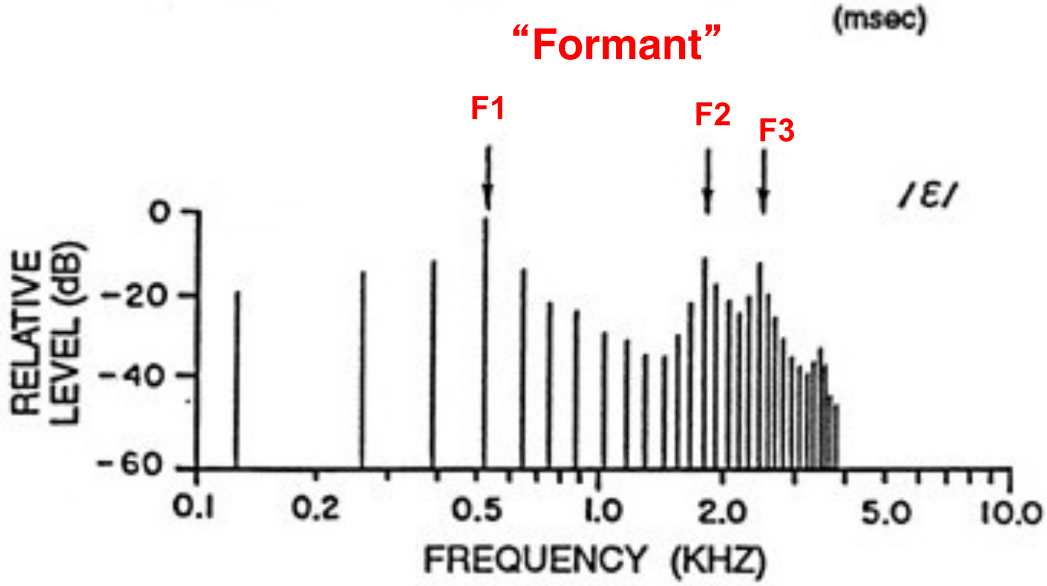
Brodmann's naming convention



Spectral and Temporal Characteristics of Speech



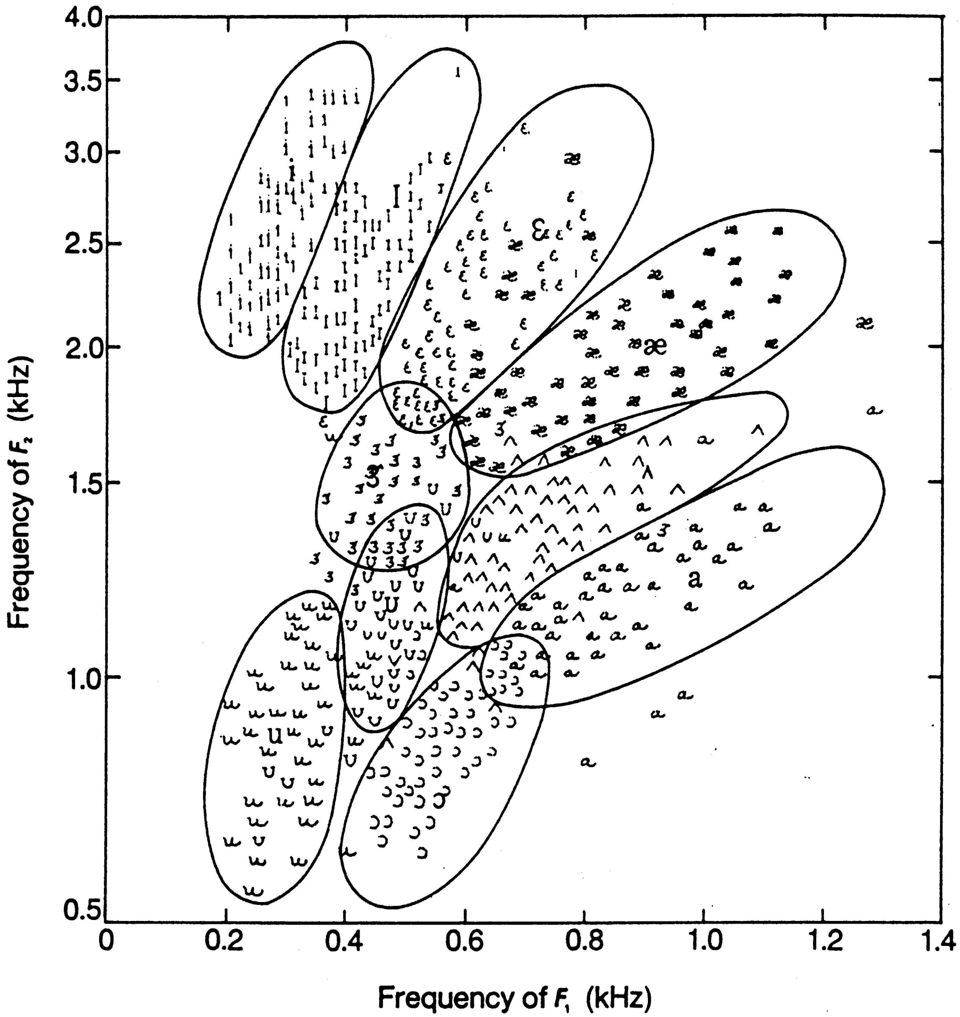
Amplitude-time Waveform



Spectrum

[From: Sachs and Young]

Formant Representation of English Vowels



Frequency of the second formant versus frequency of the first formant of English vowels

Peterson and Barney (*JASA*, 1952)

