experto en AUDIOLOGÍA

The basic physiology of the auditory nerve

Alan R. Palmer

MRC Institute of Hearing Research, University Park,
Nottingham NG7 2RD.
www.ihr.mrc.ac.uk

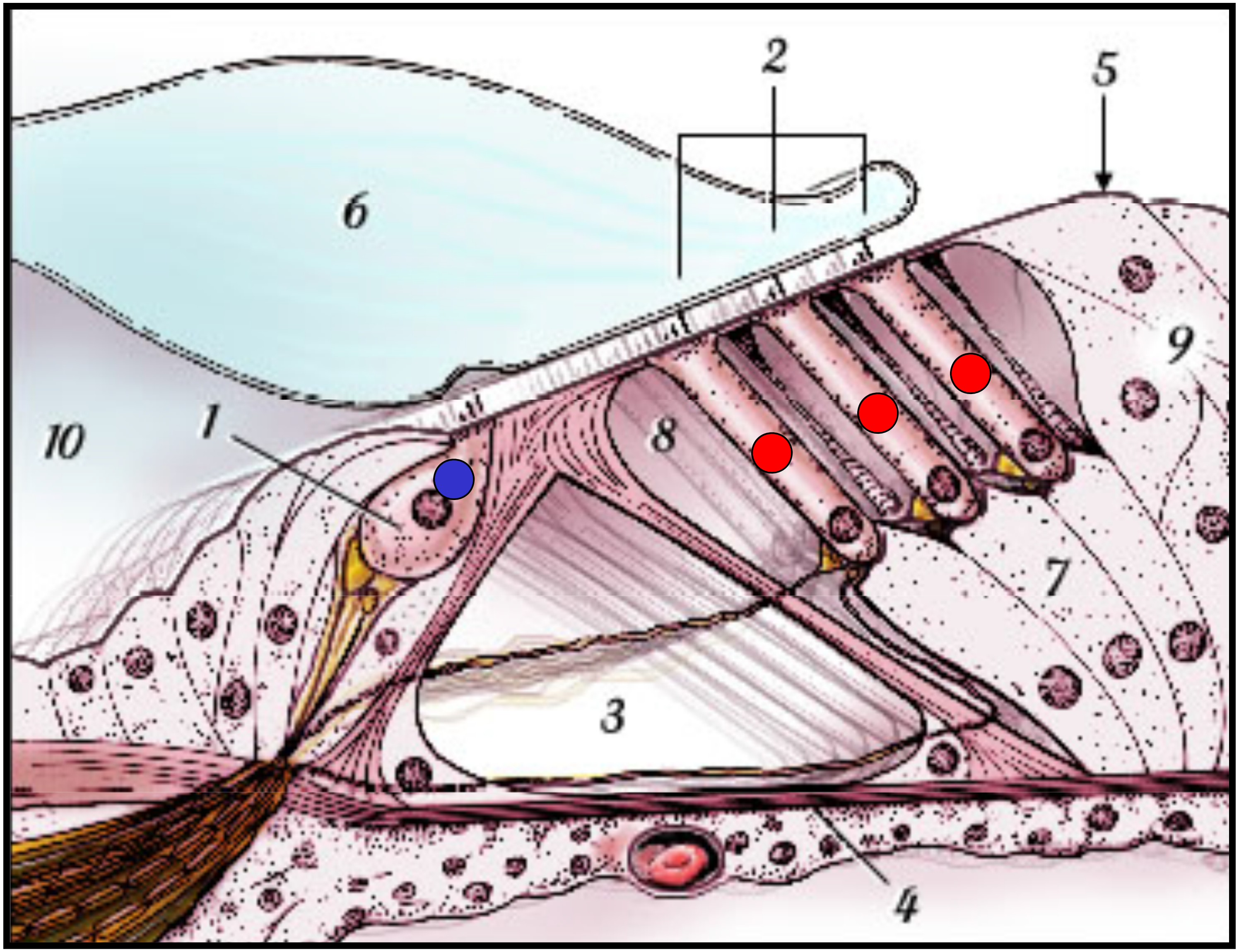
The University of Nottingham
institute of neuroscience
MRC Institute of Hearing Research

This lecture will describe the following topics:

- Responses to sound frequency
- Vulnerability of neural tuning to cochlear insults
- Responses to sound level: different fibre types
- Timing of neural discharges: adaptation, phase-locking
- Responses to complex sound: clicks, noise, 2 tones, amplitude modulation and speech sounds

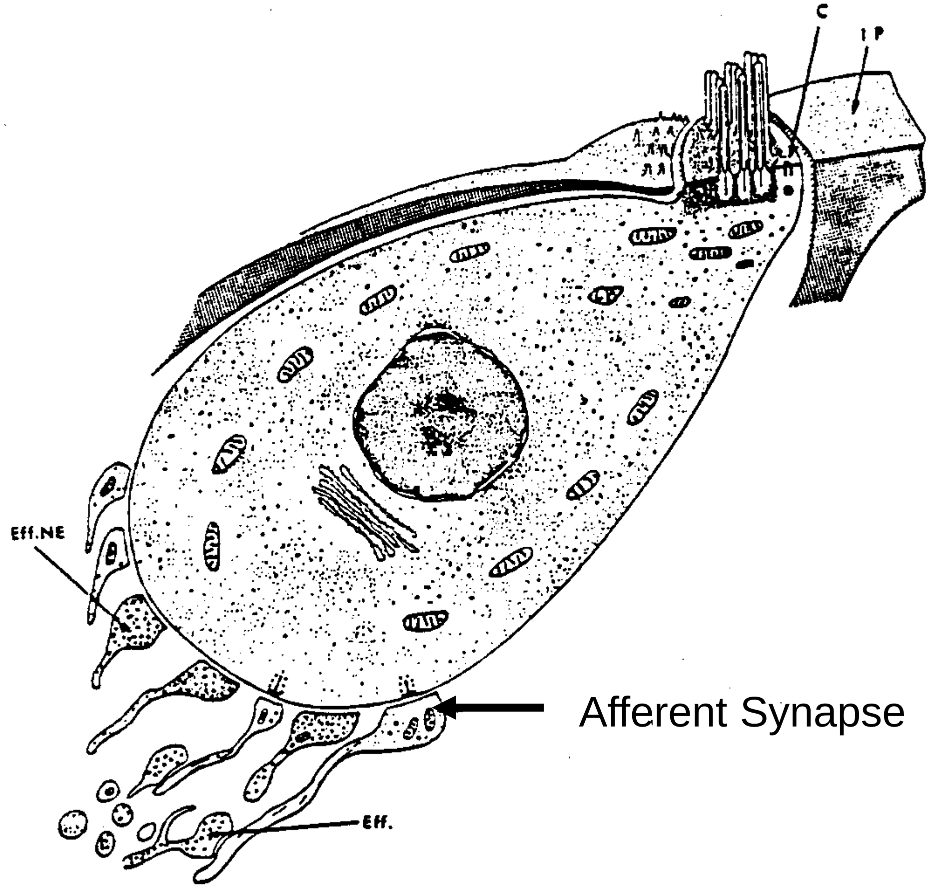
Abstract

The auditory nerve is mainly made up of nerve fibres that innervate the inner hair cells in the cochlea. Its responses are relatively homogeneous. Each nerve fibre is sharply tuned for frequency (matching the basilar membrane vibration pattern). This tuning is physiologically vulnerable: cochlear insults such as noise exposure, ototoxic drugs and hypoxia lead to the elevated threshold and broader tuning that is characteristic of sensorineural hearing loss. Auditory nerve fibres have spontaneous rates that vary from 0 to more than 120 spikes per second. Fibres with the highest rates of spontaneous activity have the lowest thresholds. Once the level of a sound exceeds the fibre's threshold the discharge rate of the fibre rises above its spontaneous rate. Eventually, when the sound is made sufficiently high in level the fibre cannot fire any faster and reaches saturated discharge rate. For high spontaneous rate fibres the shape the function relating firing rate to sound levels is sigmoidal whereas for medium and low spontaneous rate fibres it may deviate from this and even be straight over wide ranges of level. The range over which a fibre changes its discharge rate to signal sound level changes is called the dynamic range. The dynamic range is narrow for high spontaneous rate fibres and wider for medium and low spontaneous rate fibres. When a steady stimulus is turned on the discharge Is highest and then adapts to a steady or adapted rate over tens of milliseconds. On a finer time scale the exact timing of the spikes in low frequency fibres is locked to the stimulus waveform. Such phase-locking is essential for localisation of sound using interaural time differences. The presence of a second tone may suppress the activity to a simultaneously present tone due to interactions between the vibrations in the cochlear: this aids separation of strong components of complex sounds. Speech signals are very complex with many simultaneously present often harmonically related components. The spectrum of such sounds is represented across the population of auditory nerve fibres possibly in terms of the distribution of mean discharge rate, but also in terms of the temporal patterns of activity.



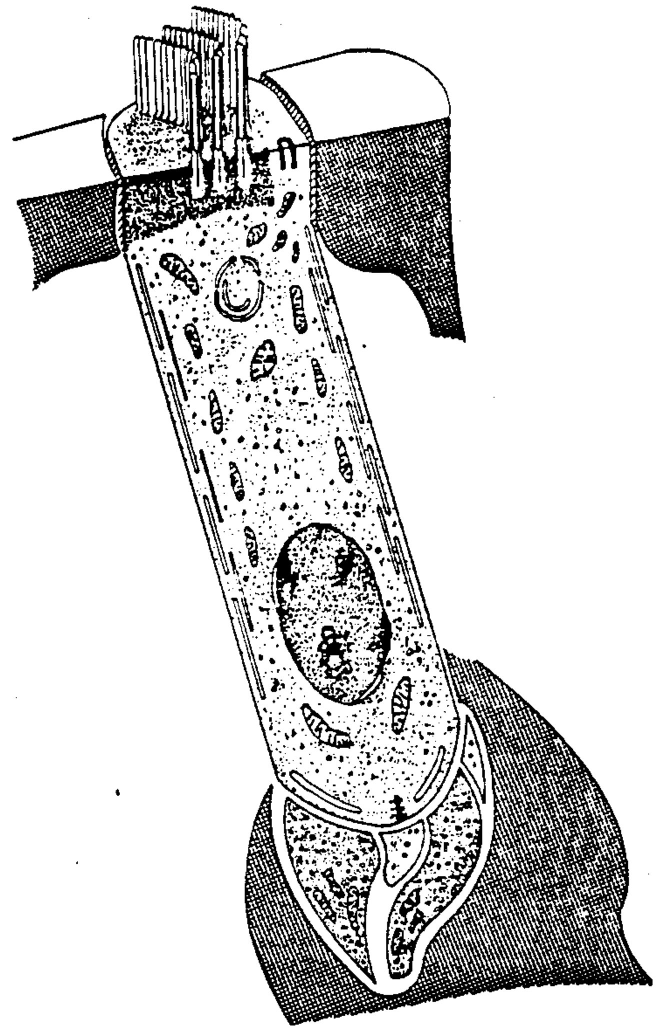
2
5
6
9
10
1
8
7
3
4

Inner Hair Cell



Afferent Synapse

Hair cell systems in the cochlea



Outer Hair Cell

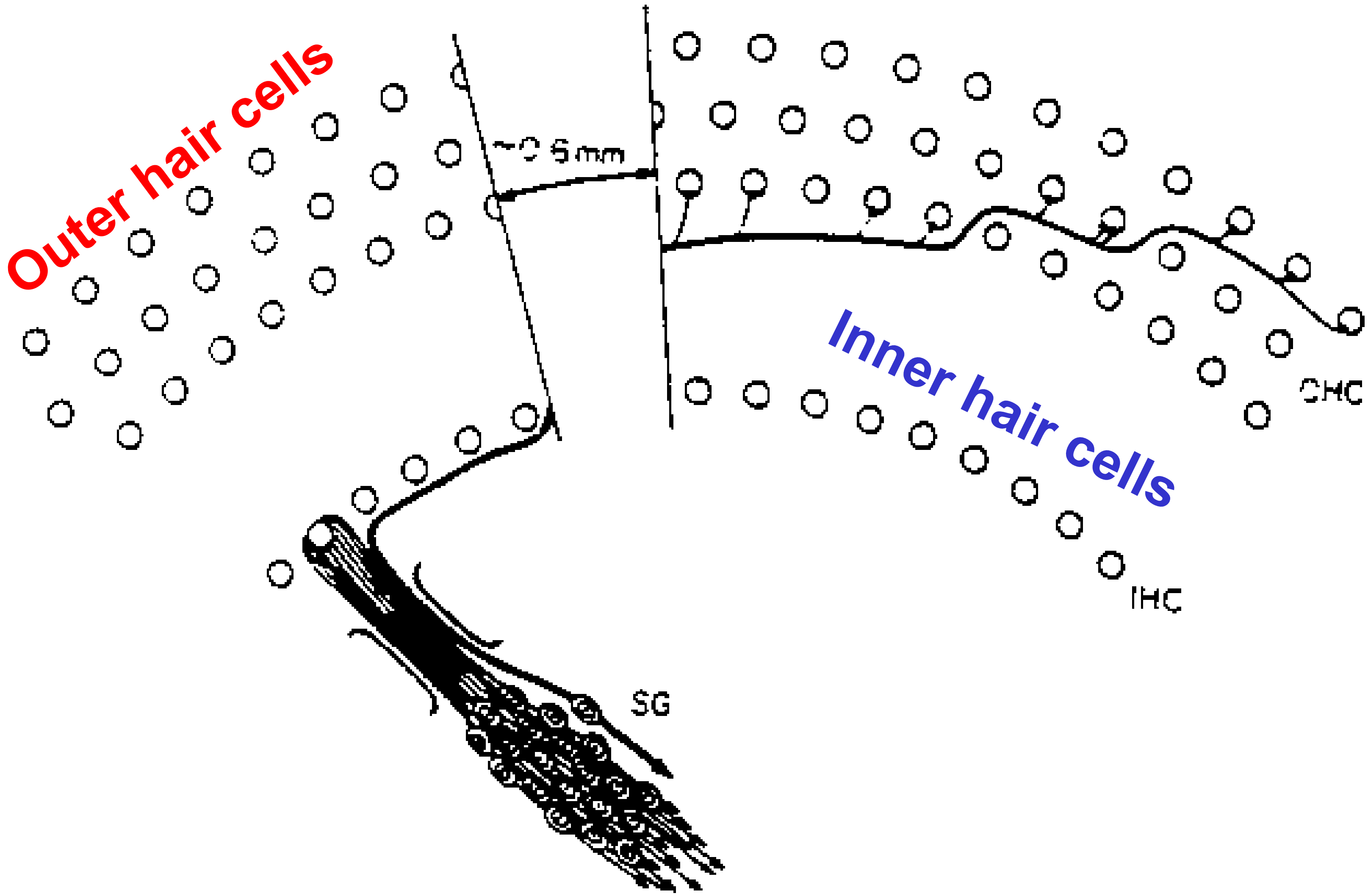
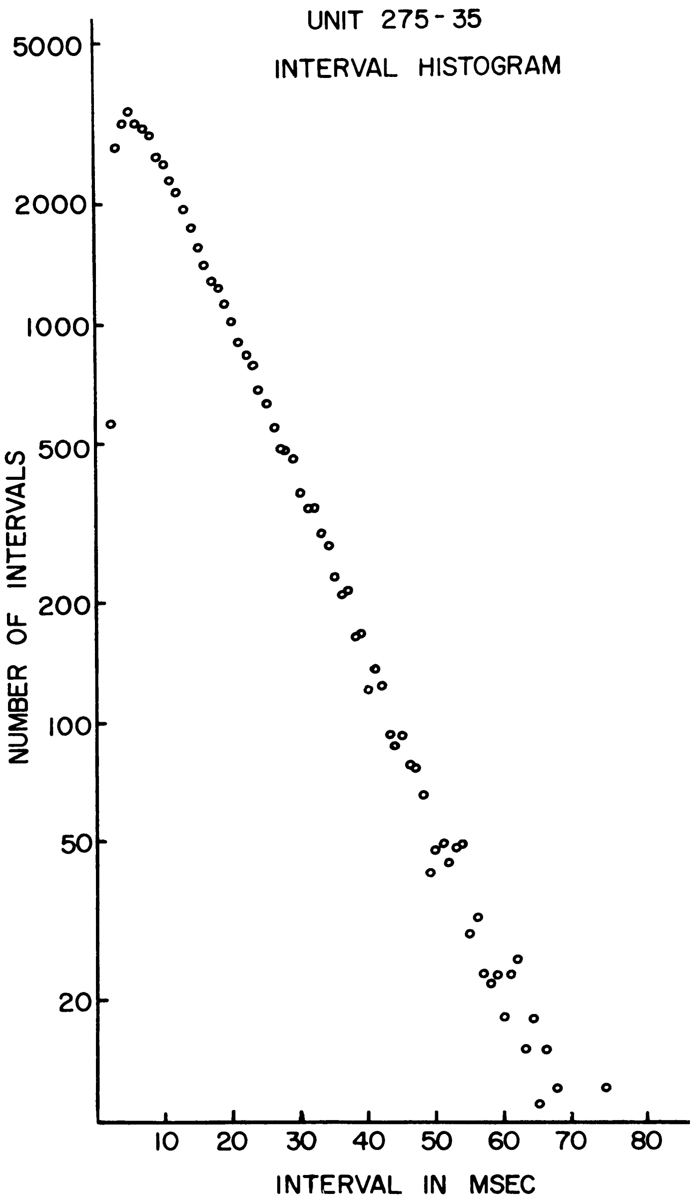


Fig. 3.6 The great majority of auditory nerve fibres connect with inner hair cells. A few fibres pass to outer hair cells, after running basally for about 0.6 mm. IHC: Inner hair cells; OHC: Outer hair cells; SG: Spiral ganglion. From Spoendlin (1978), Fig. 8.