Spectrum of English Vowels

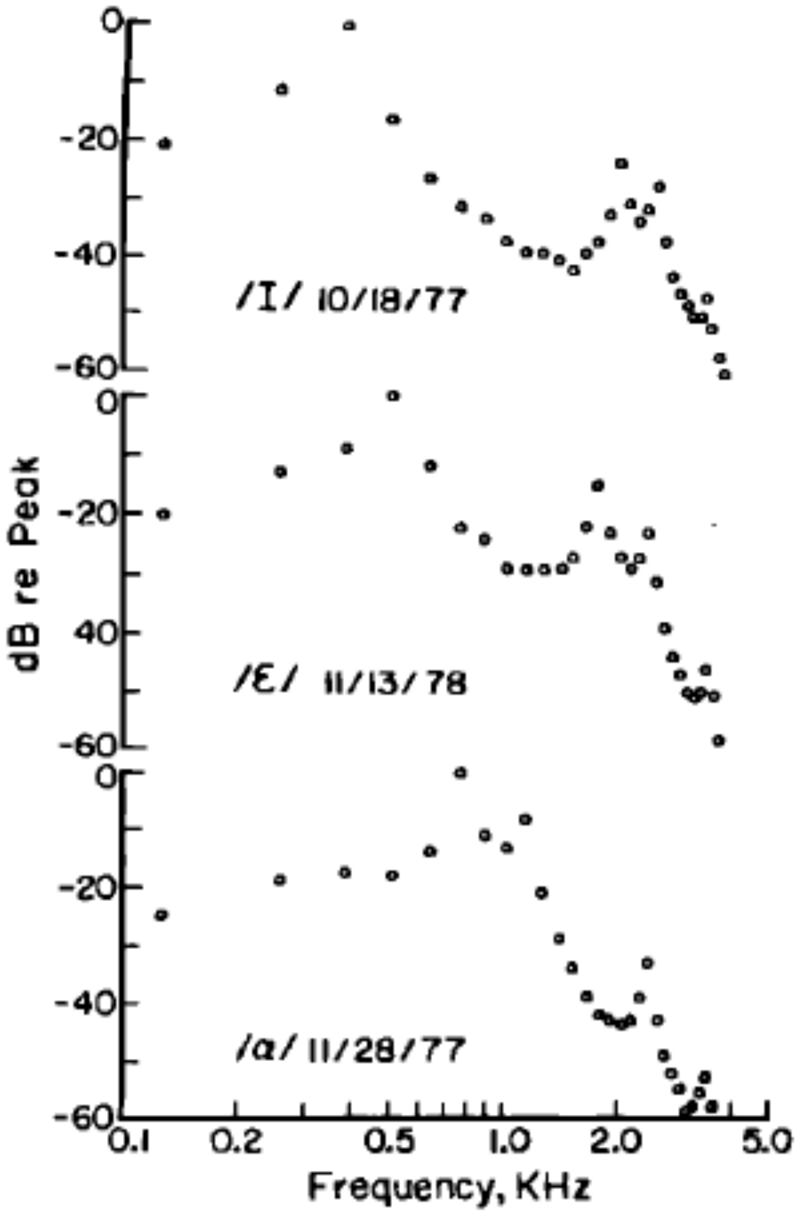


FIG. 1. Top plot shows sound pressure near the eardrum for constant amplitude electrical signal into the earspeaker. This was measured using the probe tube system described by Sokolich (1977) during experiment 10/18/77. Bottom three plots show amplitude spectra of the three vowels for which data are presented in this paper; these were measured near the cat's eardrum during the experiments. Each point is the amplitude of one harmonic of these steady-state vowels; the vowels are periodic with fundamental frequency 128 Hz.

Auditory nerve can represent speech sound (e.g., vowel) by:

1)Firing rate
2)Temporal discharge pattern

Representations of vowel spectrum by normalized firing rate of auditory nerve (AN)

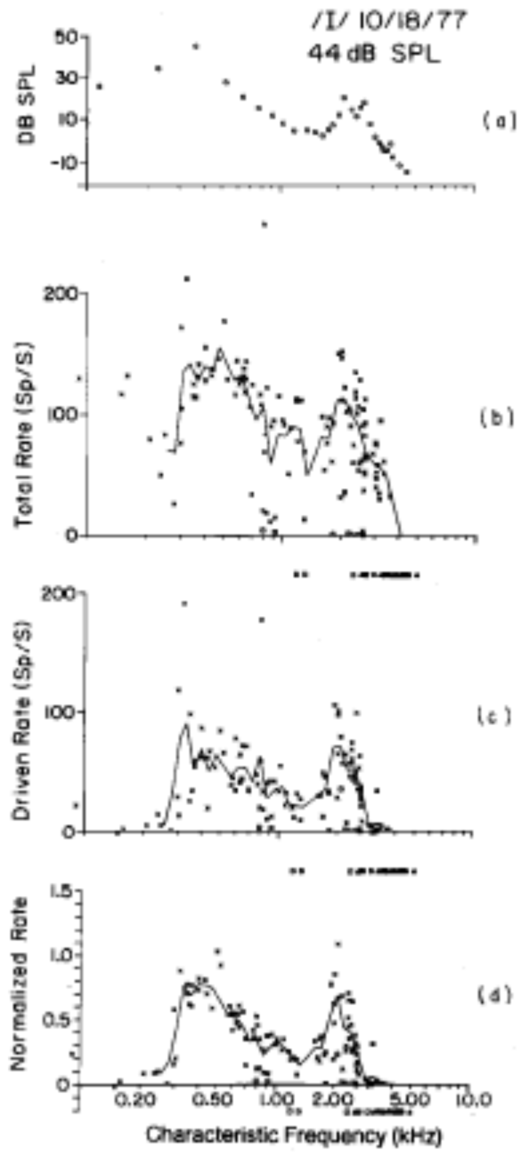


FIG. 2. (a) Spectrum of the synthesized /I/ measured near the eardrum in experiment 10/18/77; plotted as the sound-pressure level of each harmonic when the overall stimulus was at 44 dB SPL. (b) Discharge rate in response to /I/ at 44 dB SPL of each fiber studied at this sound level in experiment 10/18/77 (115 fibers). Each point is rate of one unit plotted at the unit's CF. Units with spontaneous rate less than 1/s plotted with squares; other units with X's. Line is average rate of units with spontaneous rate greater than 1/s, computed as described in the text. (c) Same data as in (b), except plotted as rate minus spontaneous rate. (d) Same data as in (b), except plotted as (rate minus spontaneous rate) divided by (saturation rate minus spontaneous rate).