Spontaneous Activity



Kiang et al (1965)

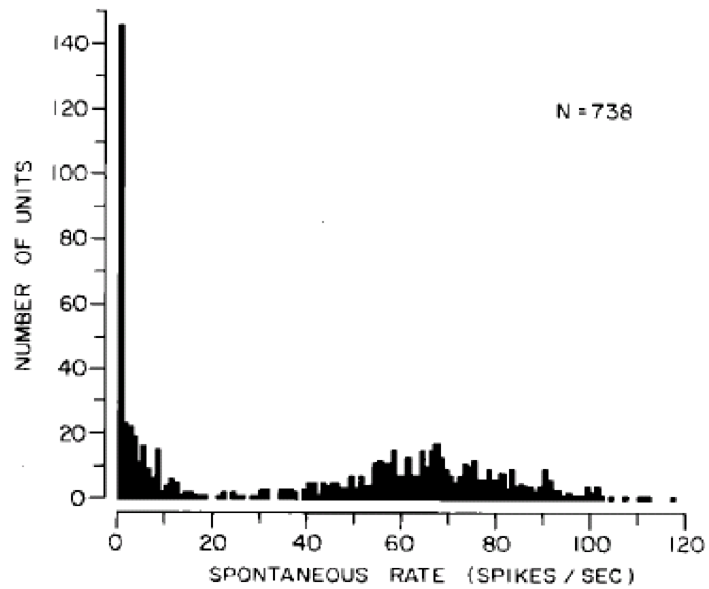
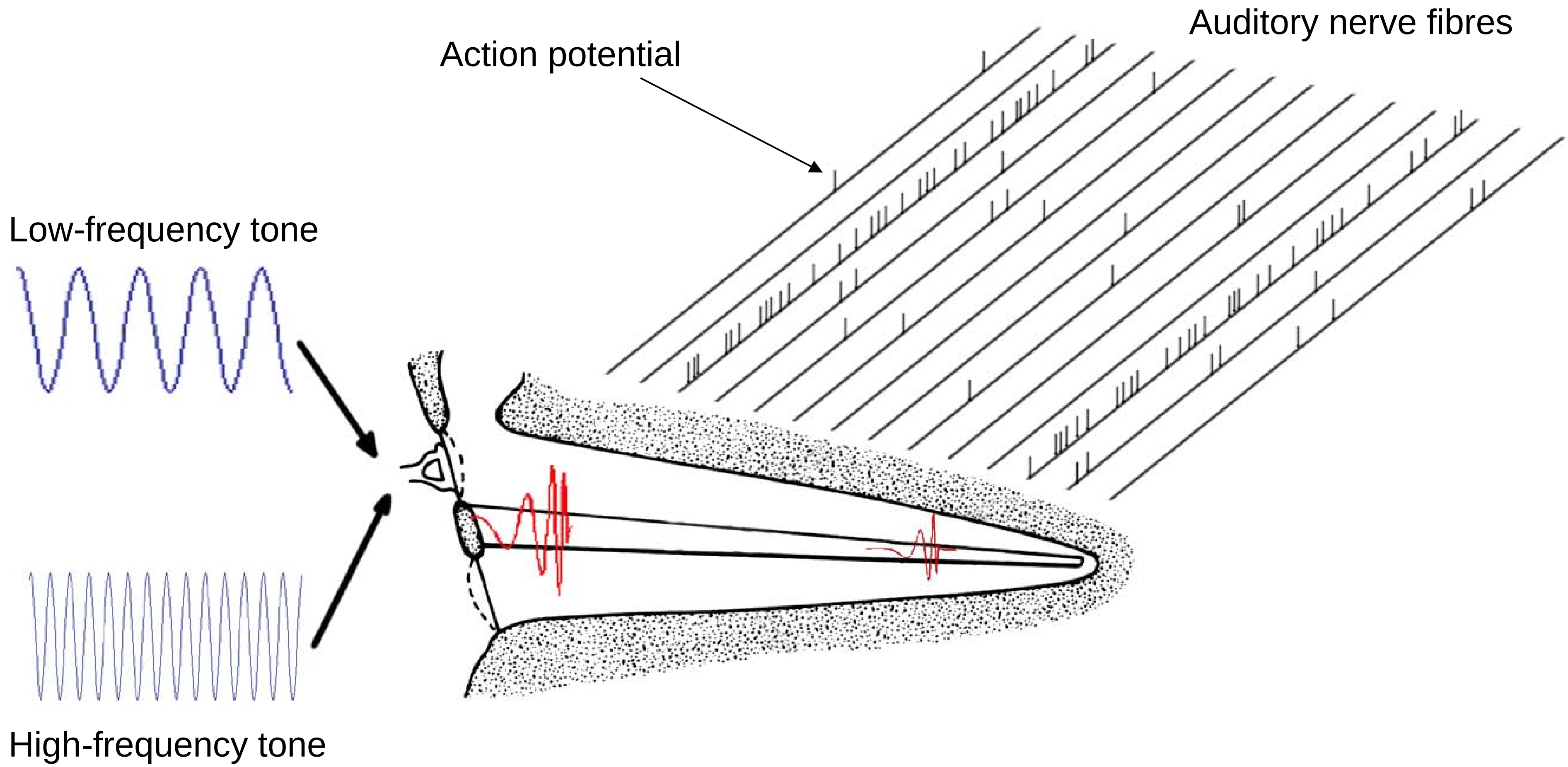


FIG. 9. Histogram of spontaneous rates sampled from the three most sensitive chamber-raised cats (MCL93, 94, 96). The bin width for the histogram is 1 spike/s. The "*N*" refers to the number of units in the sample.

Liberman (1978)

Sound Frequency: tuning in the auditory nerve


Auditory nerve fibres
Action potential
Low-frequency tone
High-frequency tone

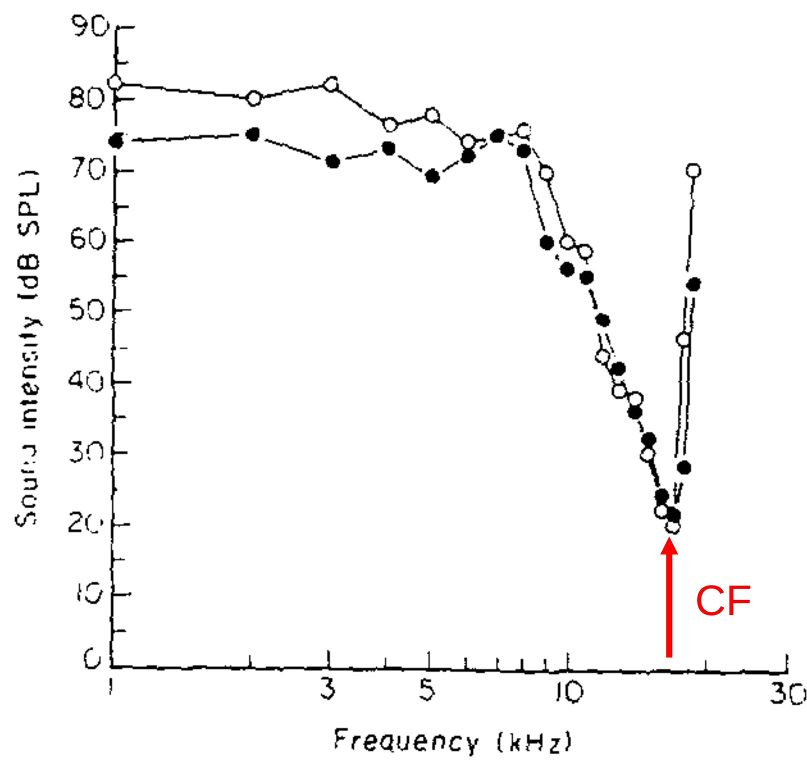
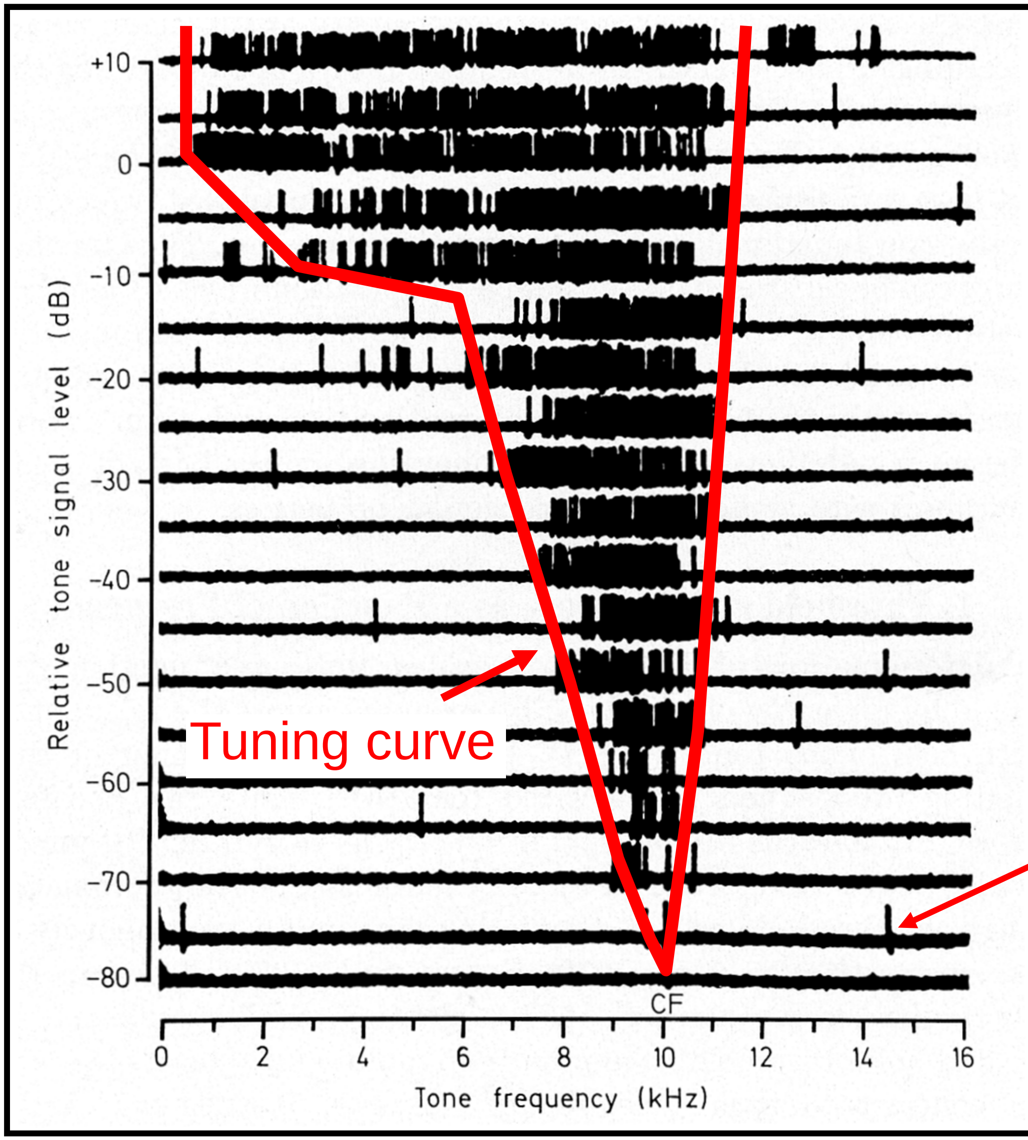


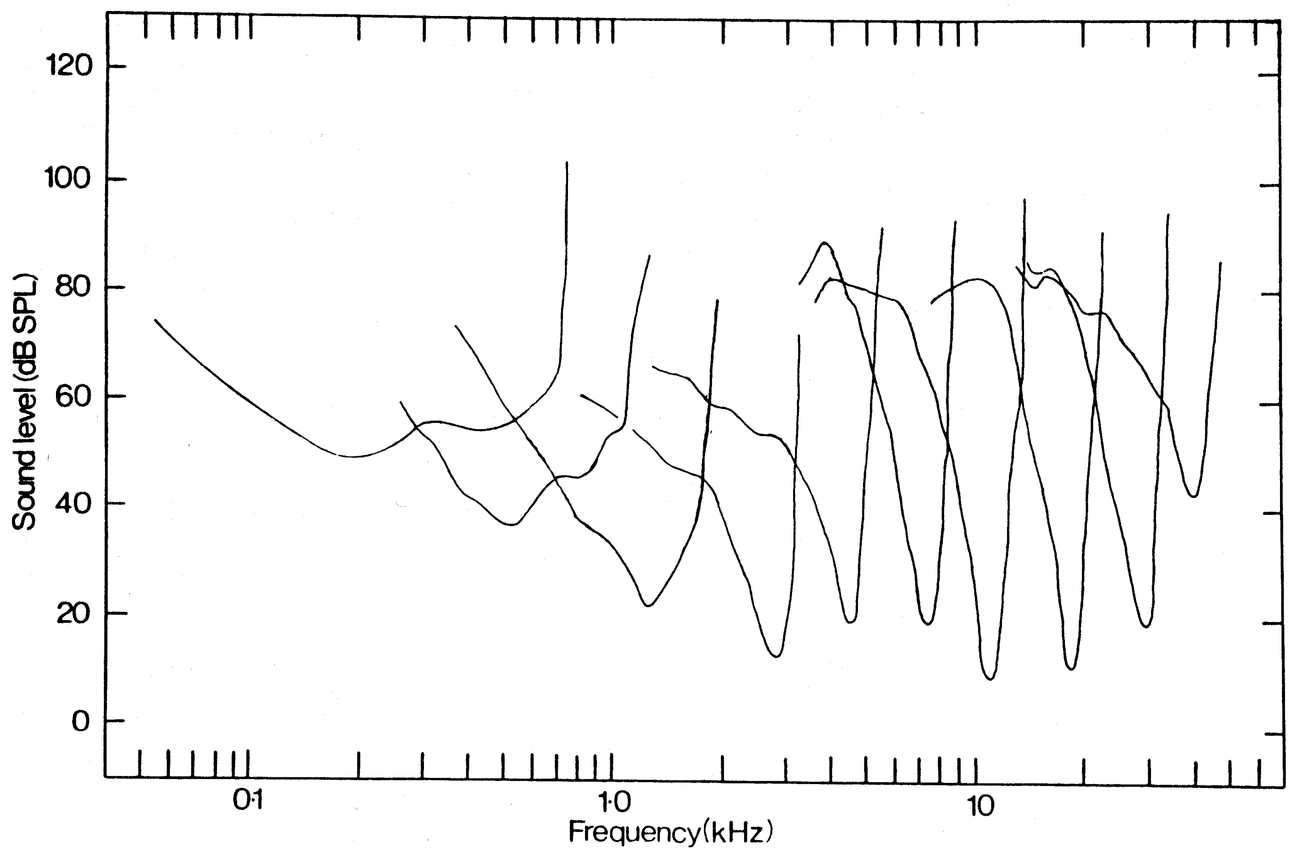
Fig. 3.19 Inner (○) and outer (●) hair cells have very similar tuning curves. The curves are also very similar to those for the mechanical response of the basilar membrane (Fig. 3.10B). From Cody and Russell (1987, Fig. 7).



Each auditory-nerve fibre responds only to a narrow range of frequencies

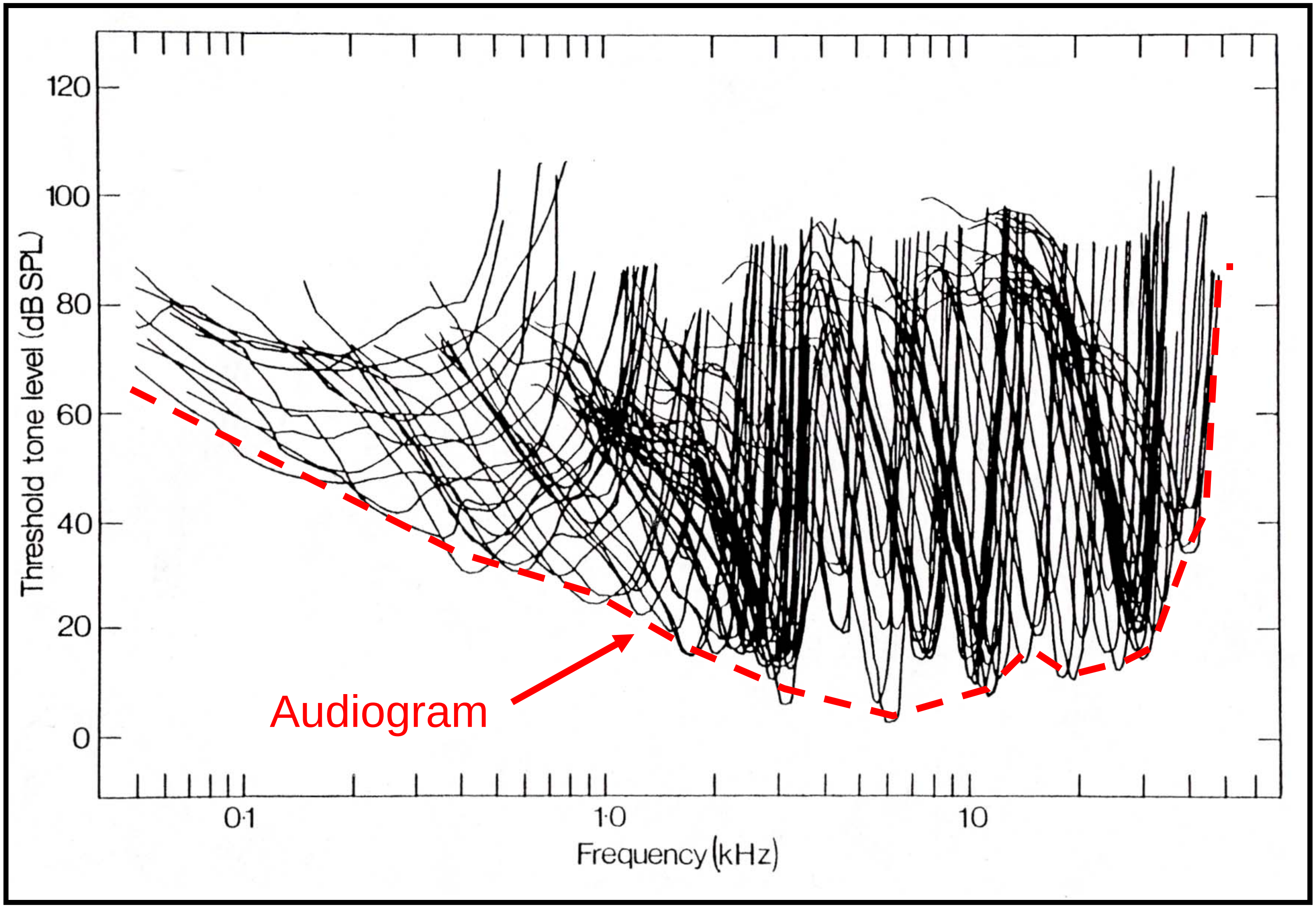
Action potential

Evans (1975)



Palmer and Evans (1975)

There are many overlapping single-fibre tuning curves in the auditory nerve

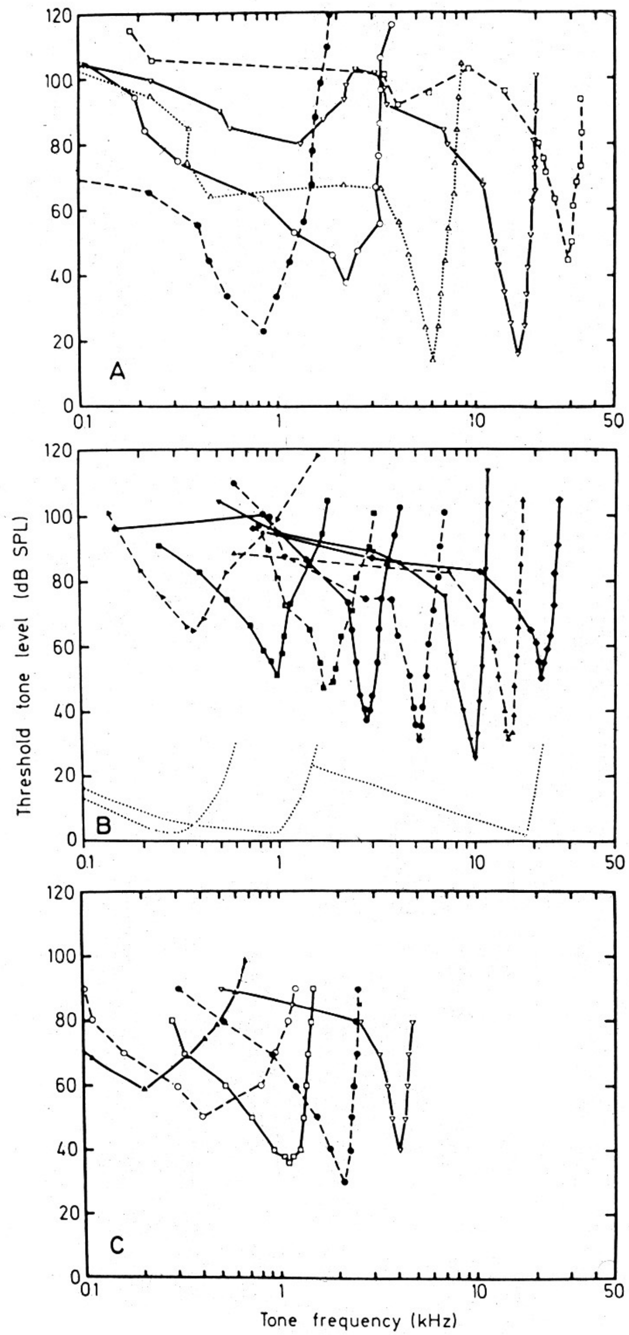


Palmer and Evans (1975)

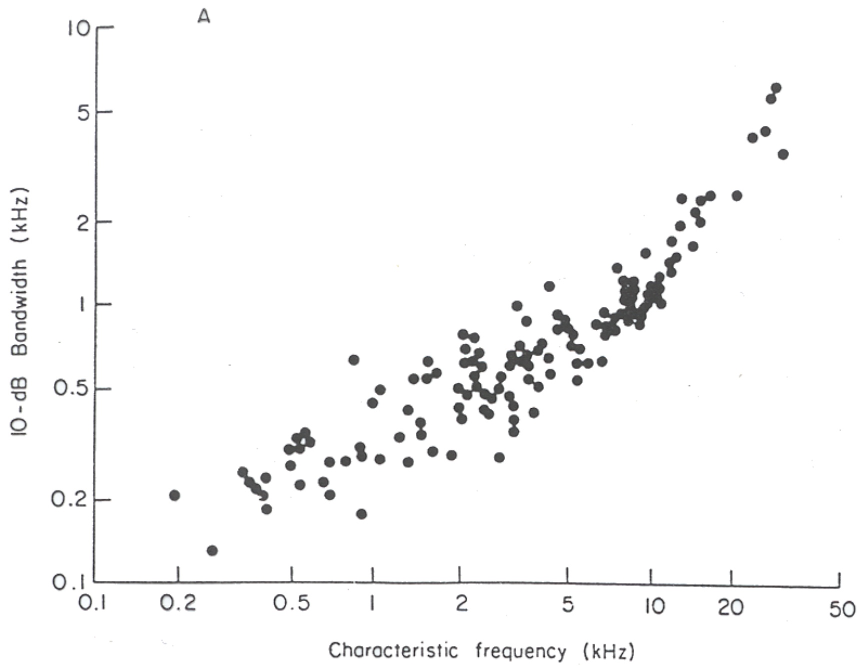
Guinea Pig

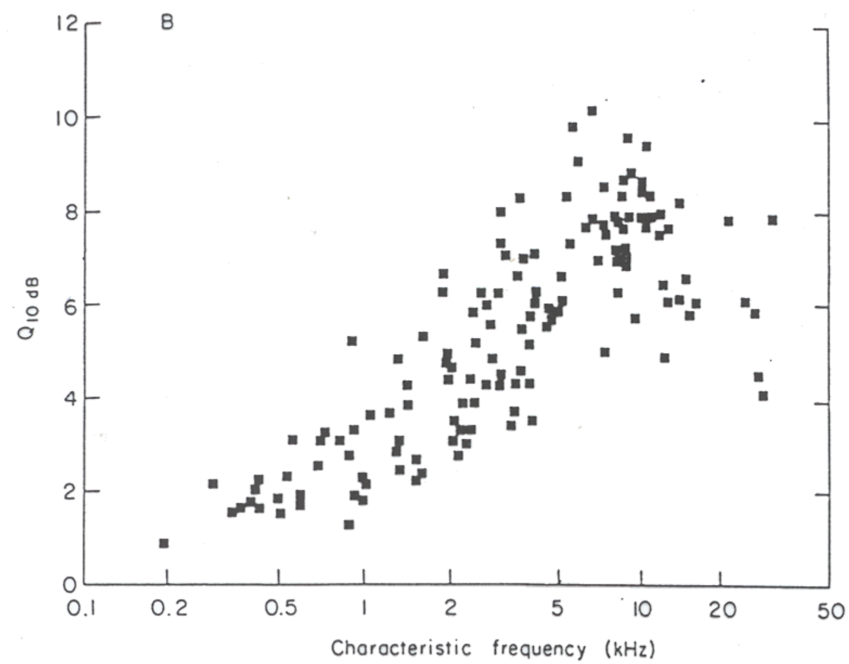
Cat

Squirrel Monkey



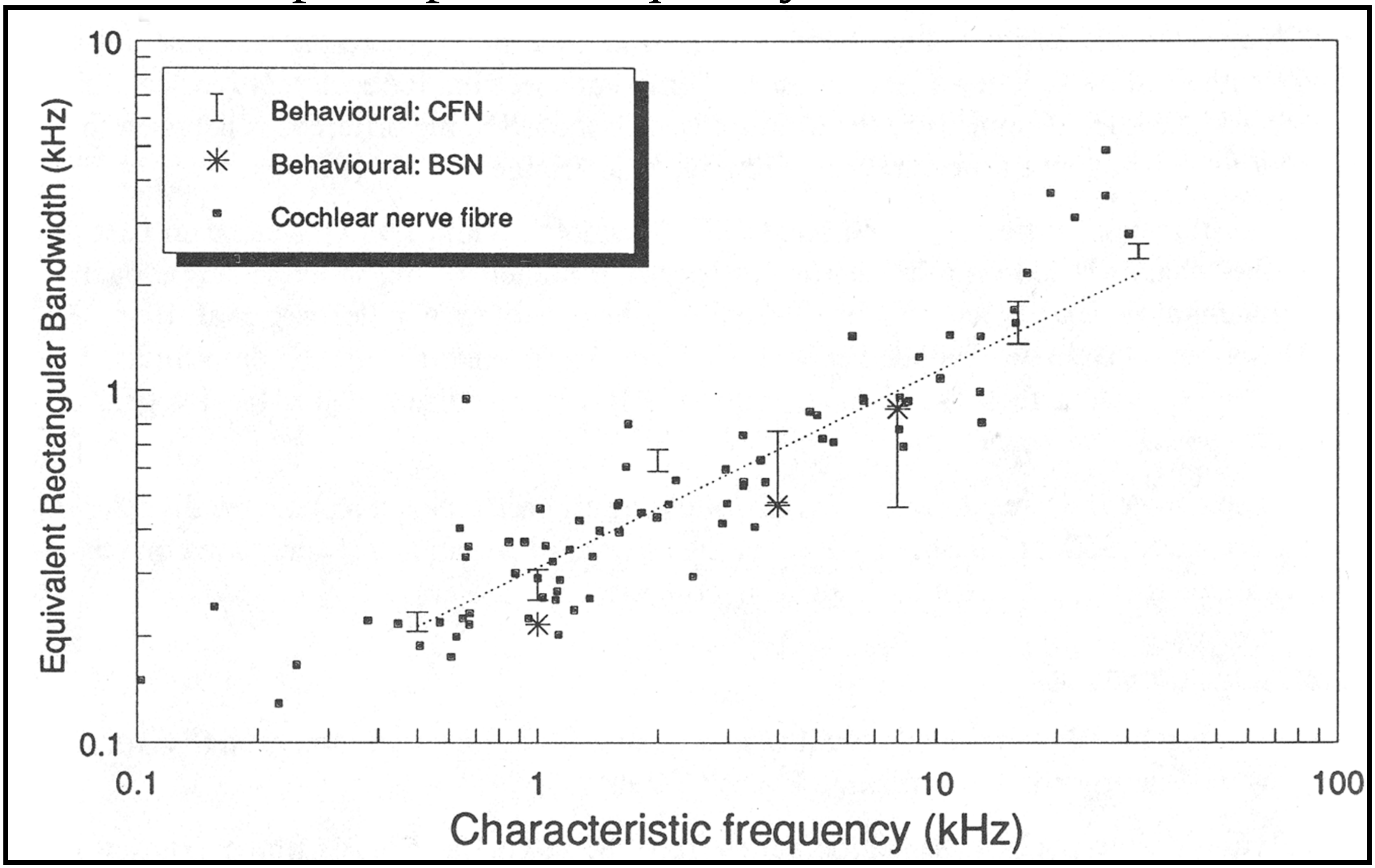
Tuning for sound frequency is ubiquitous


A
10-dB Bandwidth (kHz)
10
5
2
1
0.5
0.2
0.1
0.1
0.2
0.5
1
2
5
10
20
50
Characteristic frequency (kHz)


B
$Q_{10\ dB}$
12
10
8
6
4
2
0
0.1
0.2
0.5
1
2
5
10
20
50
Characteristic frequency (kHz)

Evans (1975)

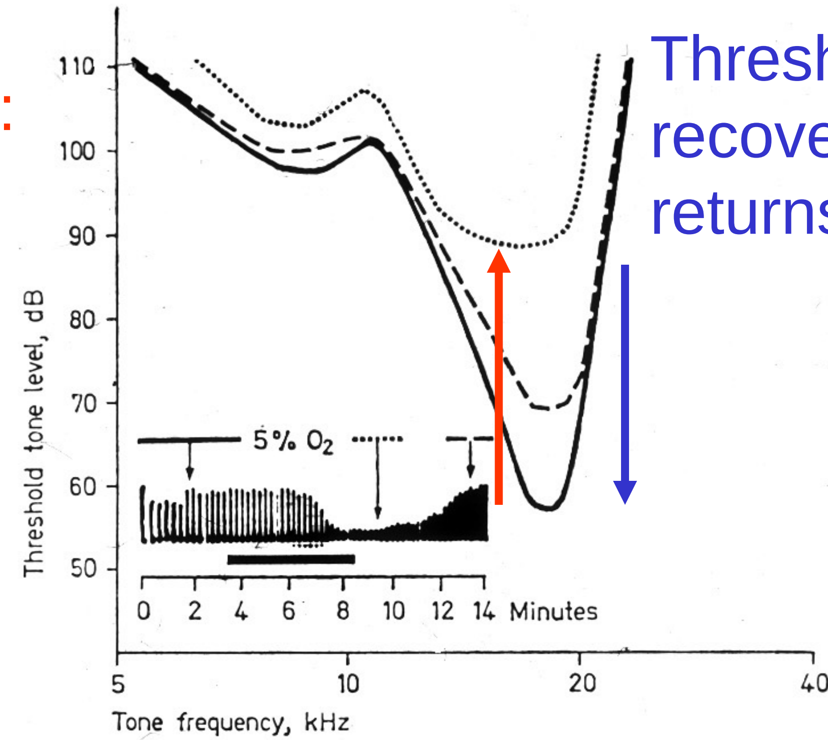
Auditory-nerve filters (tuning curves) determine the perceptual frequency resolution



Evans et al., (1989)

Vulnerability of the Tuning

Reduced oxygen:
High threshold
Broad Tuning

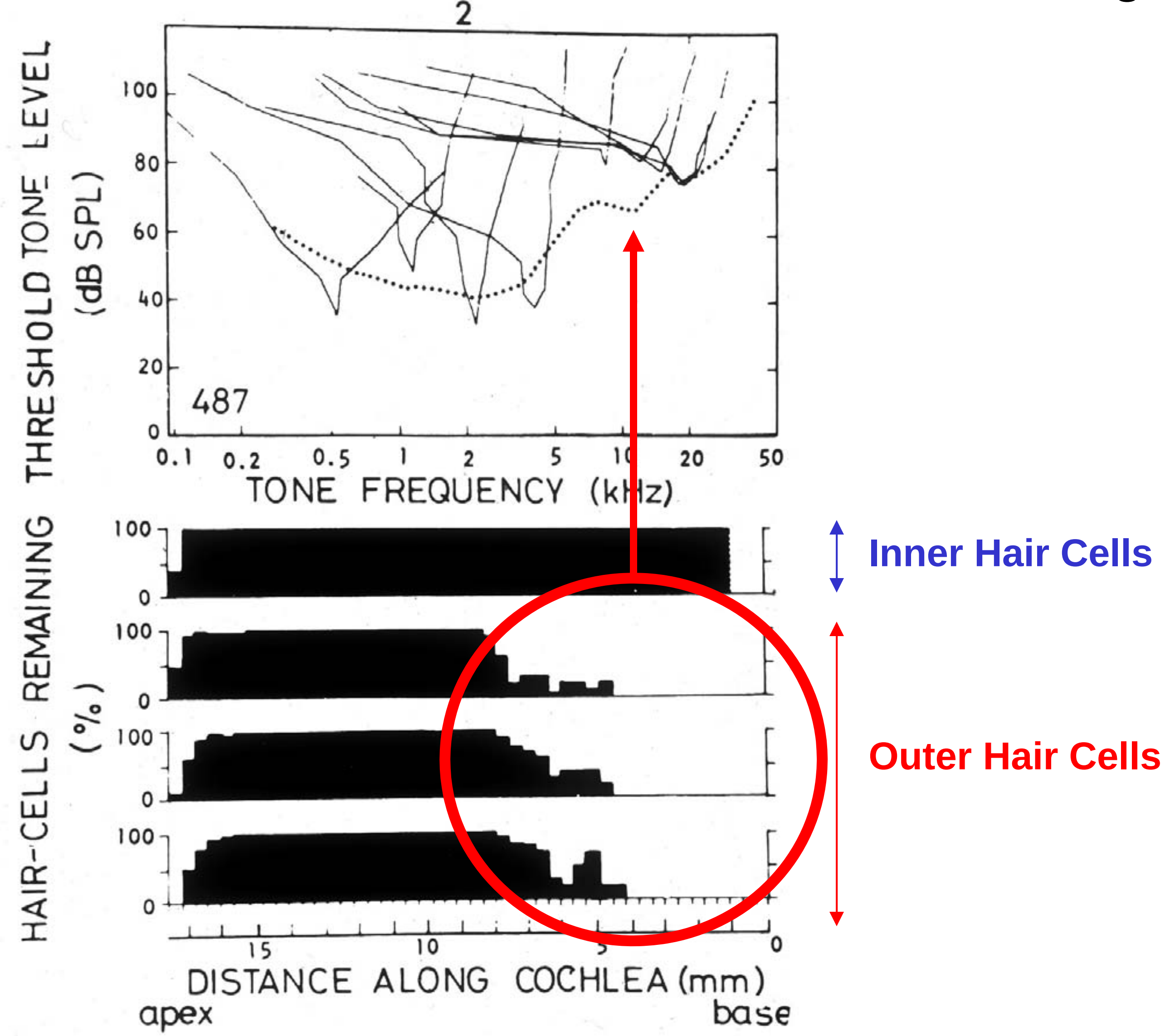


Thresholds and tuning recover when oxygen returns

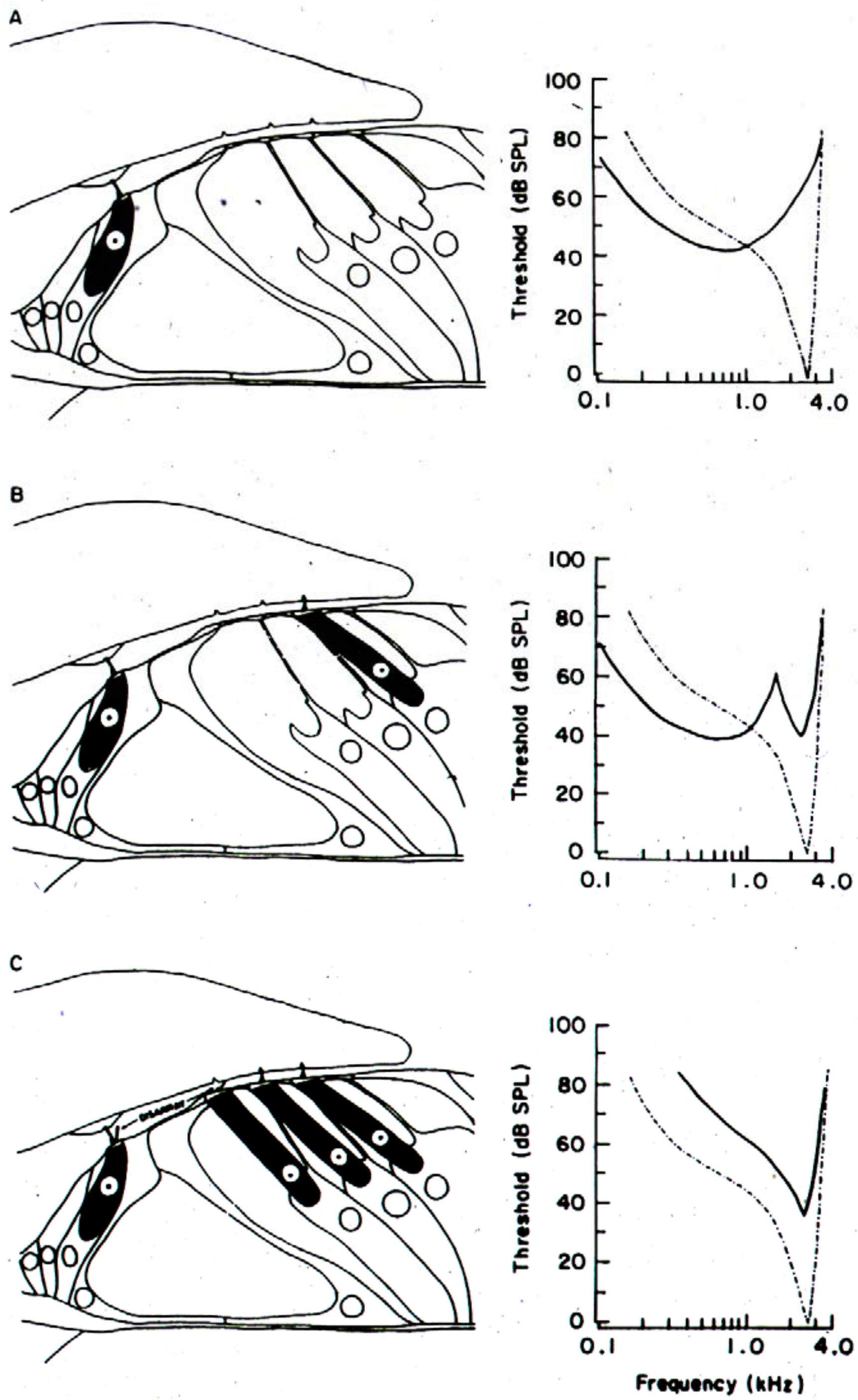
Fig. 4. Effect of hypoxia on the tuning of a single cochlear nerve fibre in the cat. Inset shows time course of gross cochlear AP response amplitude to click stimuli of constant intensity presented at a rate of 1/10 s. Black bar indicates duration of administration of 5% O_2 in N_2O. Bars over the AP record indicate the time during which determinations of the FTC for the fibre, illustrated in the main figure, were taken. The curves were determined from counts of the spike activity evoked during 60-ms tone bursts (shaped to avoid artefacts) of frequency and intensity controlled by an on-line computer to cover the frequency-intensity space of the figure in randomised order. The solid curve is the control FTC. The upper dotted curve is the FTC of the fibre at the height of the hypoxia, as judged from the AP record. The middle dashed curve was obtained during partial recovery of the cochlea from the hypoxia. (These curves have not been corrected for the characteristics of the sound system and therefore represent *relative* thresholds.)