Firing rate representation of AN degrades at high sound levels

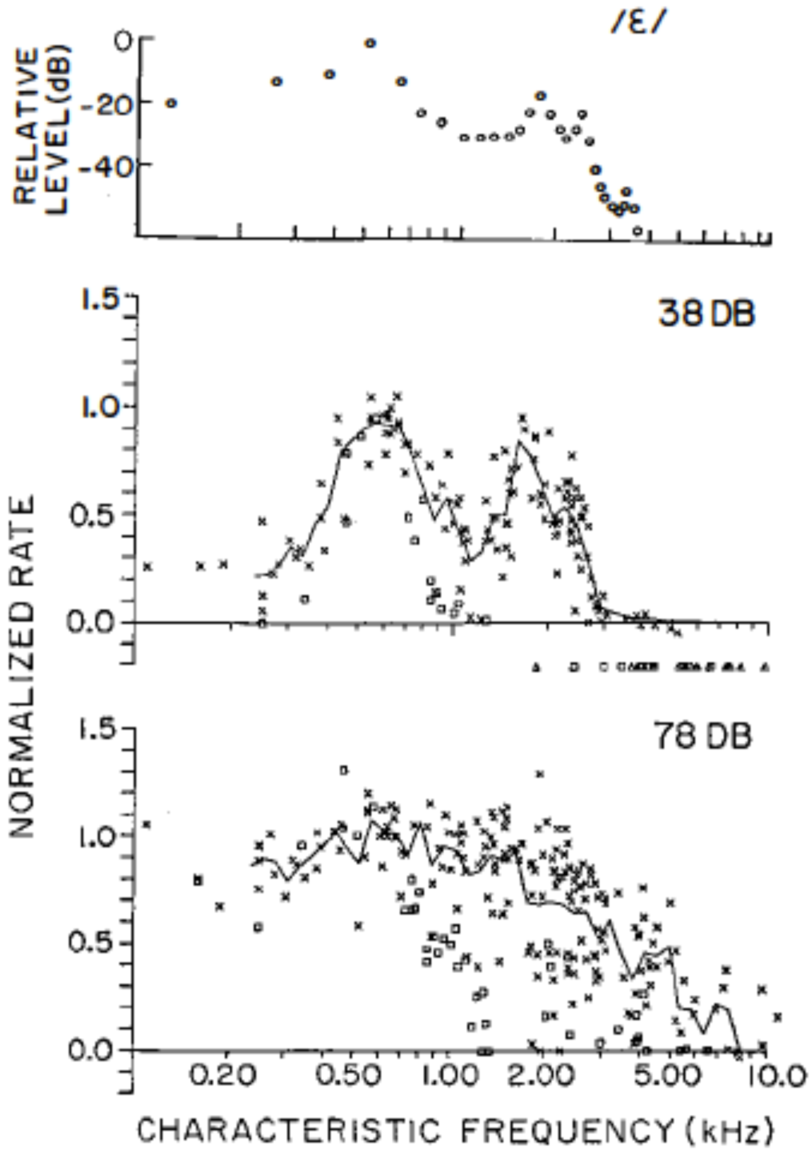


Figure 2 Top: Amplitude spectrum of /ɛ/. *Middle:* Plot of normalized rate vs characteristic frequency for units studied on 11/13/78 with /ɛ/ as the stimulus at 38 dB SPL. *Bottom:* Same as middle but at stimulus level of 78 dB SPL.

Sachs and Young 1979

Low-spontaneous AN can represent vowel spectrum by firing rate at high sound levels

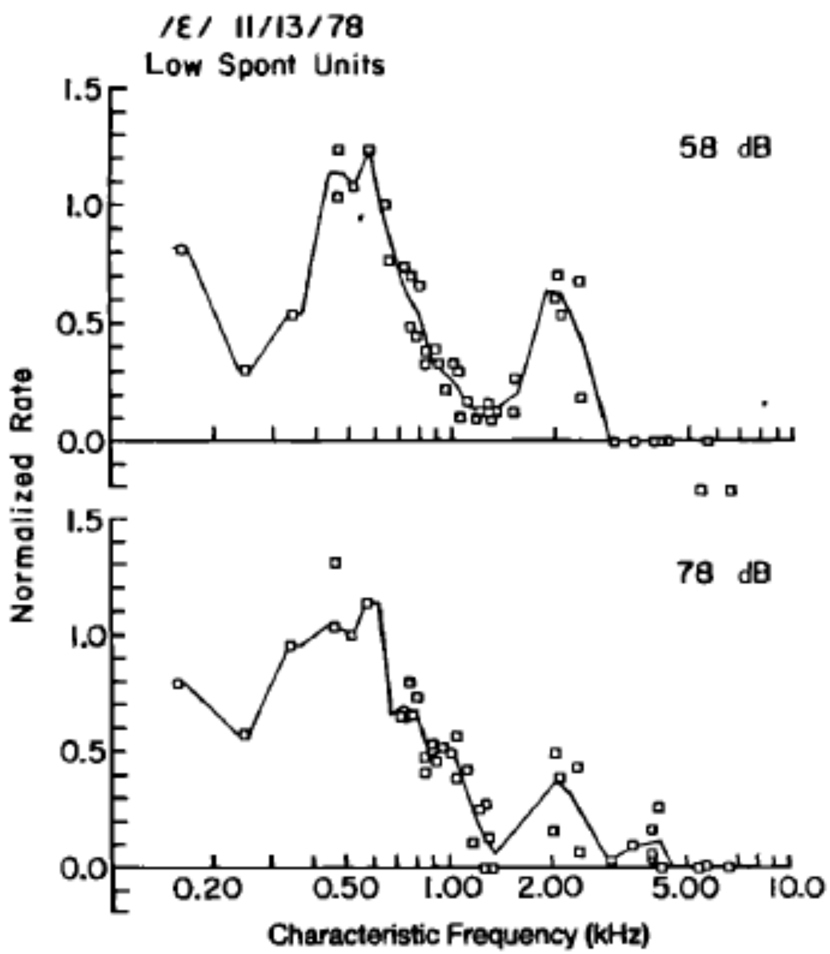
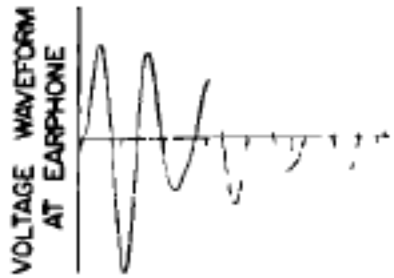


FIG. 12. Normalized rate vs CF for low spontaneous rate units (less than 1/s) studied on 11/13/78 with /ɛ/ as the stimulus. Data are replotted from Fig. 6. In this case, the average curves include all windows containing at least one unit instead of at least three as in other plots.