Evans (1975)

Ototoxic drugs also cause threshold loss and broad tuning

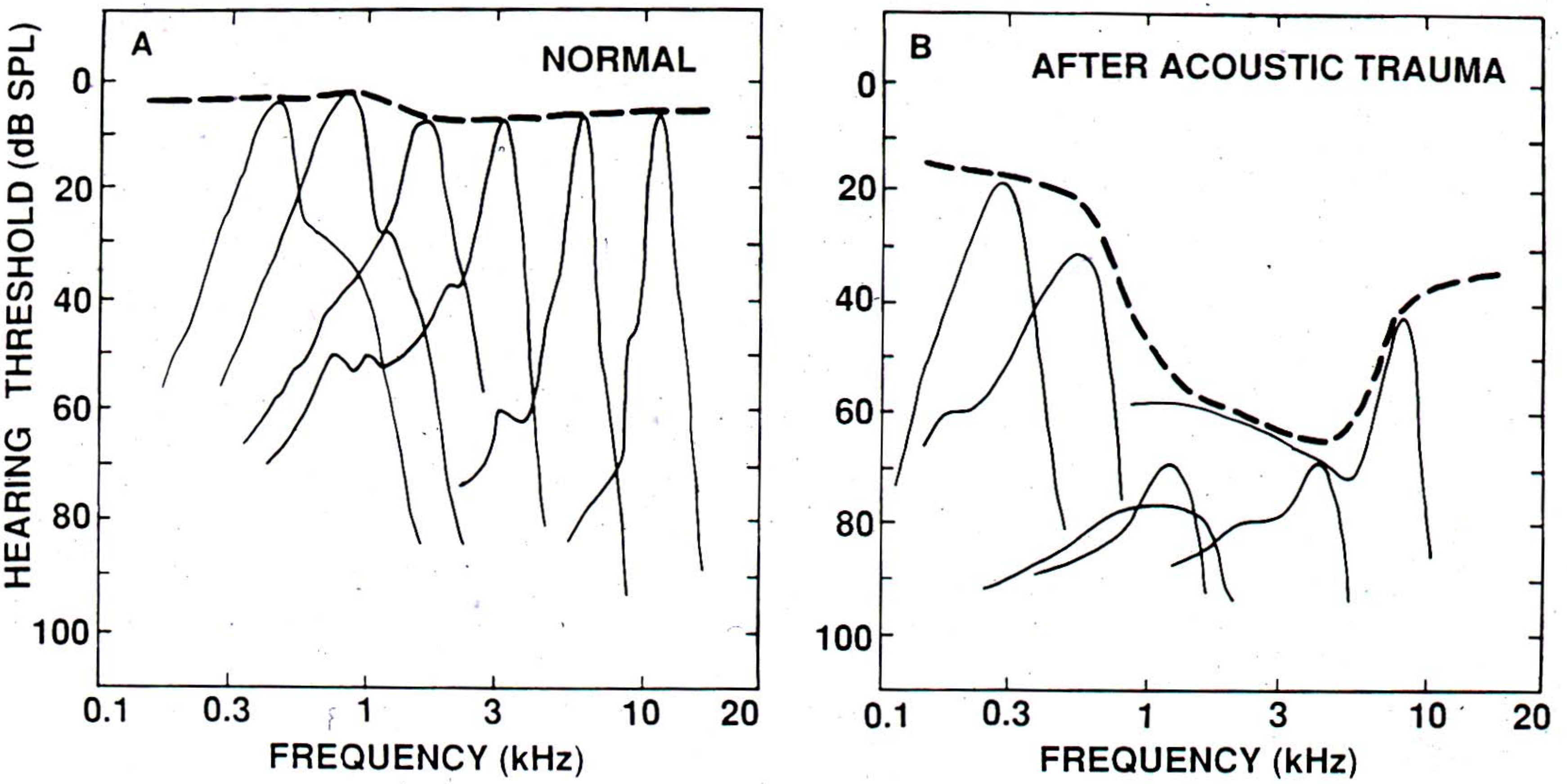


Harrison and Evans (1975)



As does noise exposure

Liberman and Dodds



A
NORMAL
HEARING THRESHOLD (dB SPL)
0
20
40
60
80
100
0.1
0.3
1
3
10
20
FREQUENCY (kHz)
B
AFTER ACOUSTIC TRAUMA
0
20
40
60
80
100
0.1
0.3
1
3
10
20
FREQUENCY (kHz)

Wightman

Sound Level

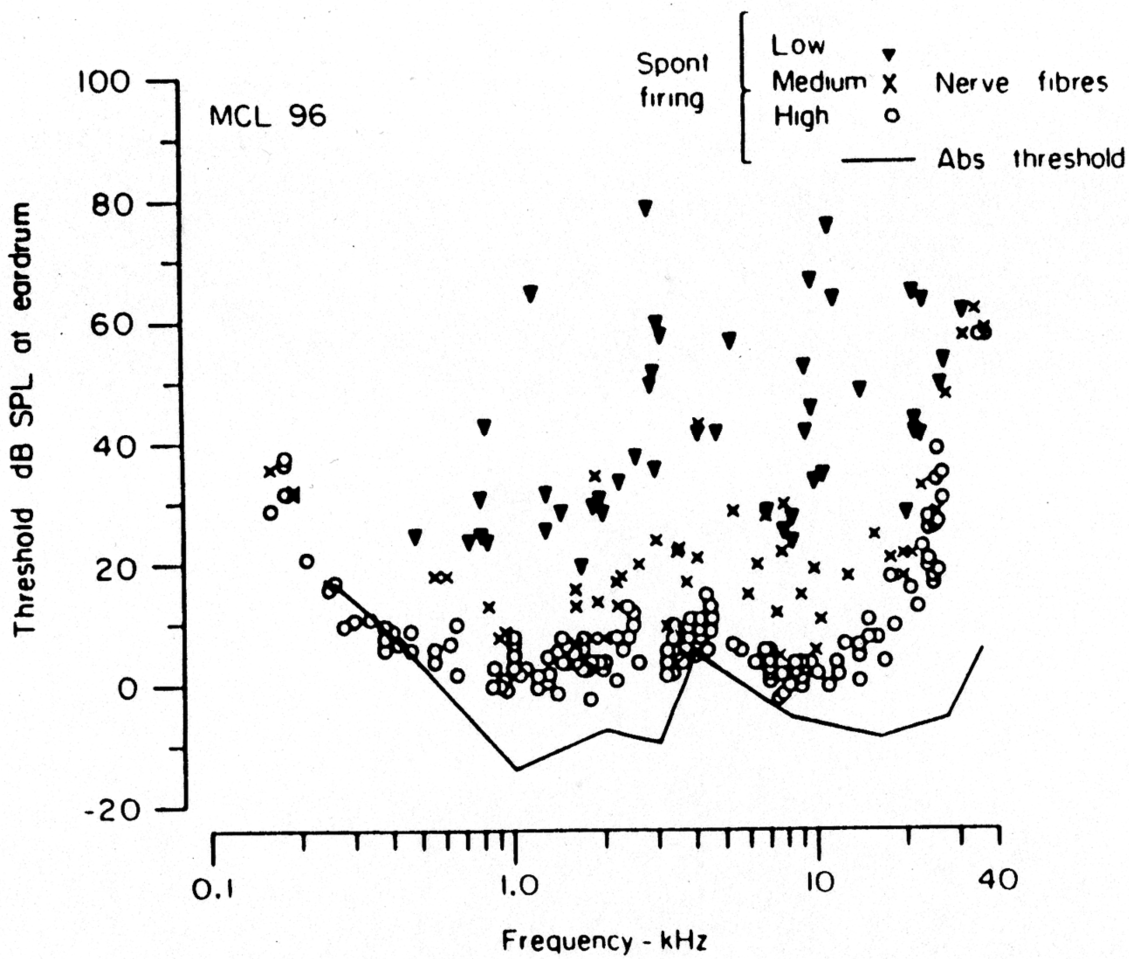
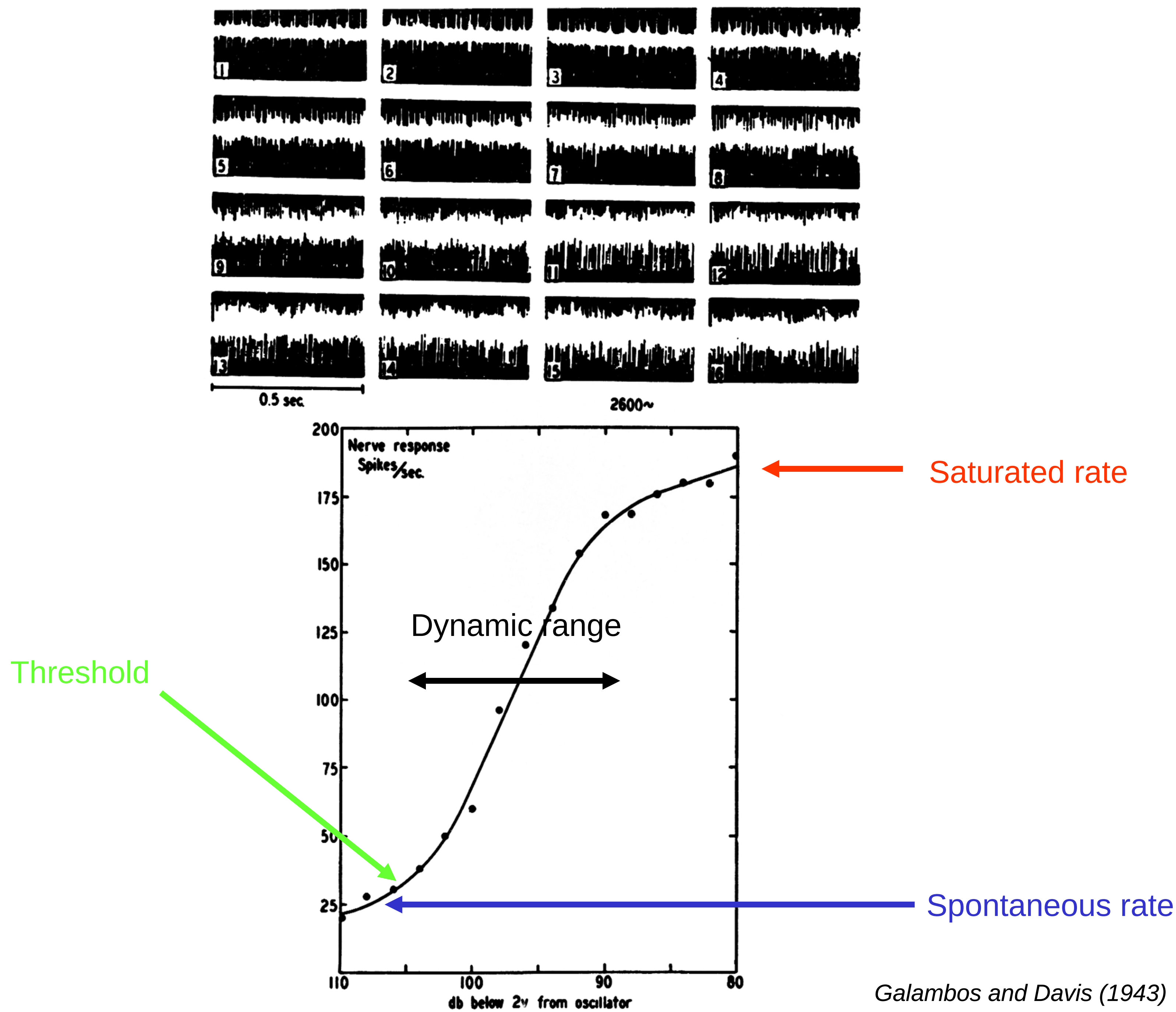
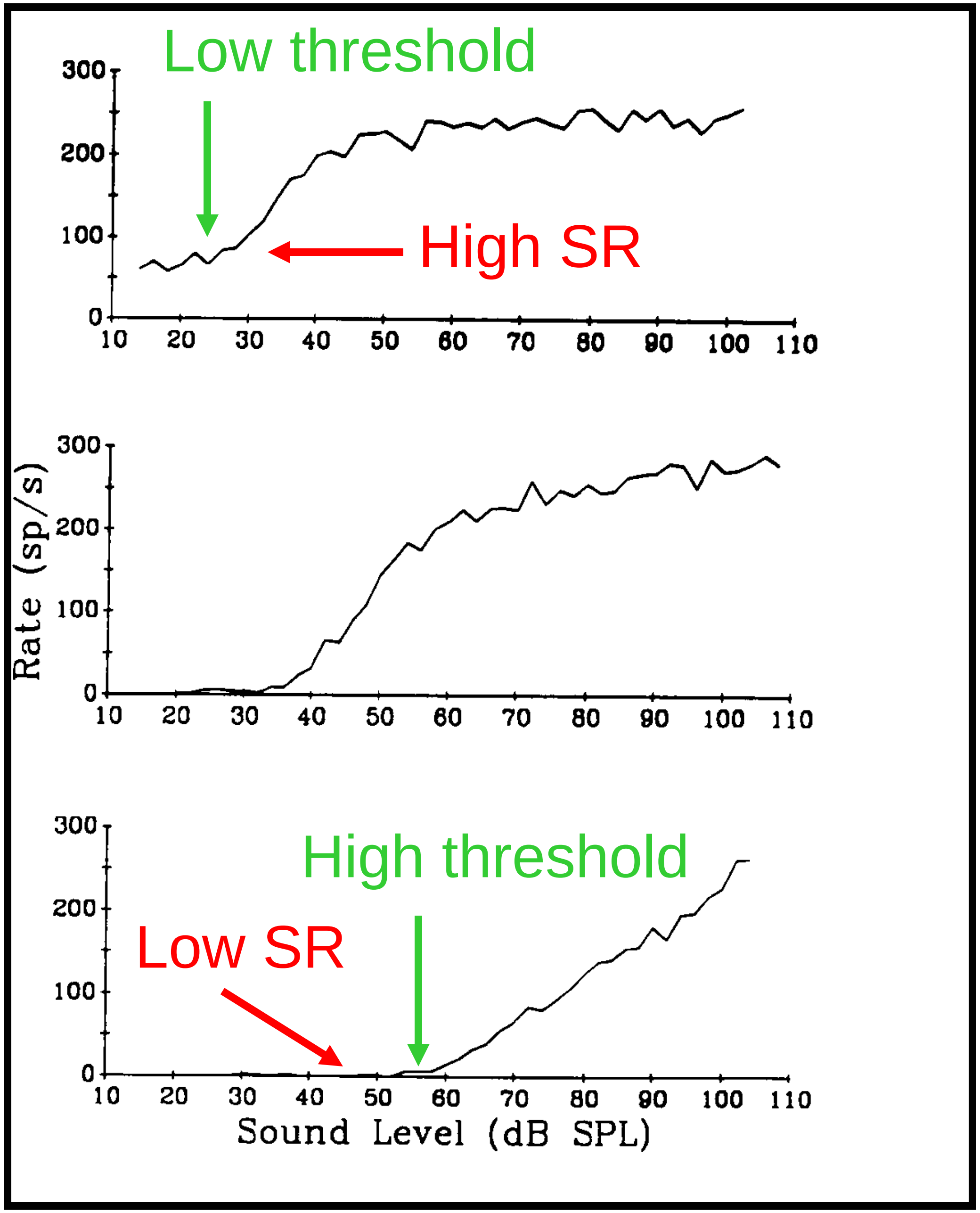


Fig 4.4 Distribution of best thresholds of auditory nerve fibres in one cat. Fibres with high spontaneous firing rates (○, ≥18/s) have low thresholds, and those with low spontaneous firing rates (▼, <0.5/s) have high thresholds. Fibres with intermediate spontaneous firing rates (×) have thresholds in between. The behavioural absolute threshold of the cat, expressed in terms of the intensity at the eardrum, lies just below the lowest thresholds of the auditory nerve fibres. Neural data from Liberman and Kiang (1978, Fig. 2). Behavioural data from Elliott *et al.* (1960).



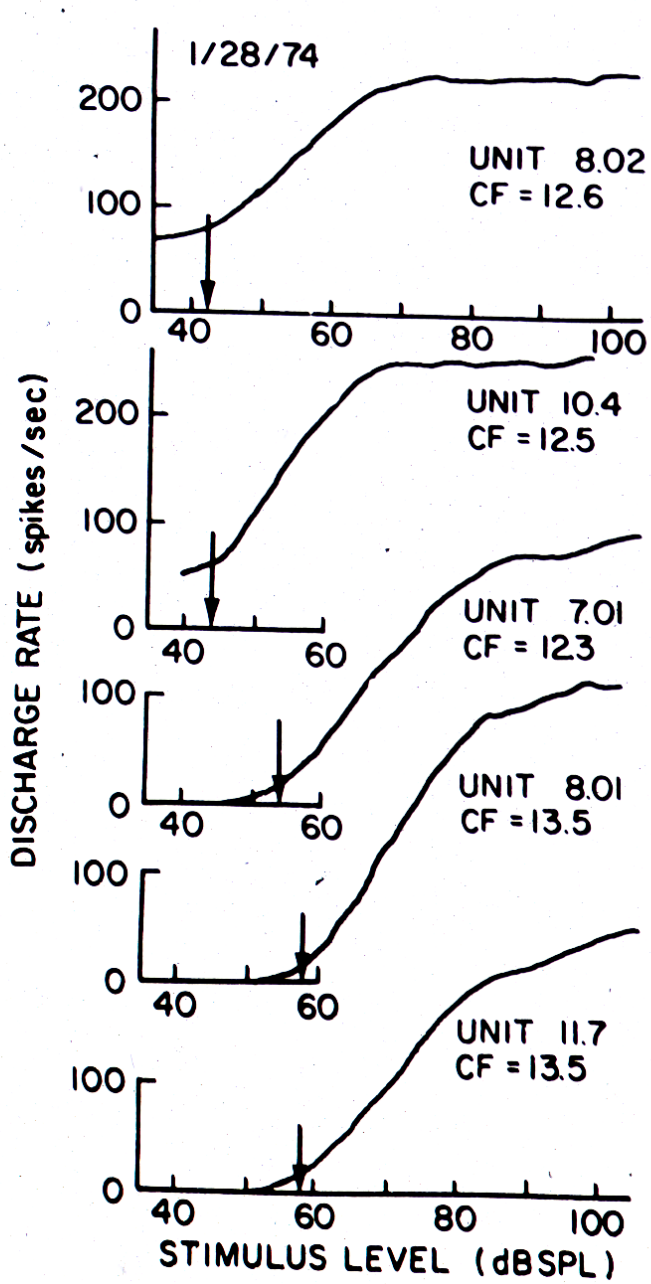
Galambos and Davis (1943)



Guinea pig

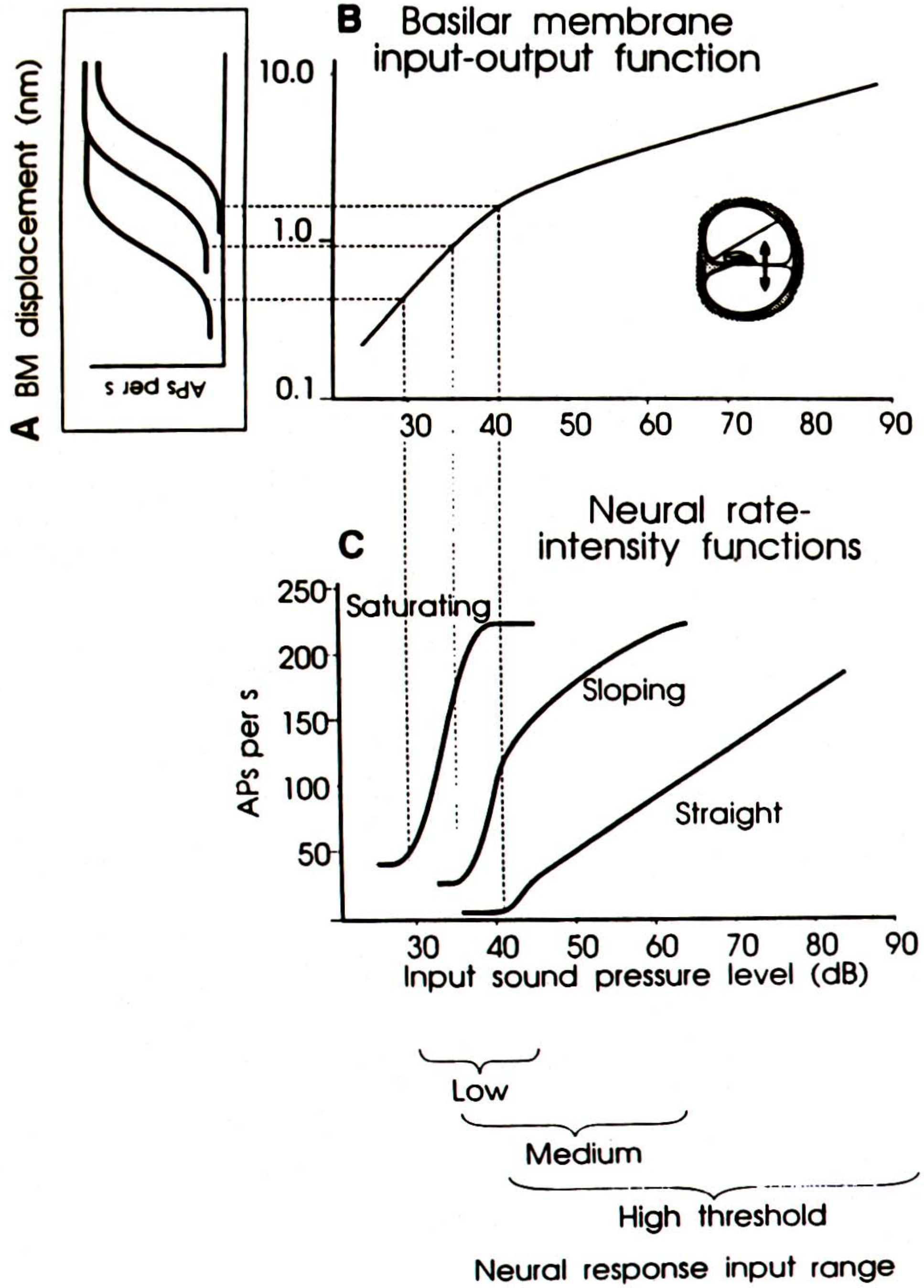
At each frequency, auditory nerve fibres differ in their spontaneous rate, input/output function and dynamic range - these covary.