Temporal Responses to Vowel in AN



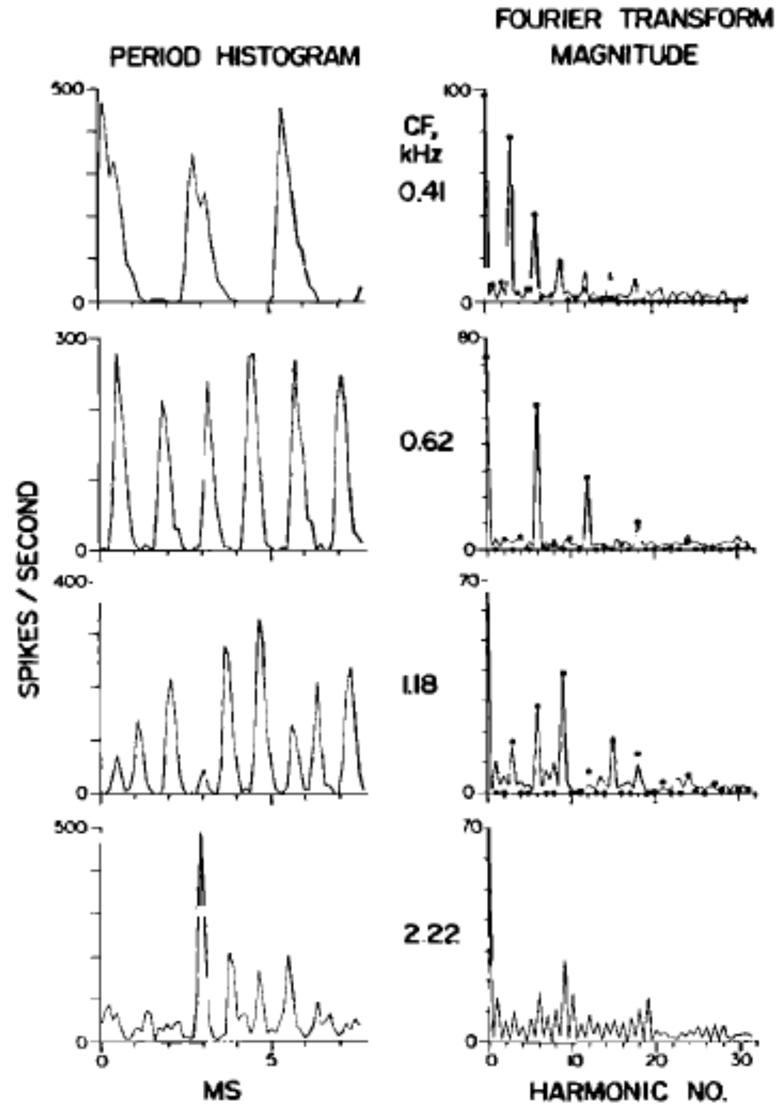


FIG. 2. Period histograms (left column) and amplitude spectra of Fourier transforms of the period histograms (right column) for four single fibers studied on 11/28/77 using /ɑ/ as the stimulus. CFs of the units are shown in the center column. Period histograms are estimates of instantaneous discharge rate as a function of time through one cycle of the vowel; computed with 64 bins per cycle. One pitch period of the vowel (electrical signal at earphone input) is shown at the top of the left column; time scale is the same as the period histograms. Fourier transforms computed from two cycle period histogram which introduces a "noise" point between each adjacent pair of stimulus harmonics. The dots on the top three Fourier transform plots show the spectra of model histograms fit to these period histograms using the method discussed in the text and in the Appendix.

$$r(n) = R_0 + 2 \sum_{k=1}^{N/2-1} R_k \cos(2\pi kn/N + \theta_k) ,$$

$$n = 0, 1, 2, \ldots, N-1 .$$

The magnitudes of the Fourier transforms (the R_k)

Representing Vowel Spectrum by Synchronized (phase-locked) Firing
"Average localized synchronized rate (ALSR)"

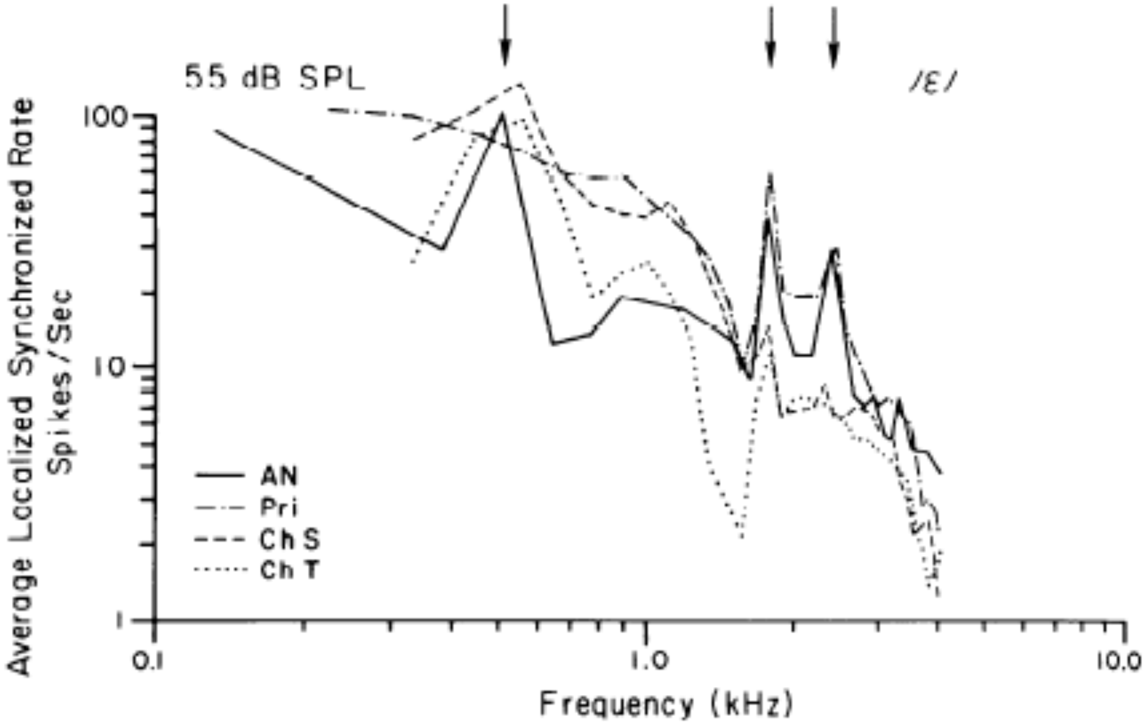


FIG. 18. Average localized synchronized rate profiles of responses of ANFs (solid line), Pri units (dot-dashed line), ChS units (dashed line), and ChT units (dotted line) to /ε/ at 55 dB SPL. All lines are plotted on the same scale. ANF data from Young and Sachs (1981).

$$\mathrm{ALSR}(k) = \frac{1}{M_k} \sum_{l \in C_k} R_{kl}$$

where C_k is the set of units with CF between $0.707kf_0$ and $1.414kf_0$; M_k is the number of units in C_k; and f_0 is the fundamental frequency of the vowel.