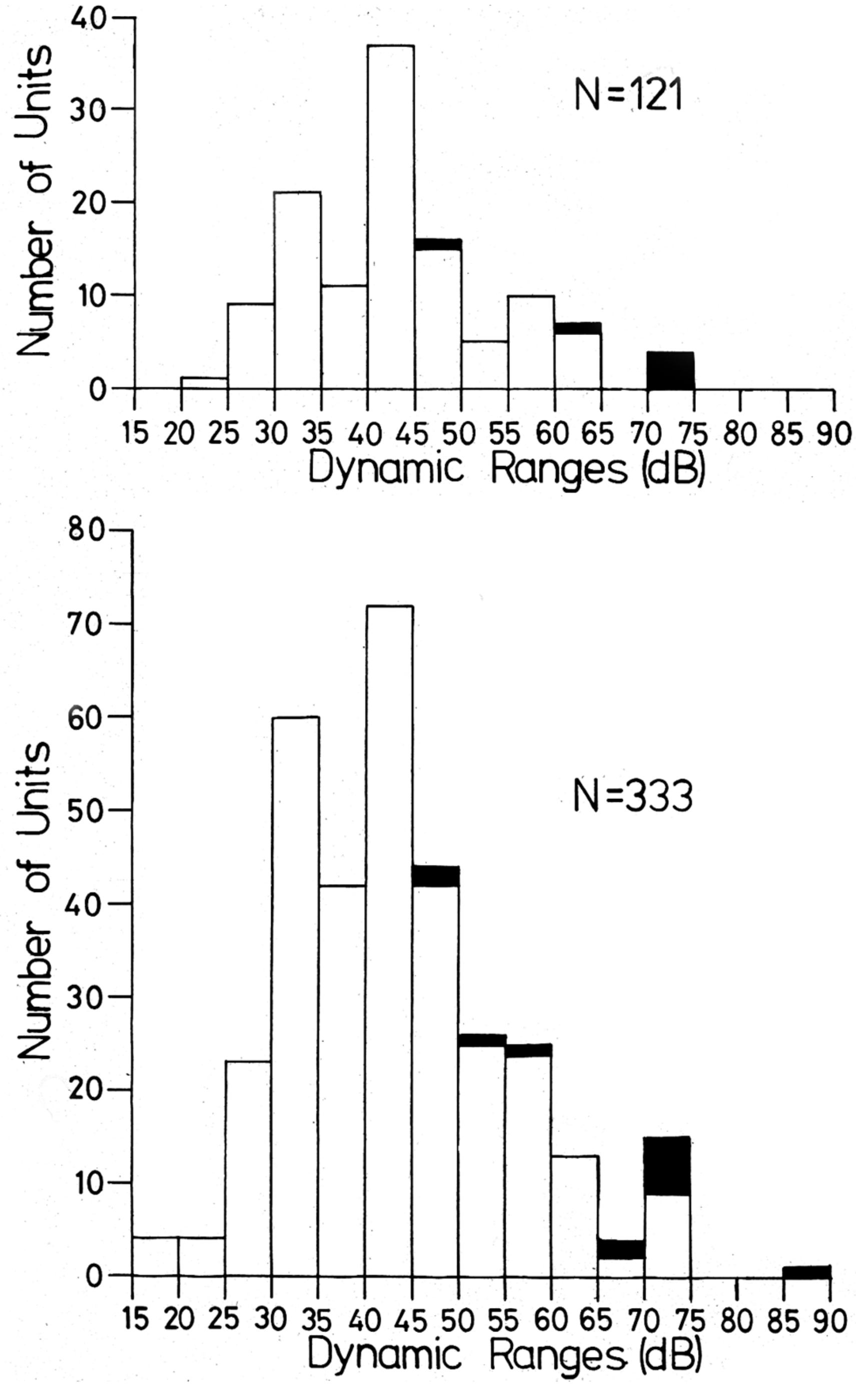
Winter and Palmer



Cat

Sachs and Abbas (1974)


A
BM displacement (nm)
APs per s
B Basilar membrane input-output function
10.0
1.0
0.1
30
40
50
60
70
80
90
C
Neural rate-intensity functions
250
200
150
100
50
APs per s
Saturating
Sloping
Straight
30
40
50
60
70
80
90
Input sound pressure level (dB)
Low
Medium
High threshold
Neural response input range


N=121
Number of Units
Dynamic Ranges (dB)
N=333
Number of Units
Dynamic Ranges (dB)

Palmer (1975)

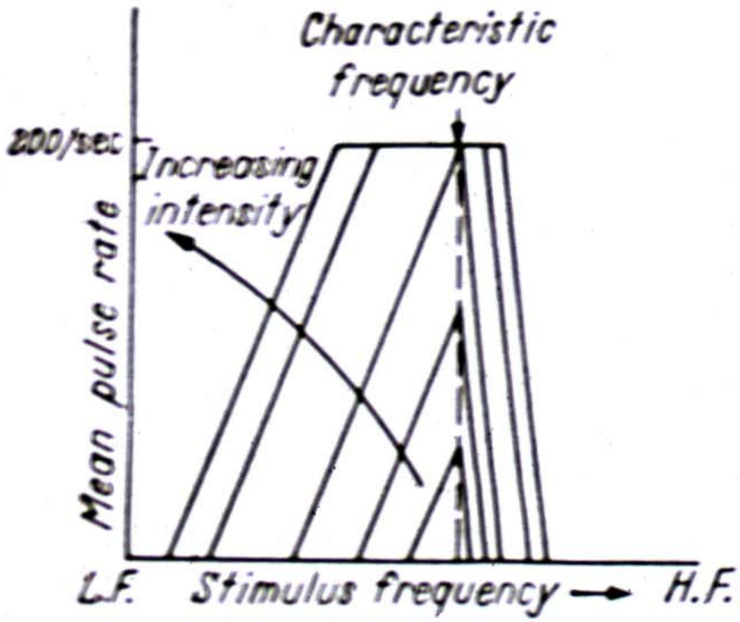


Figure 1.

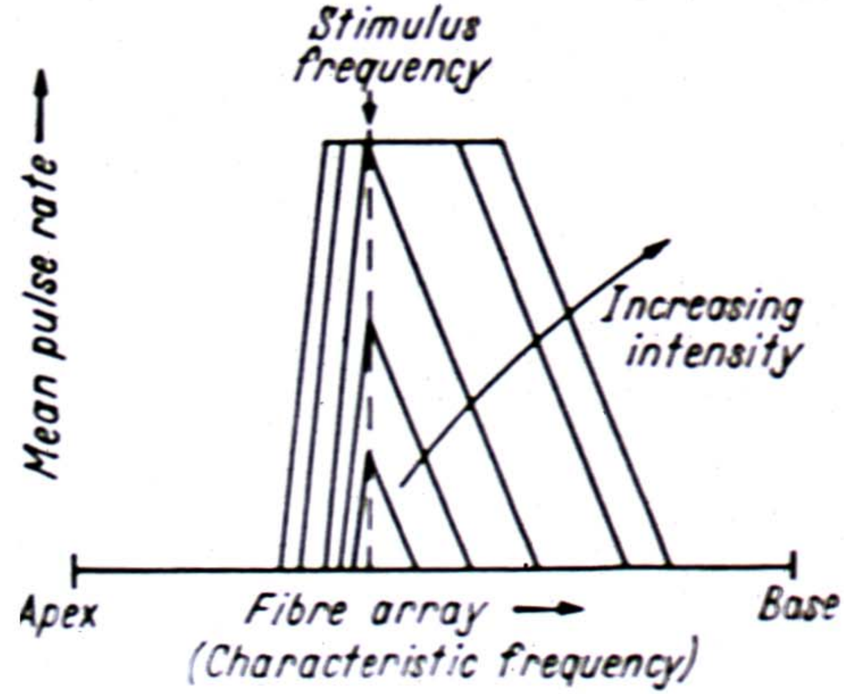
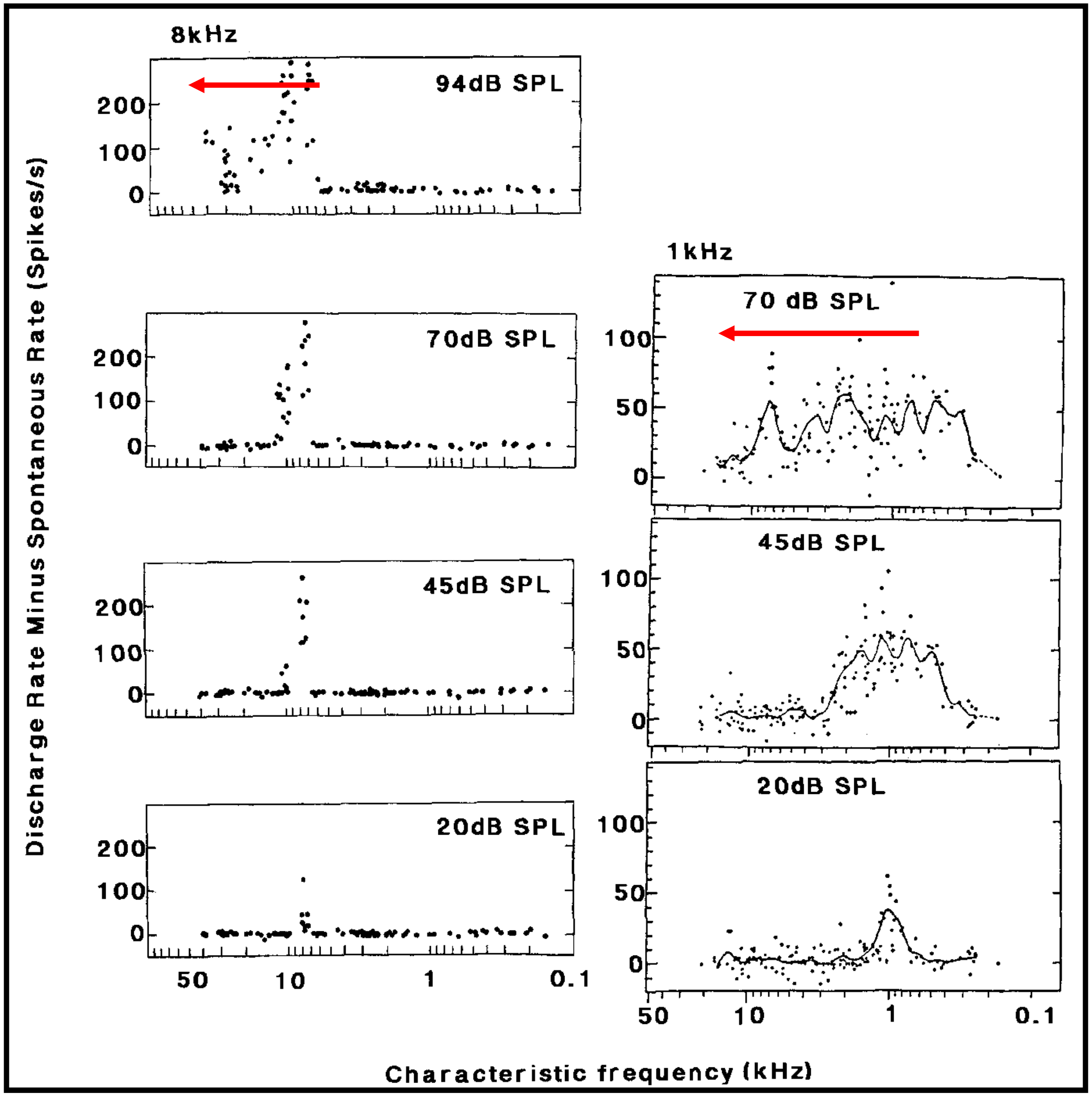


Figure 2.

Whitfield (1965)

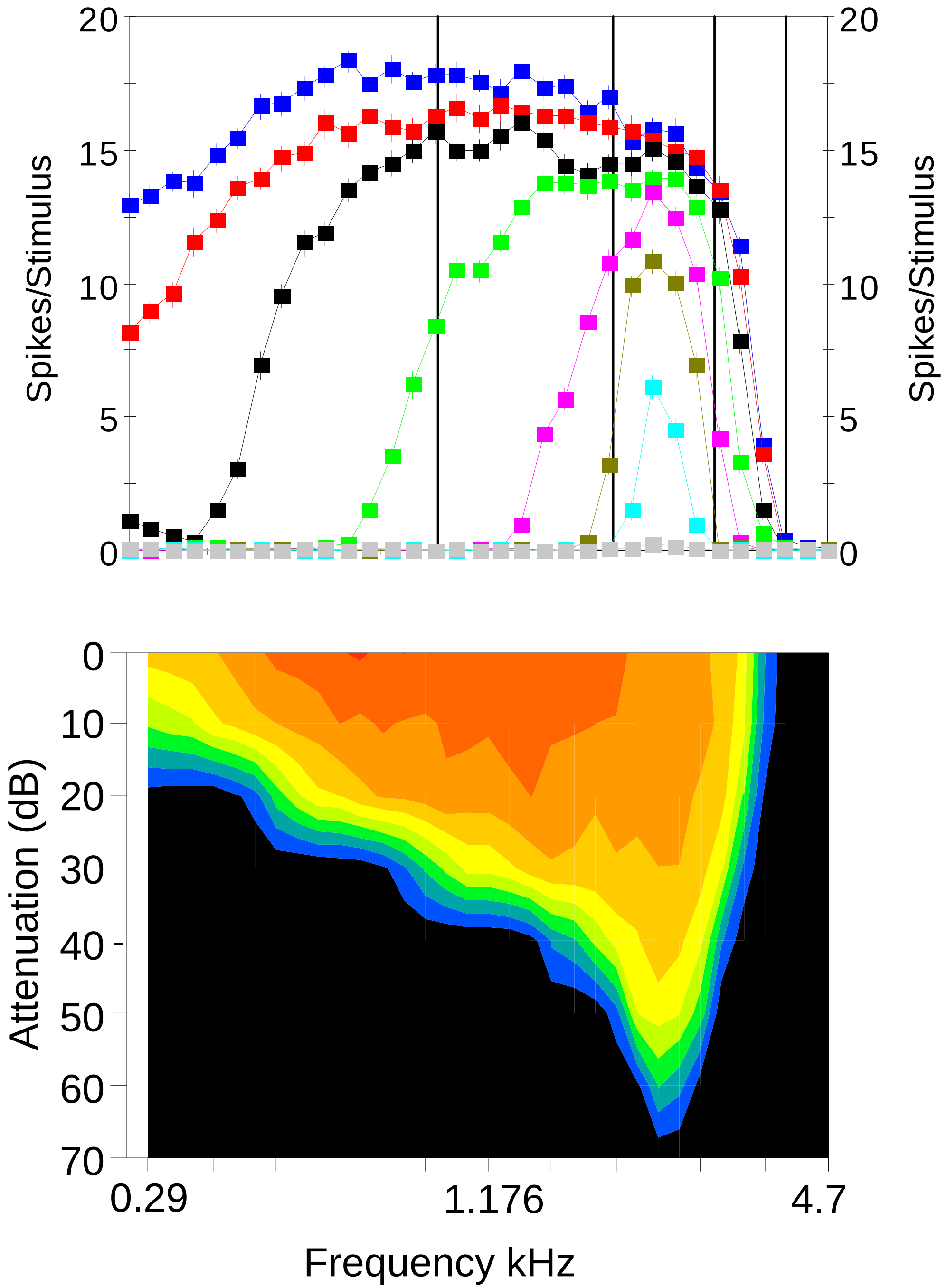


Because of the asymmetrical "V" shape of tuning curves, activity spreads to higher frequencies

Palmer and Evans

Kim and Molnar (1979)

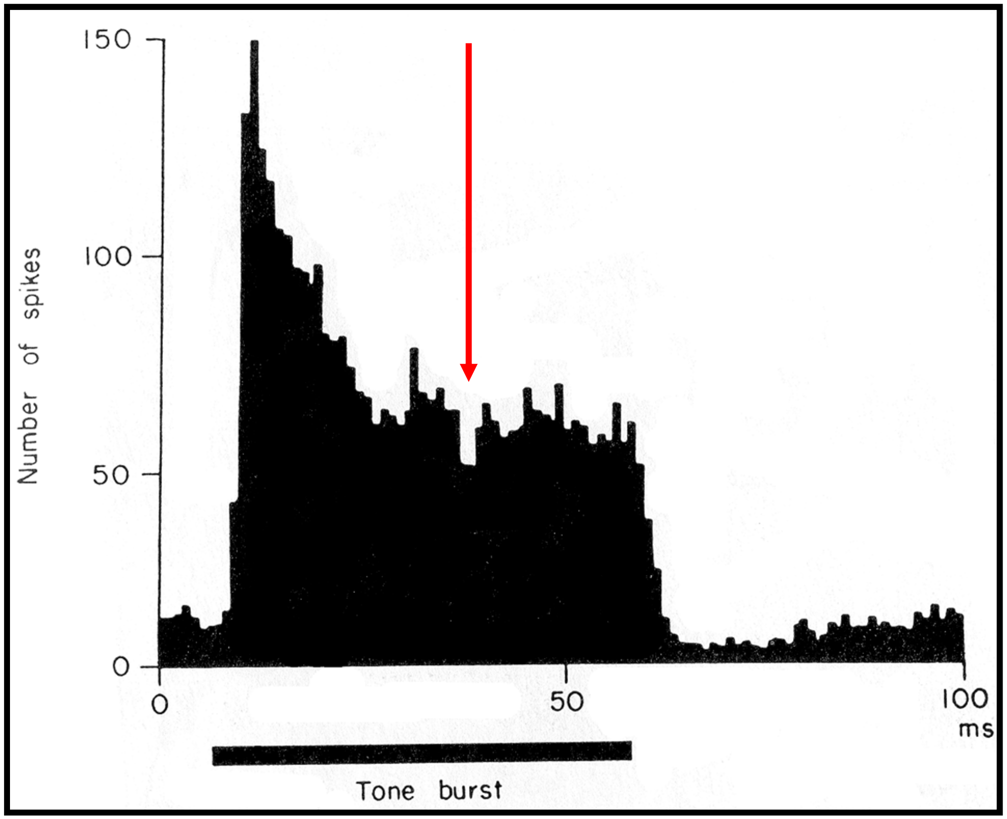
Iso-level response functions



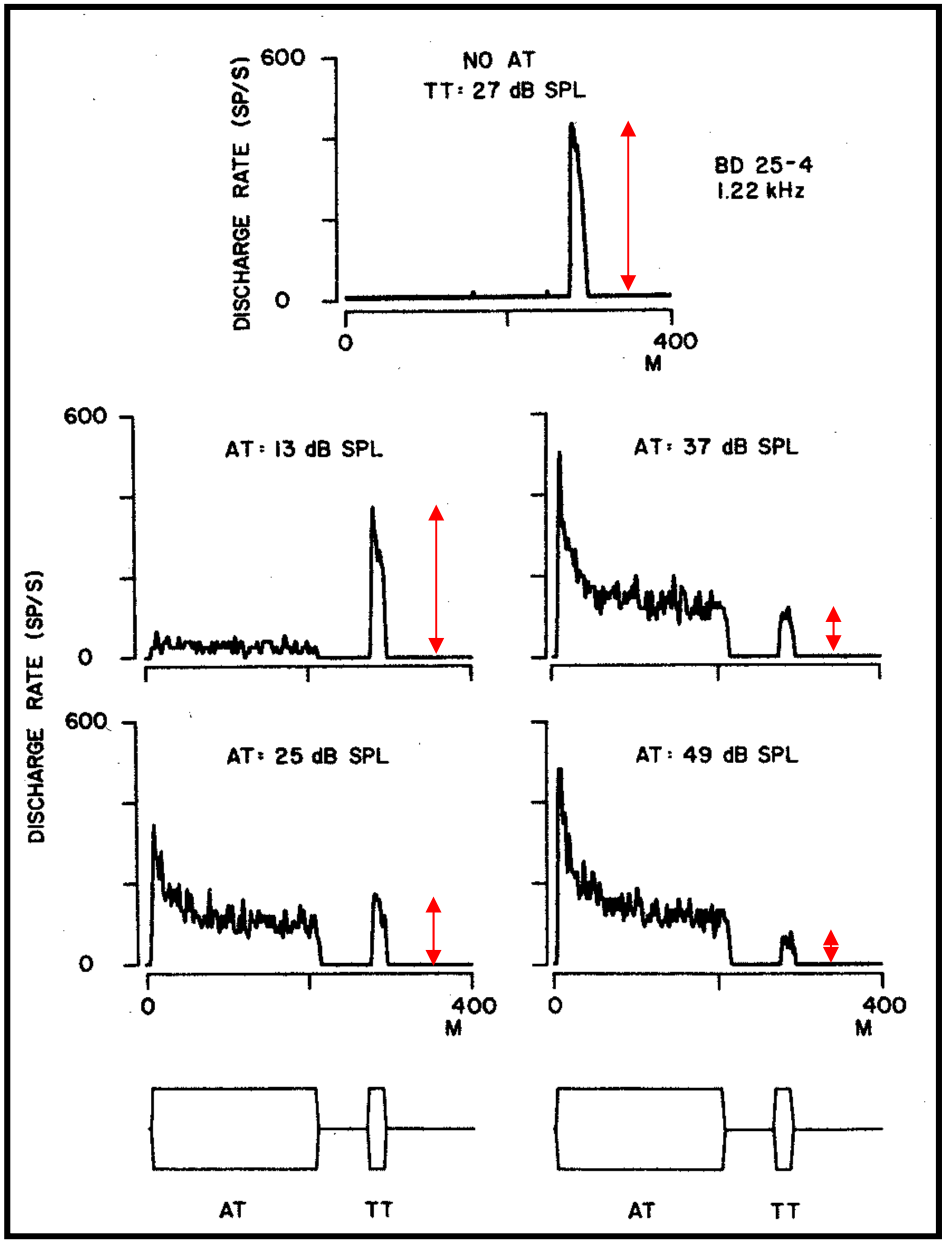
Palmer unpublished

Timing

When a novel stimulus occurs within a frequency channel the discharge rate is immediately increased and then falls (*adapts*) over a few tens of milliseconds



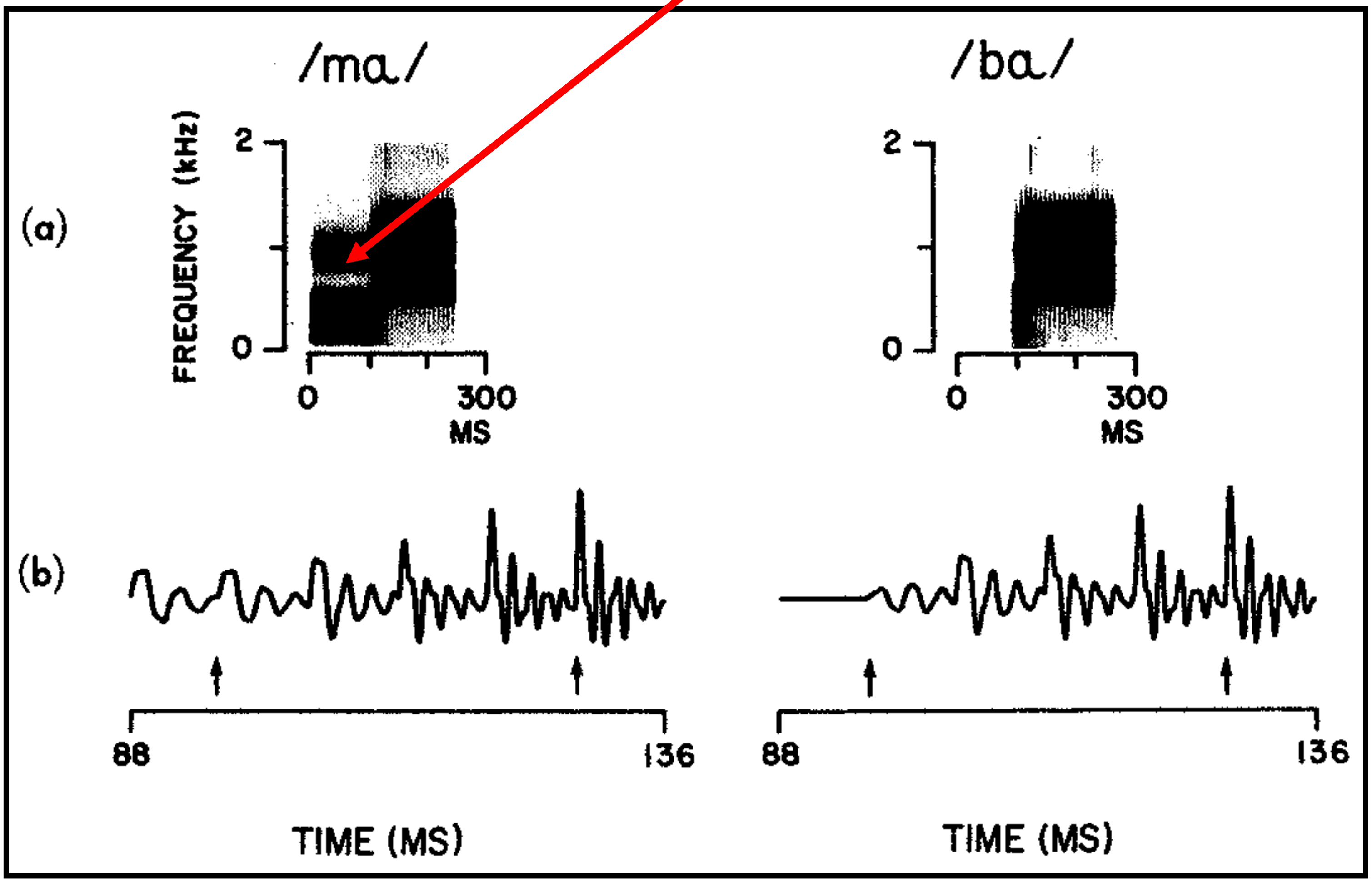
Kiang et al. (1965)



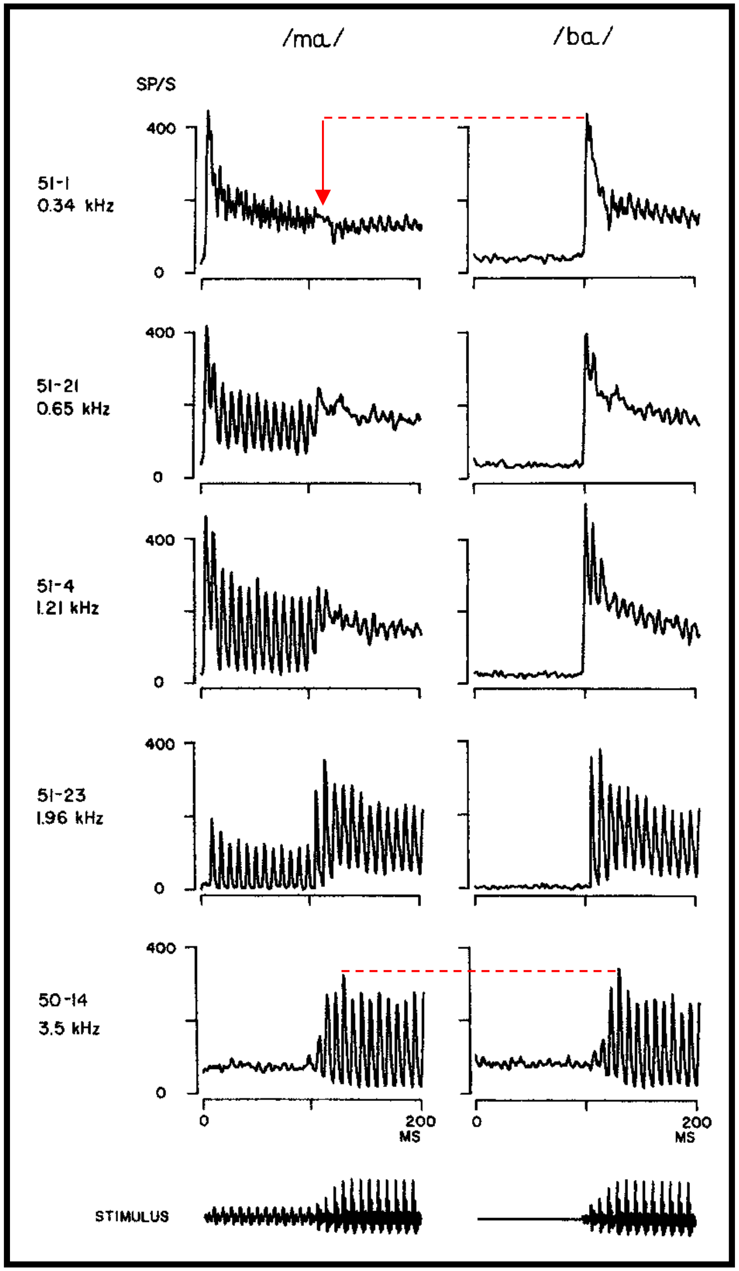
Adaptation within a single frequency channel can reduce the activity to following signals

Delgutte (1984)

/ma/ and /ba/ have the same vowel /a/,
but preceded in /ma/ by low-frequency energy



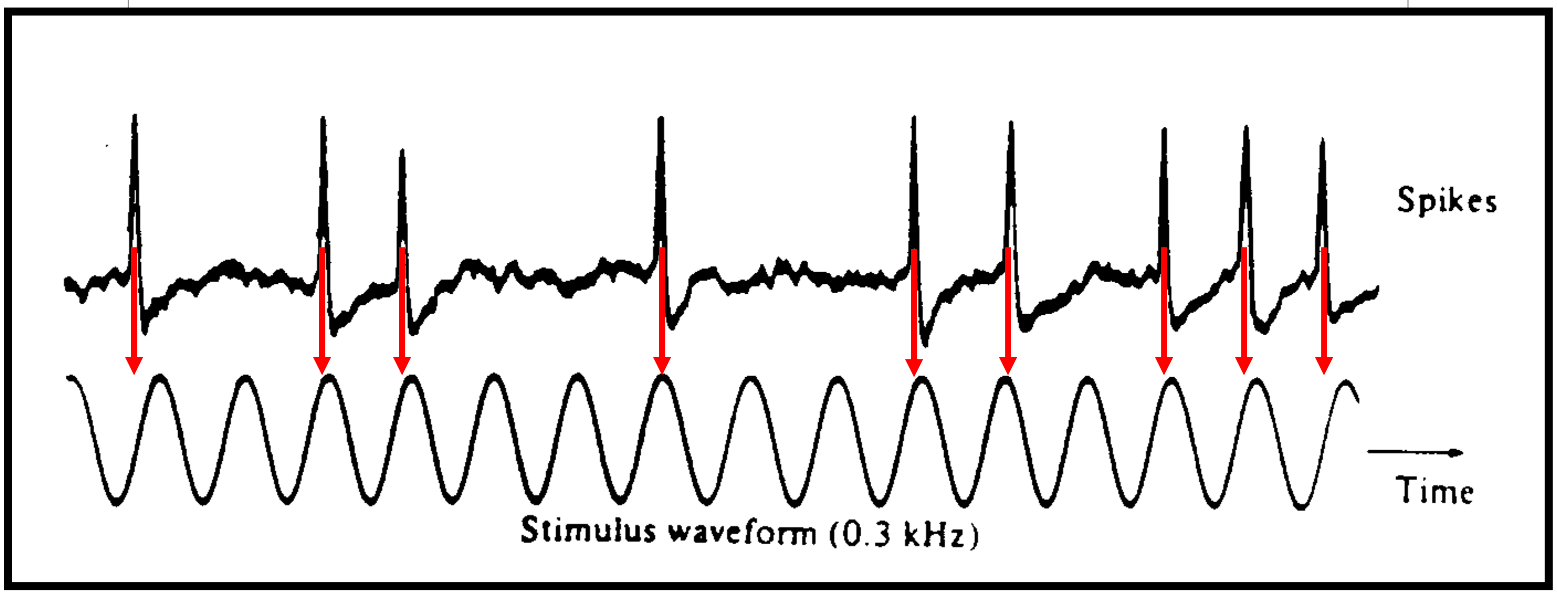
Delgutte (1984)



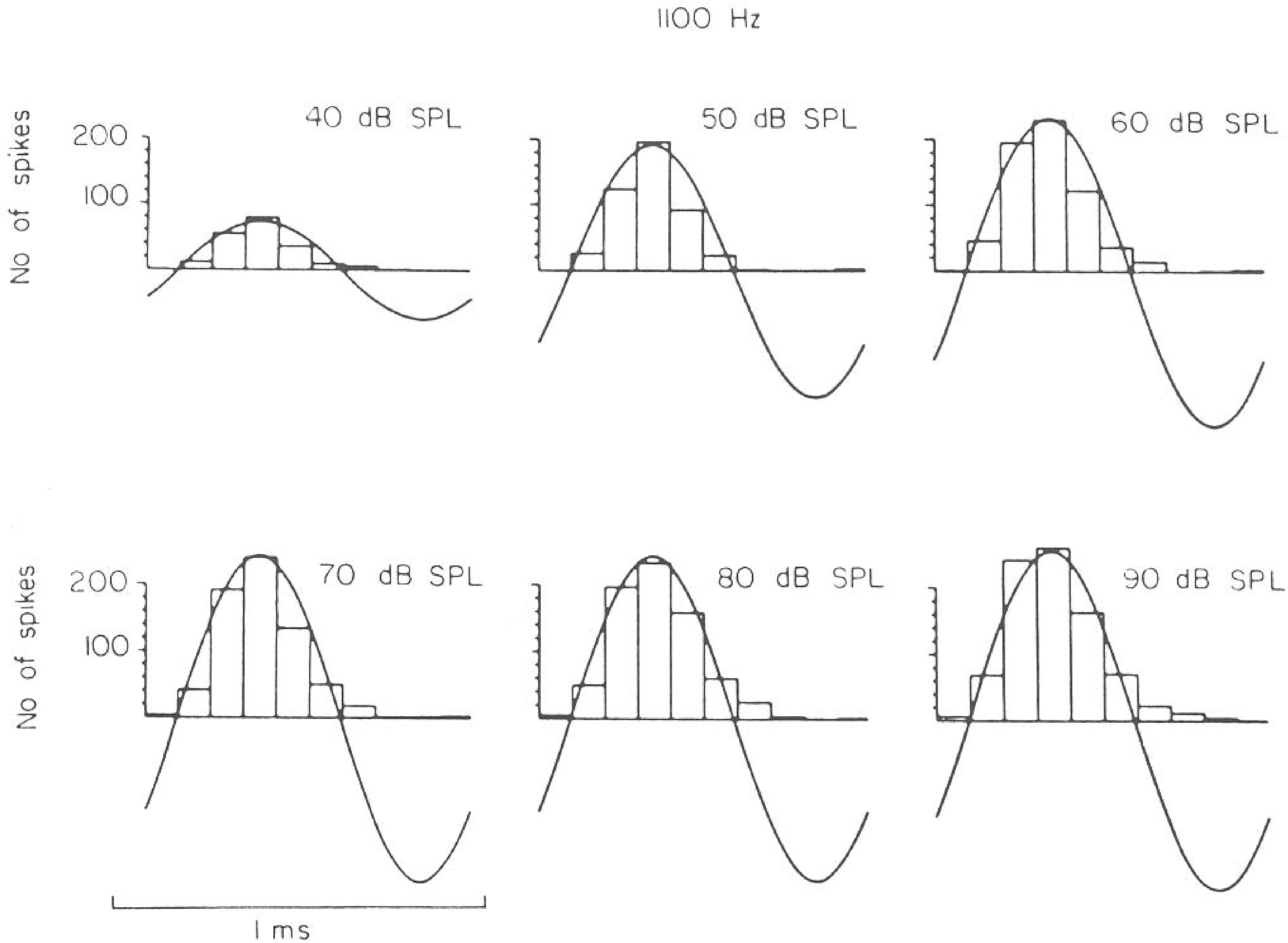
When adapting energy is present in a frequency channel the high spike rate at the onset of a signal is reduced or absent

Delgutte (1984)

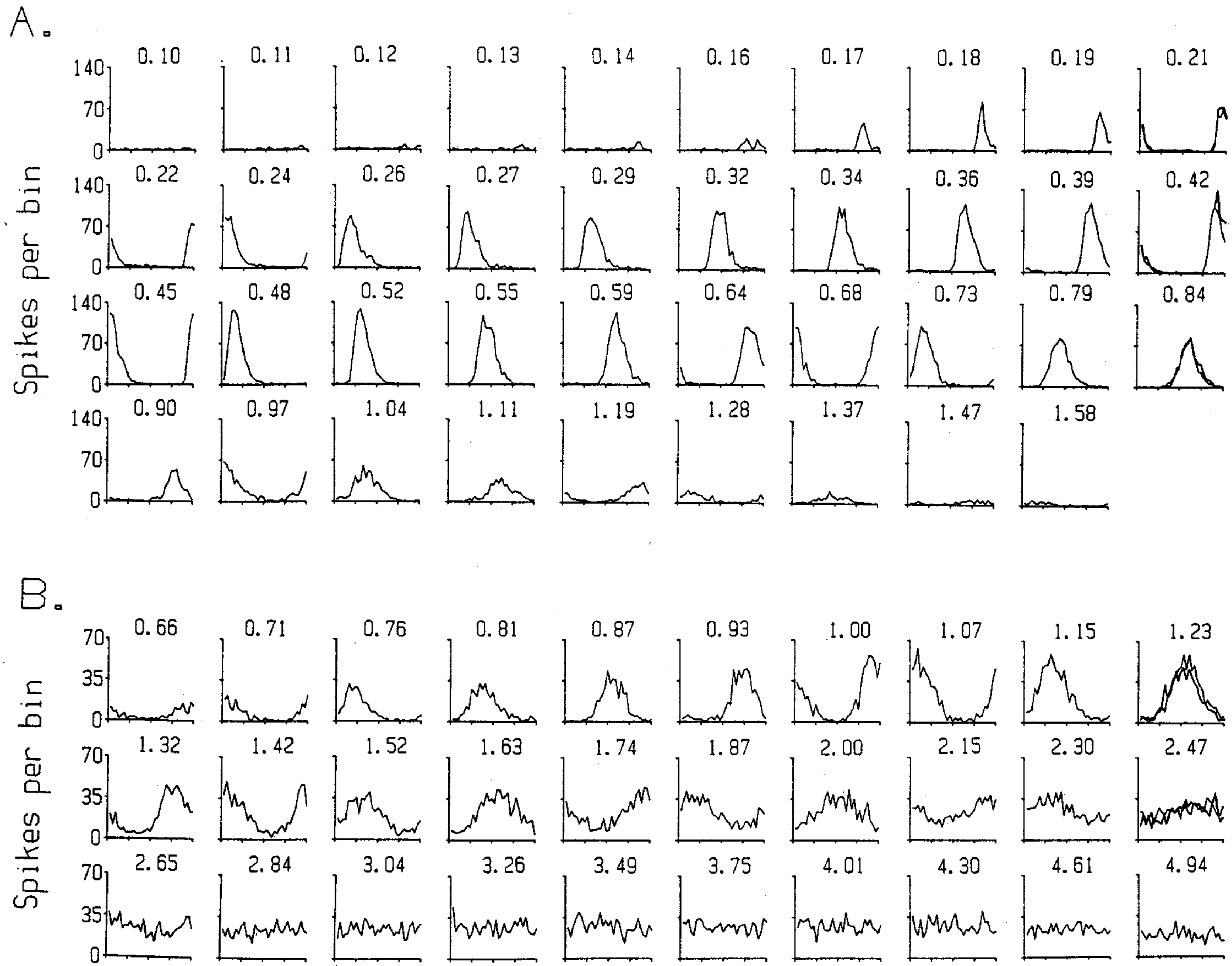
The discharges of cochlear nerve fibres to low-frequency sounds are not random;
they occur at particular times (*phase locking*).