Firing Synchrony Representation Maintained at High Sound Levels

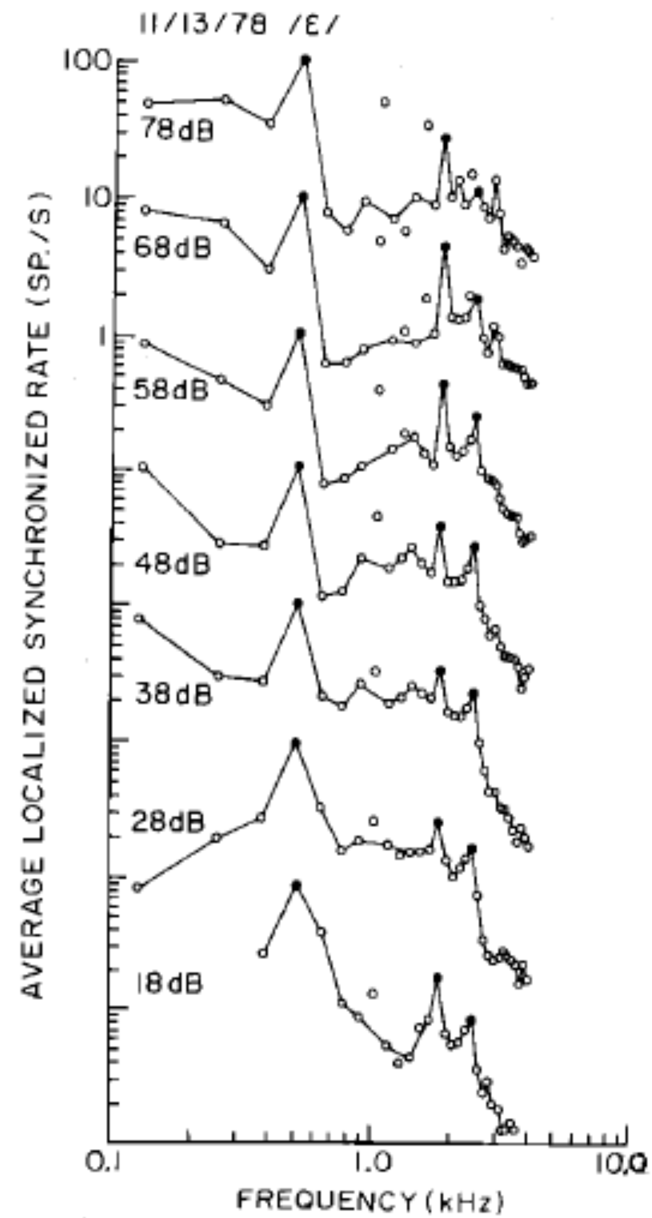
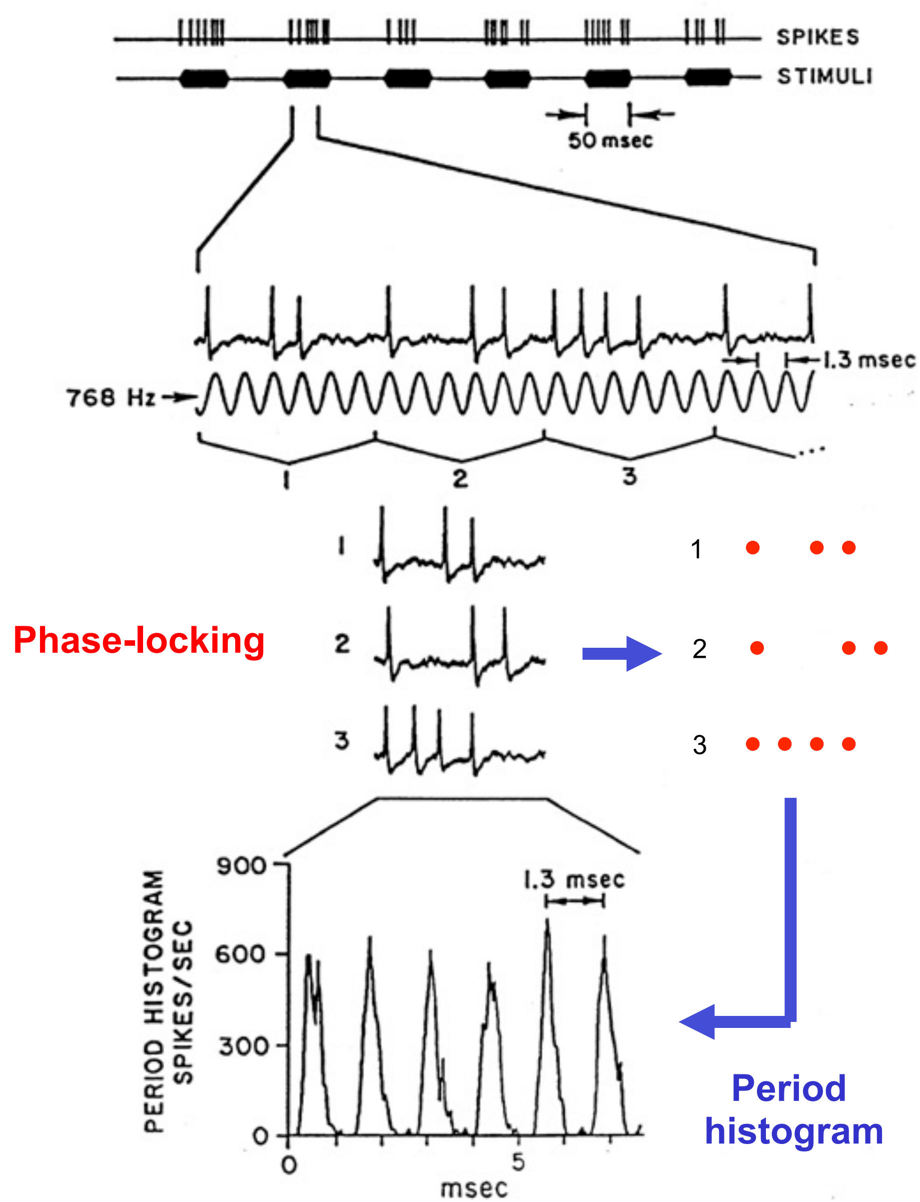


FIG. 6. The points show average localized synchronized rate computed according to Eq. (3) for responses to /ε/ at all sound levels used in experiment 11/13/78. There is one point for each harmonic up to the 32nd. Points corresponding to formant frequencies are plotted with filled circles. Ordinate is scaled logarithmically. Plots are shifted vertically from one another by one order of magnitude for clarity. Maximum response in each plot is about 100 spikes/s. The lines are drawn through all points except those corresponding to the 2nd and 3rd harmonics and the sum and difference tones of the first two formants. See rules given in text.

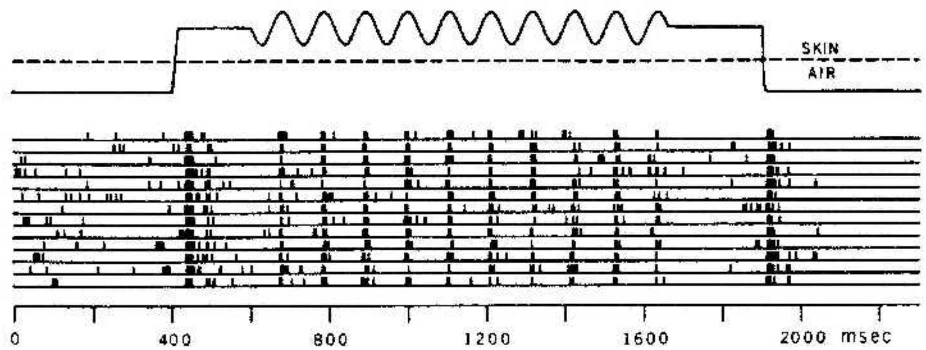
Temporal Structure of Spike Trains

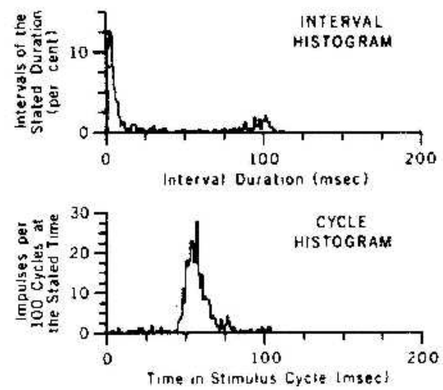
This figures illustrates a phenomenon called "phase-locking" and how to characterize it using the *period histogram*. When burst of tone of a given frequency (represented by the black bars) 50 msec in duration are presented to the ear, auditory-nerve fibers respond with an increase in firing rate of spikes. On an expanded time scale we can see individual cycles of the tone as well as the spikes in more detail. When a spike occurs it always occurs at about the same point (or phase) in the tone cycle. We call this alignment of spikes "phase-locking". We get a quantitative measure of phase-locking as follows: We extract short segment of the spike train (six stimulus cycles long in this case, although the number of cycles used is arbitrary); we line the segments up so tat their starting points coincide. From many such segments (say a total of 5 seconds of spike train record) we construct a histogram of the times when the spikes occur relative to the waveform of the stimulus over a 6-cycle period. This histogram is called a "period histogram" because the response is aligned with the stimulus periods. Phase-locking is shown by the peaks in the period histogram which occur once each stimulus cycle (every 1.3 msec here, corresponding to a frequency of 768 Hz).



Phase-locking in the discharges of somatosensory neurons

Composite showing stimulus pattern, replicas of several individual responses, and examples of the four basis methods of analysis. Stimulus-pattern and spike train replicas share the same time axis (top). The stimulus probe, initially in the air above the skin, is moved to indent the skin 500 um and then after a 200-msec delay set into sinusoidal movement for a period of 1 sec. After a further 300-msec delay the probe is removed from the skin. Typically this procedure is repeated 16 times at a rate of one presentation each 5 sec before the sine-wave frequency and/or amplitude is changed. All other parameters are fixed. Transient discharges at onset and removal of the step stimulus are typical of quickly adapting neurons. For the histogram analyses shown in this figure only data collected during actual sinusoidal stimulation are used. Note that the period of the stimulating sine wave is approximately 105 msec. This defines the rightmost meaningful bin in the period histogram (also referred to as the cycle histogram). The multiple discharges seen in the impulse-train replicas is characteristic of the responses to very low frequency sinusoidal stimulation. It obscures the representation of the period of the stimulating since wave and its subharmonics which are frequently seen in inter-spike interval histograms.





Inter-spike Interval histogram

Period histogram

Phase-locking in a spike train can be quantified by synchronization index or vector strength

Method-1:

$$VS = \frac{1}{n}\sqrt{x^2 + y^2} \quad x = \sum_{i=1}^{n} \cos\theta_i \quad y = \sum_{i=1}^{n} \sin\theta_i \quad \theta_i = 2\pi \frac{t_i}{T}$$

where n is the total number of spikes, t_i is the time of spike occurrence and T is the period of the stimulus, VS is the vector strength.