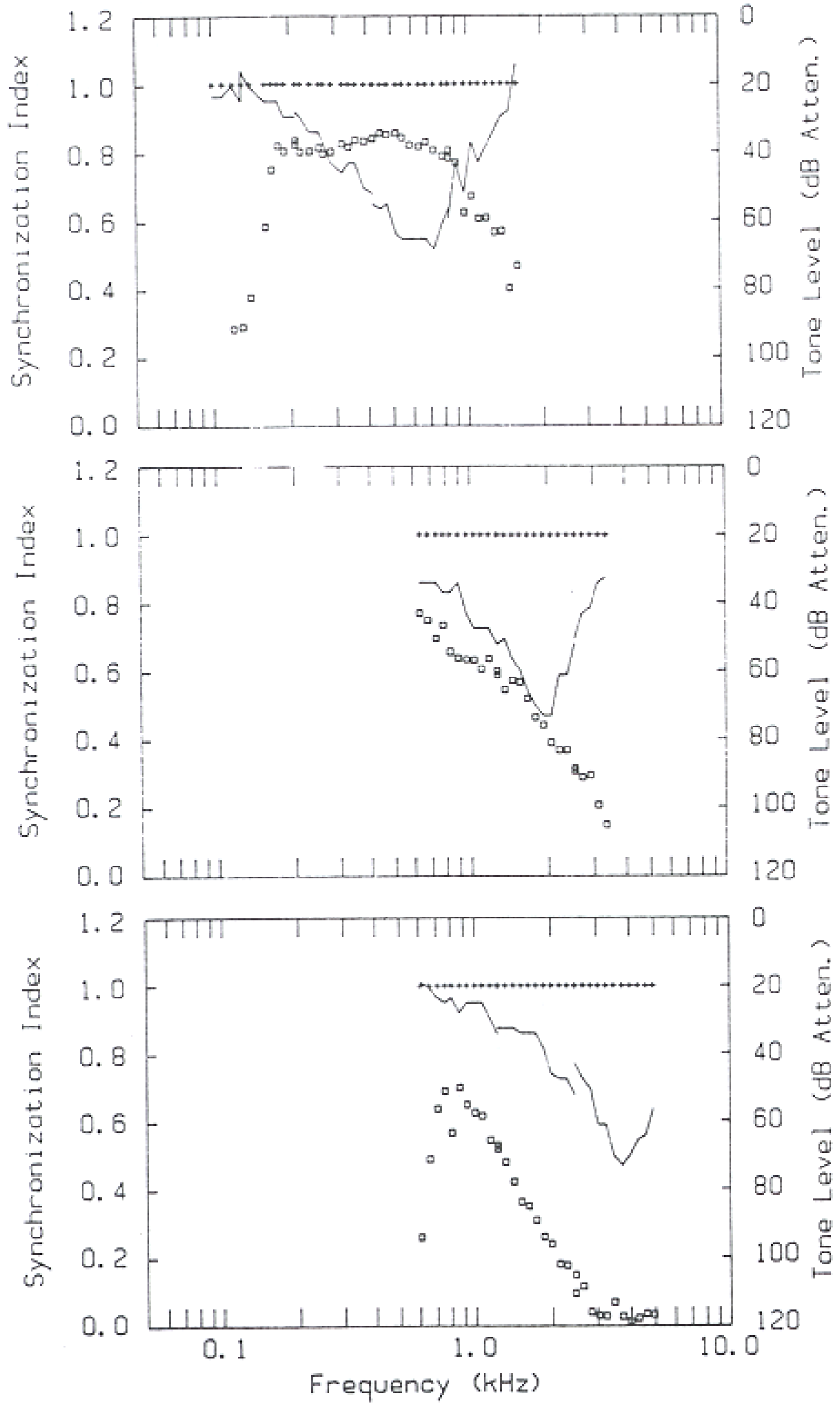
Evans (1975)



Rose et al (1971)

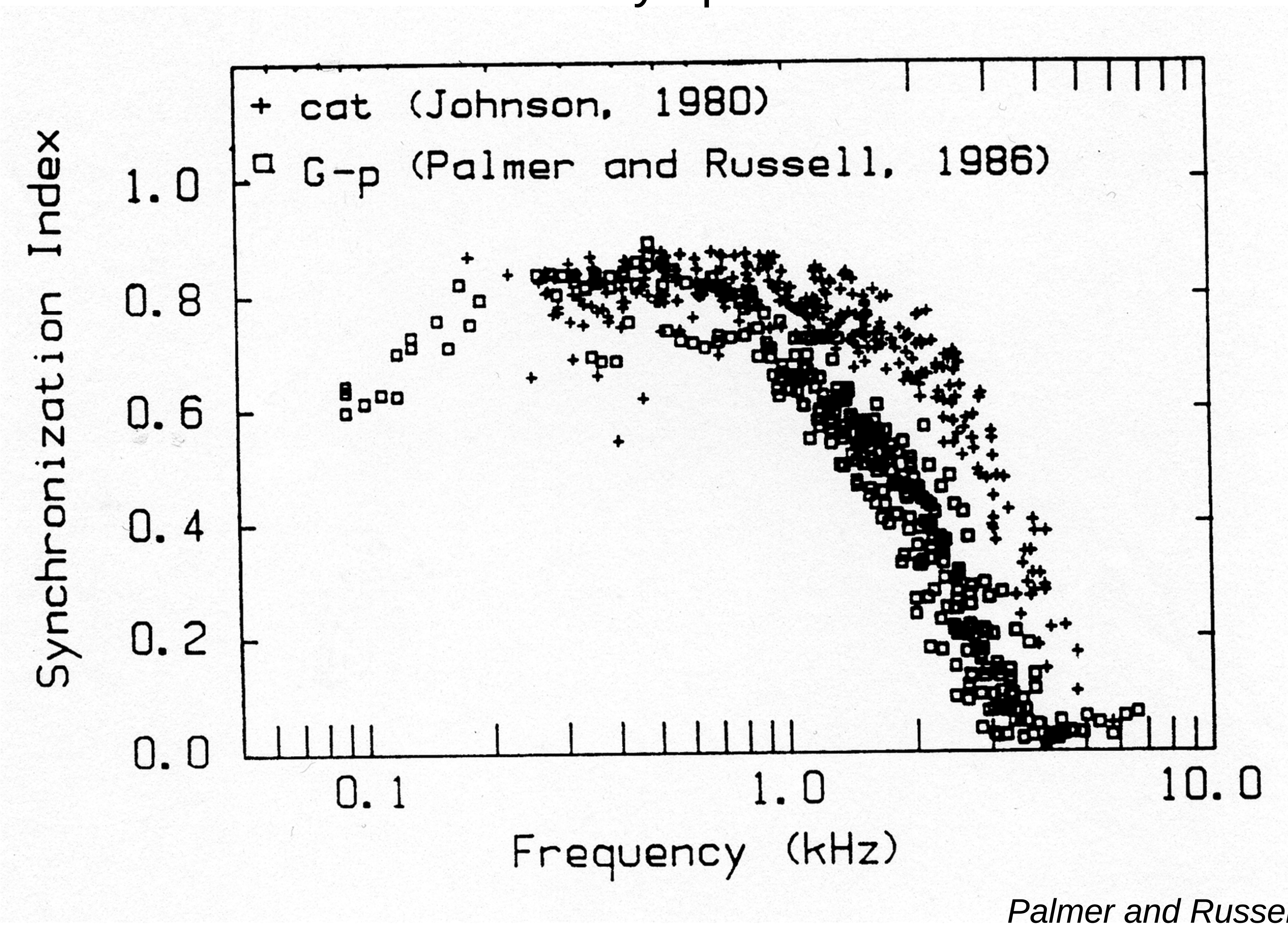


Palmer and Russell (1986)



Palmer and Russell (1986)

Phase-locking in the auditory nerve is species dependent, but in mammals occurs only up to about 5 kHz



Palmer and Russell (1986)

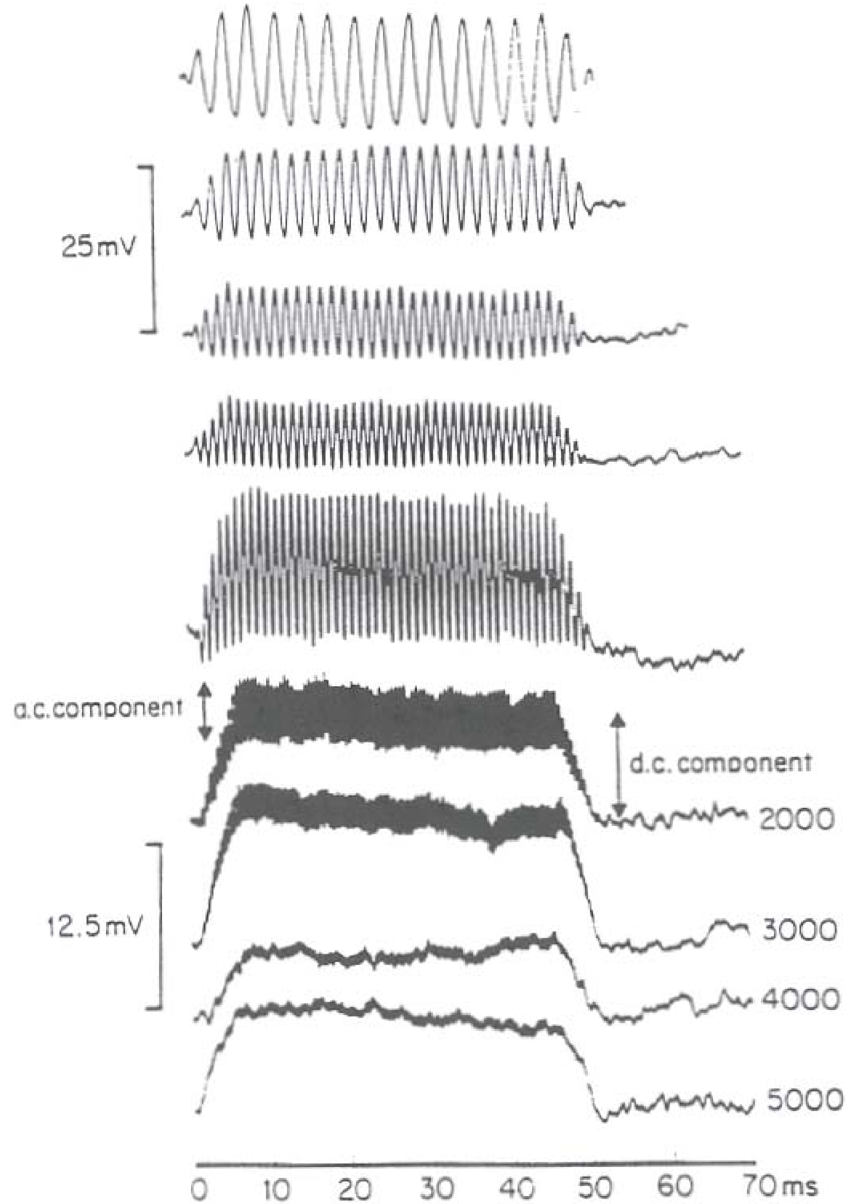
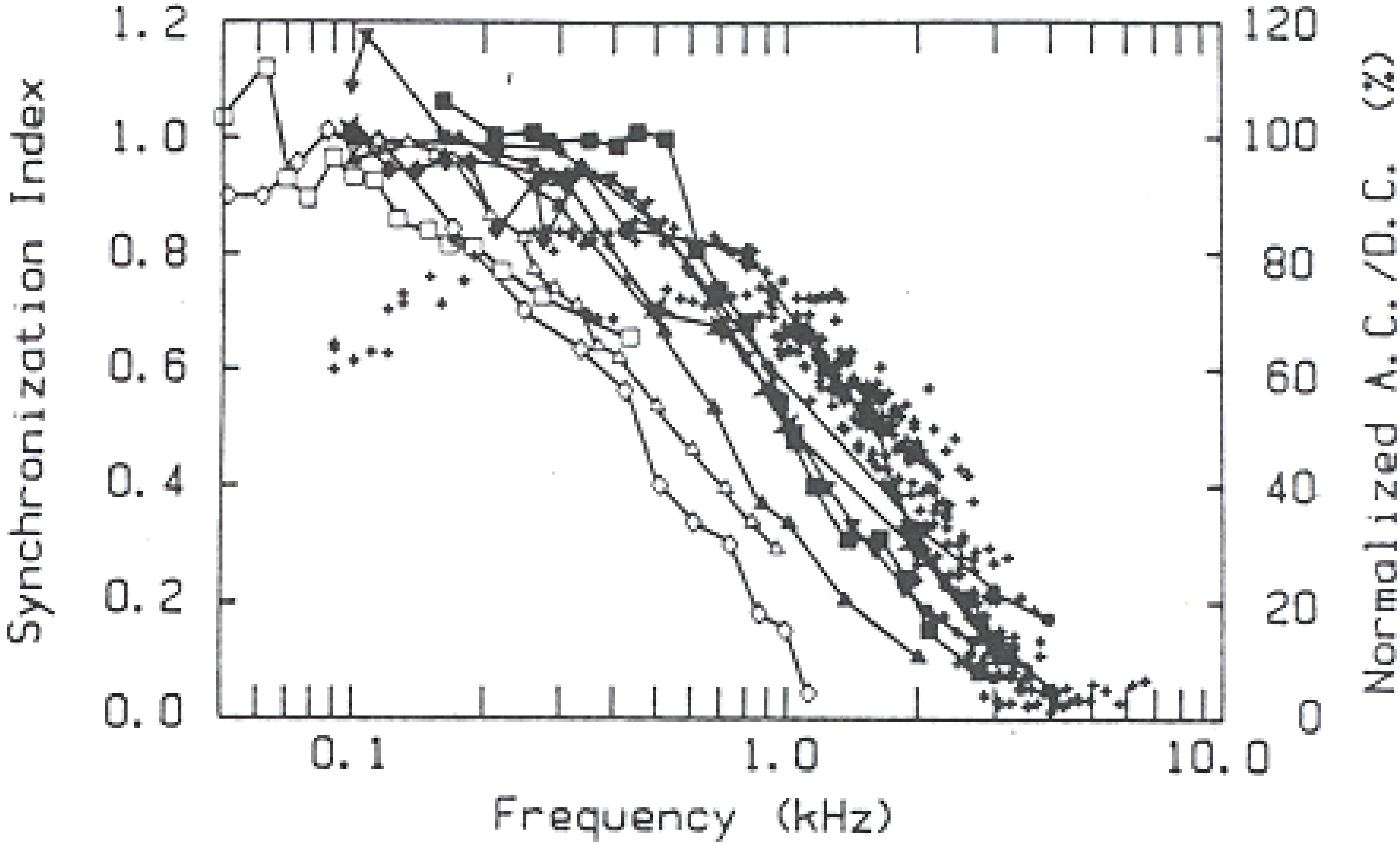


Fig. 3.18 Intracellular voltage changes in an inner hair cell for different frequencies of stimulation. show that the relative size of the a.c. component declines at higher stimulus frequencies (numbers on right of curves). Note change of scale for the lower four traces. From Palmer and Russell (1986, Fig. 9).



Palmer and Russell (1986)

Responses to broadband stimuli: clicks and noise

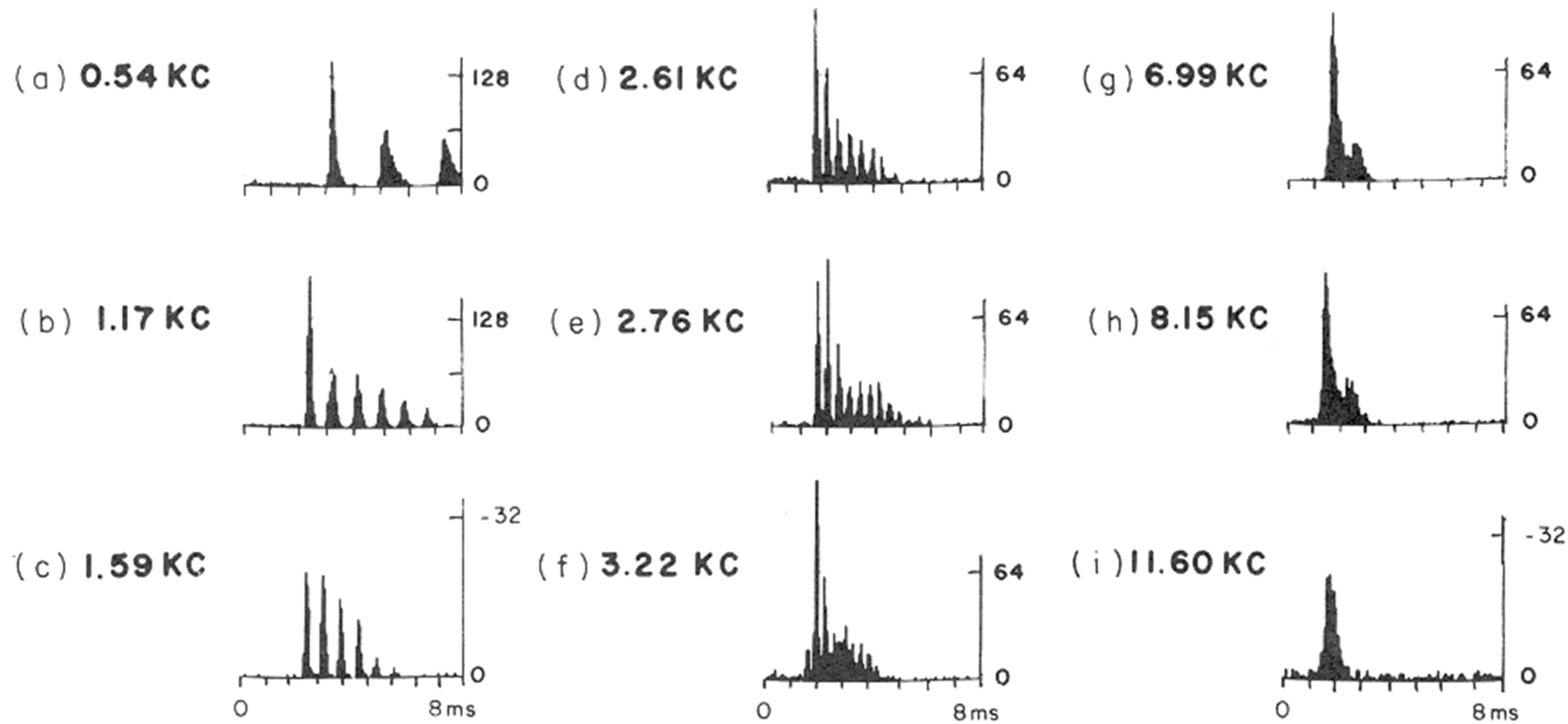


Fig. 4.9 The form of the post-stimulus–time histograms to clicks depends on the CF of the fibre. Low-frequency fibres show ringing (a–f), high-frequency fibres do not (g–i). High-frequency fibres also show a later phase of activation (f–h). Reprinted from *Discharge Patterns of Single Fibers of the Cat's Auditory Nerve* by N. Y.-S. Kiang *et al.* (Fig. 4.7), by permission of The MIT Press, Cambridge, Massachusetts. © The MIT Press, 1965.