Method-2:

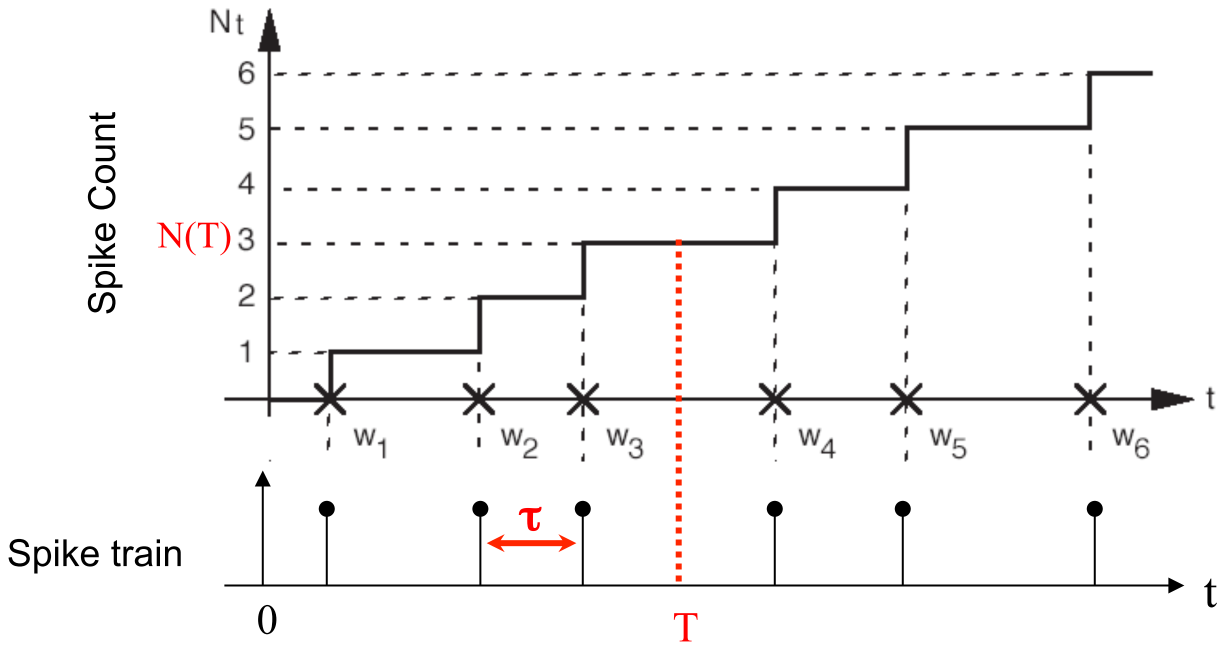
- Find the magnitude of the power spectrum component $R(f_0)$ at stimulus frequency ($f_0 = 1/T$), and then normalize $R(f_0)$ by average discharge rate of the spike train R(0).

Synchronization Index = $R(f_0)$ / R(0)

Spike trains can be modeled as a Poisson process

Spike count: Poisson distribution

$$\mathbf{P(N_T=n) = [(\lambda T)^n/n!] * \exp(-\lambda T)}$$



Inter-spike interval (ISI): Exponential distribution

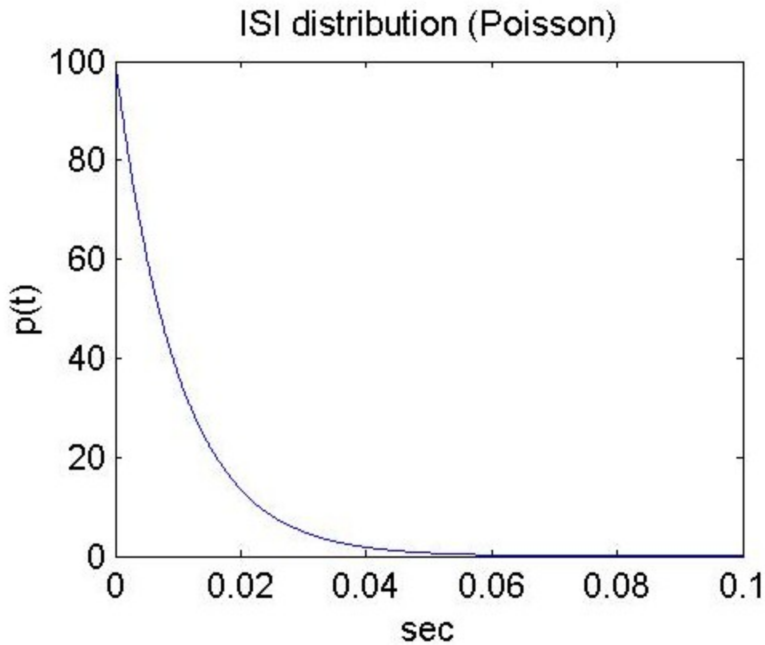
$$\boldsymbol{p(\tau) = \lambda * \exp(-\lambda\tau)}$$

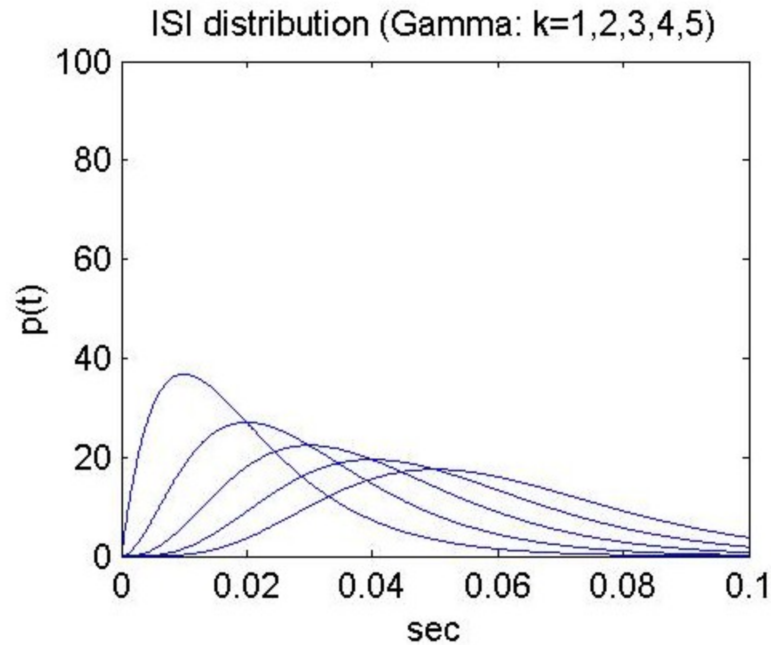
This figure illustrates that a spike train can be modeled as a Poisson processing. There are two equivalent ways to characterize a Poisson process, as a counting process (Poisson distribution) or as an interval process (exponential distribution). The latter is often more convenient for analyzing spike trains.

Refractory periods modify the Poisson process model

$$p(\tau) = \lambda \exp(-\lambda\tau)$$

$$p(\tau) = \lambda(\lambda\tau)^k \exp(-\lambda\tau)/k!$$



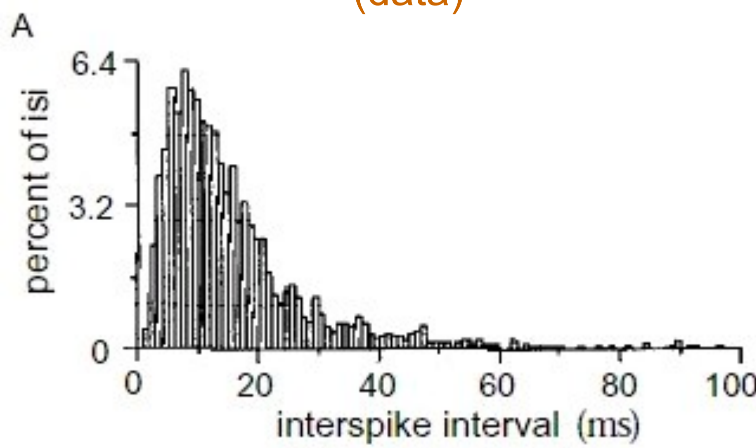


Inter-spike-interval (ISI) distributions for homogeneous Poisson process with exponential function (*left*) and for modified Poisson processes with Gamma functions (*right*).

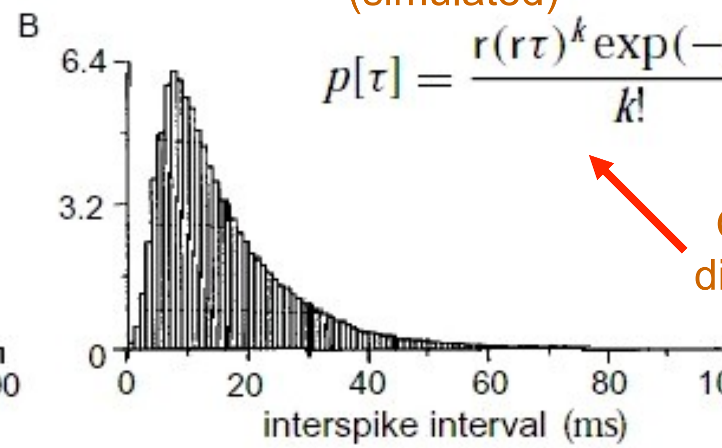
Refractory periods modify the Poisson process model (cont.)

Real world:

ISI histogram
(data)



ISI histogram
(simulated)



$$p[\tau] = \frac{r(r\tau)^k \exp(-r\tau)}{k!}$$

Gamma distribution

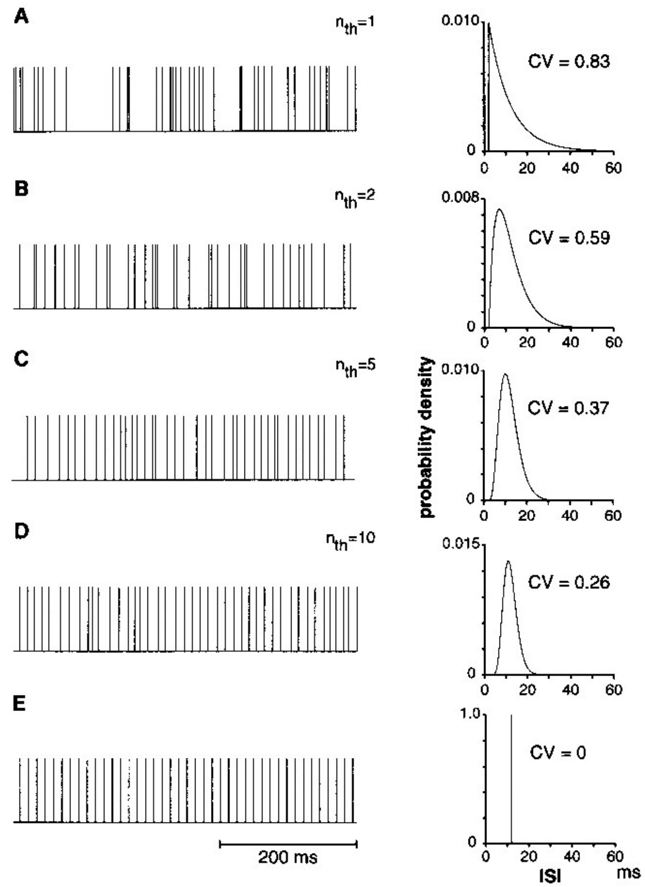
(**A**) Inter-spike interval distribution from a visual neuron responding to a moving random dot image. The probability of inter-spike intervals falling into the different bins, expressed as a percentage, is plotted against inter-spike interval. (**B**) Inter-spike interval histogram generated from a Poisson model with a stochastic refractory period.

The randomness of a spike train can be quantified by Coefficient of Variation (CV) analysis.

$CV = \sigma(\tau) / E(\tau)$

Poisson process:

$E(\tau) = 1/\lambda$
$\sigma^2(\tau) = 1/\lambda^2$
$CV = 1$



Sample spike trains and inter-spike interval (ISl) distributions from various models in response to a constant current input into a perfect integrator model. All models have an absolute refractory period of 2 msec and a mean firing rate of 83 Hz. (A) Poisson-distributed (i.e., exponential) random voltage threshold yields the most irregular spike train and an exponential ISI distribution. In the absence of a refractory period, CV would be 1. (B-D) Gamma-distributed random thresholds of order 2, 5, and 10 yield increasingly regular ISI distributions, which are gamma-distributed of order 2, 5, and 10, respectively. (E) Integrate-and-fire model yields a perfectly regular spike train.

How to simulate a Poisson process?

General Method:

If u is a random variable of uniform distribution [0, 1], and $F(t)$ is the probability distribution function of random variable τ, then

$w=F^{-1}(u)$ is a random variable with probability distribution function $F(t)$.

Poisson process:

$$F(t) = 1 - exp(-\lambda\, t)$$

$$w = F^{-1}(u) = -1/\lambda * ln(1-u)$$

Suggested reading:

1) “*Neuroscience*” textbook, Chapter 13: The auditory system

2) Sachs MB, Young ED. Encoding of steady-state vowels in the auditory nerve: representation in terms of discharge rate. J Acoust Soc Am. 1979 Aug;66(2):470-9.

3) Young ED, Sachs MB. Representation of steady-state vowels in the temporal aspects of the discharge patterns of populations of auditory-nerve fibers. J Acoust Soc Am. 1979 Nov;66(5):1381-1403.