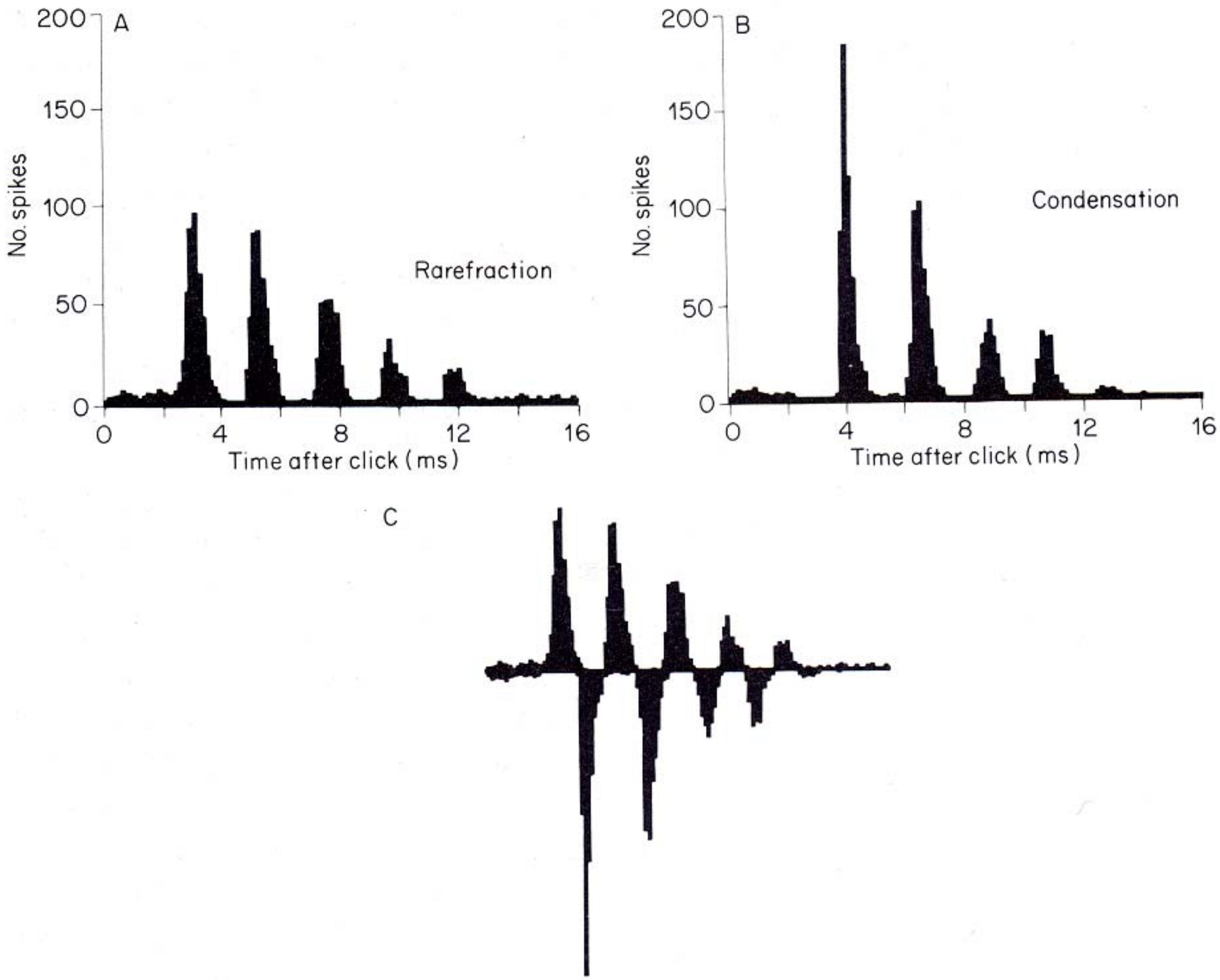


Fig. 4.10 (A) Post-stimulus–time histograms to (A) rarefaction and (B) condensation clicks show that the peaks and troughs occur in complementary places for the two stimuli. Fibre CF: 450 Hz. Reprinted from *Discharge Patterns of Single Fibers of the Cat's Auditory Nerve* by N. Y.-S. Kiang *et al.*, by permission of The MIT Press, Cambridge, Massachusetts. © The MIT Press, 1965. (C) A compound histogram is formed by inverting the histogram to condensation clicks under that to rarefaction clicks.

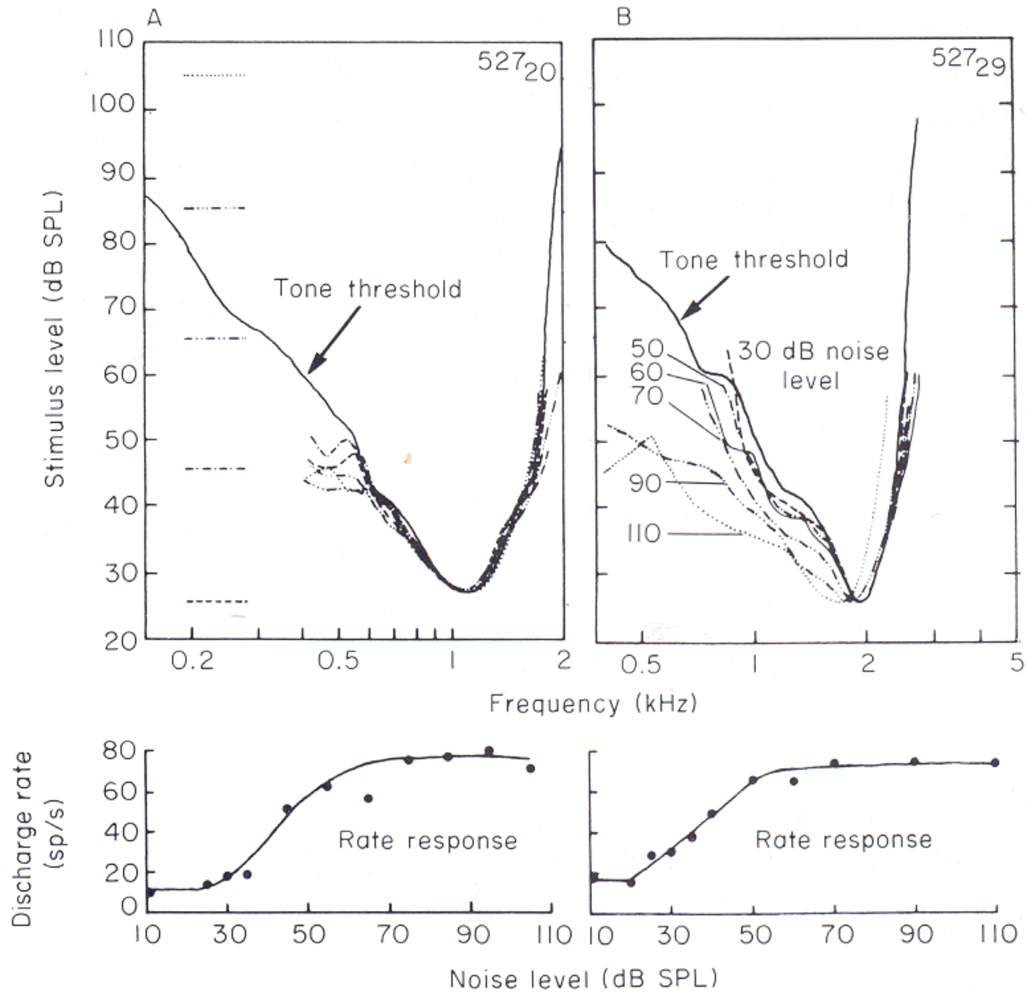
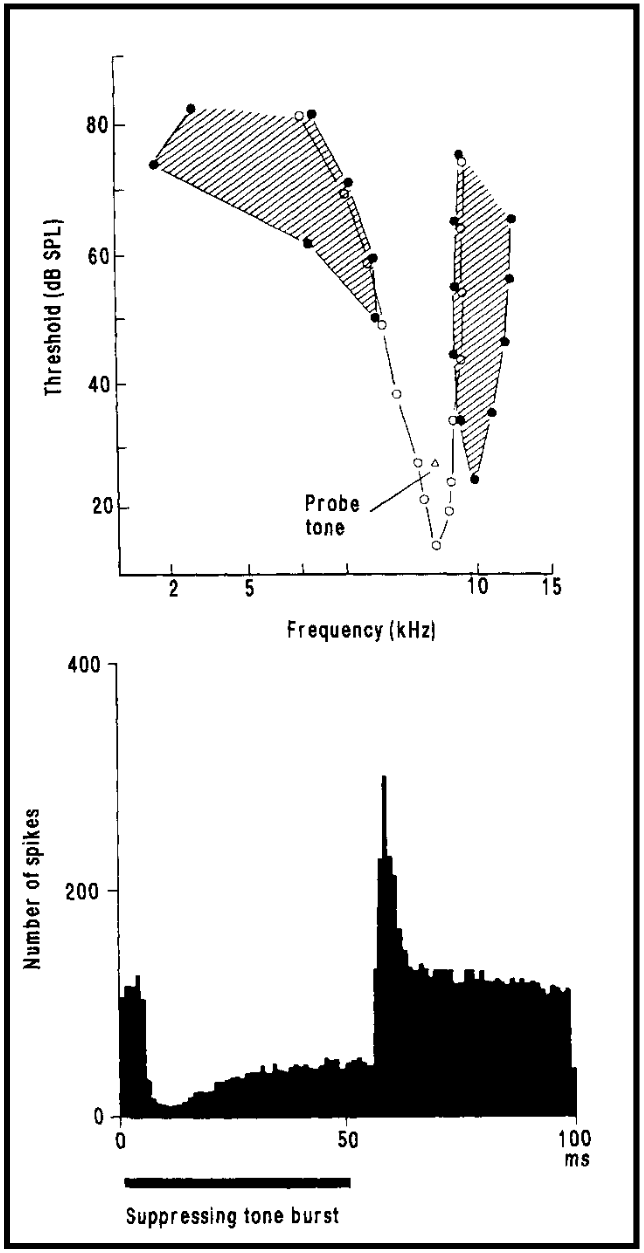


Fig. 4.13 Two fibres studied by the reverse correlation technique. (A) The Fourier transformation of the impulse response (broken lines), as recovered by the reverse correlation technique, shows good agreement with the tuning curve obtained with tones at threshold (solid line), over the bottom 15 dB of the tuning curve, even though the mean firing rate is 40 dB into saturation (rate response: bottom). (B) The 2-kHz fibre shows some deterioration of tuning as the intensity is raised, together with a downward shift in best frequency. Some tuning is still preserved, even though the intensity is 60 dB above that producing saturation of the firing. From Evans (1977, Figs 4 and 5).

Complex Stimuli

1. Two tones: suppression



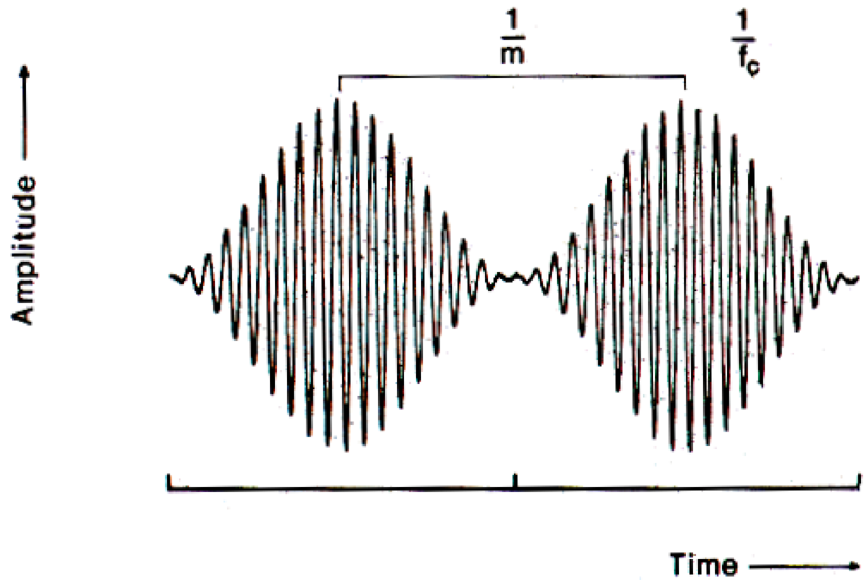
When two or more frequency components are simultaneously present, interactions on the basilar membrane can result in suppression of the activity.

This appears to
be very important for the population response to high-level speech sounds.

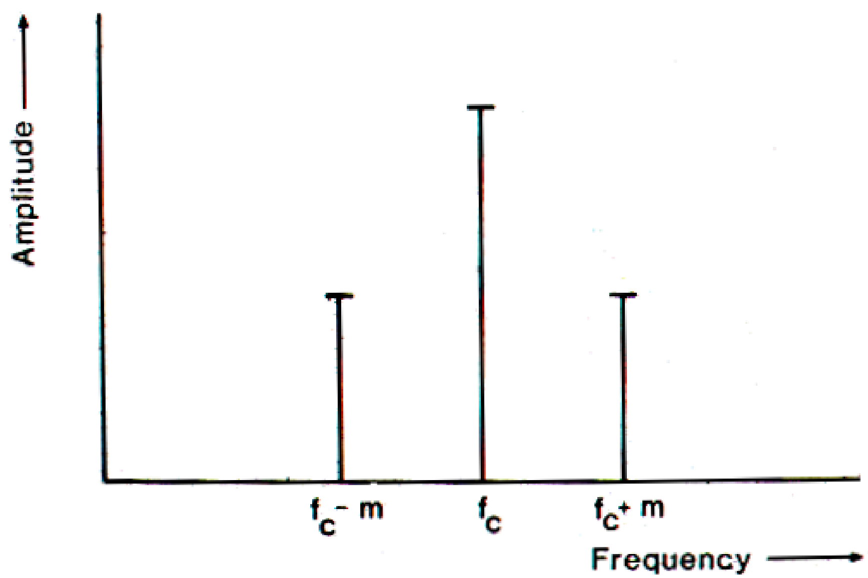
Arthur et al (1971)

Complex Stimuli

2. Three tones: amplitude modulation

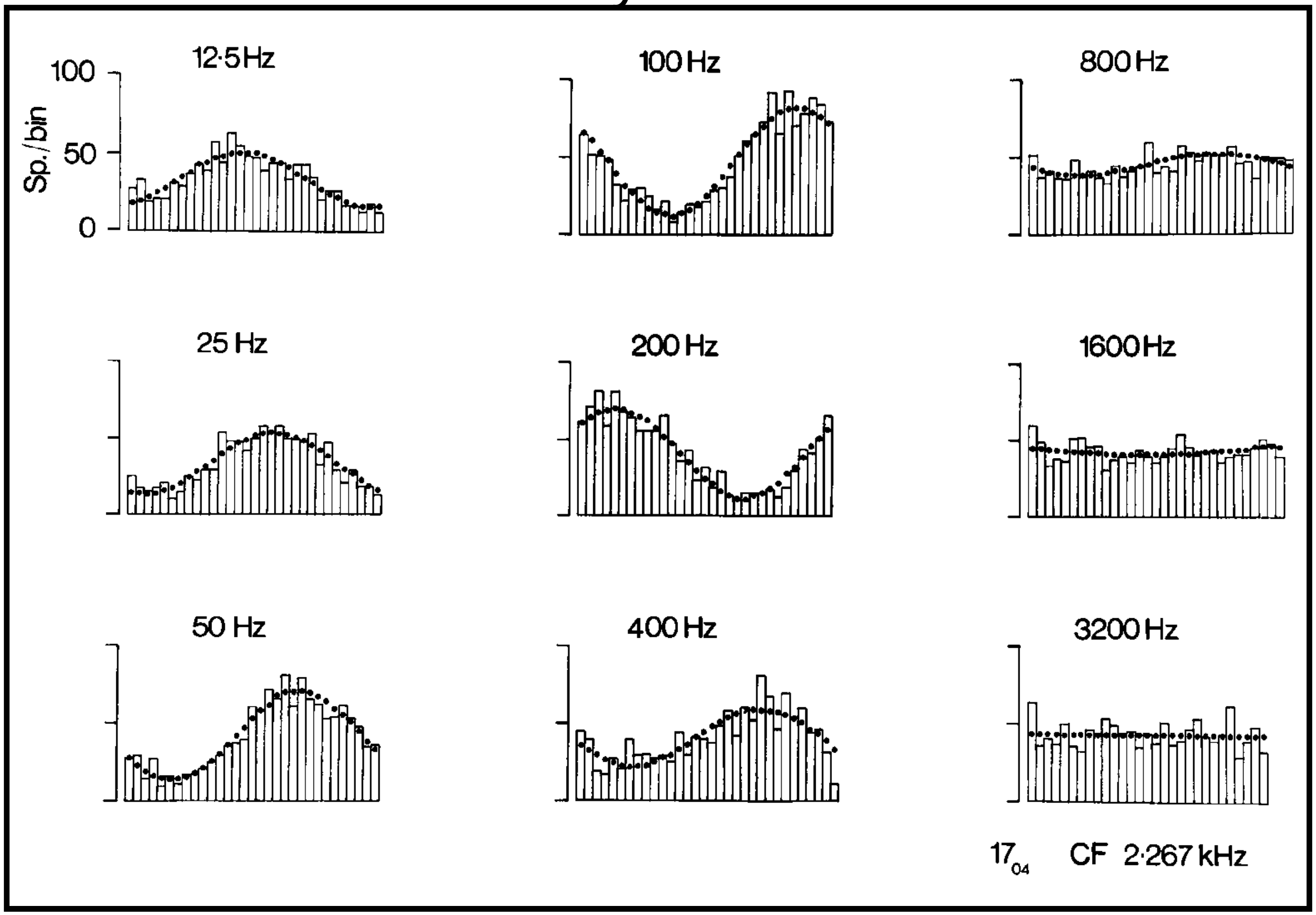


$\frac{1}{m}$
$\frac{1}{f_c}$
Amplitude
Time



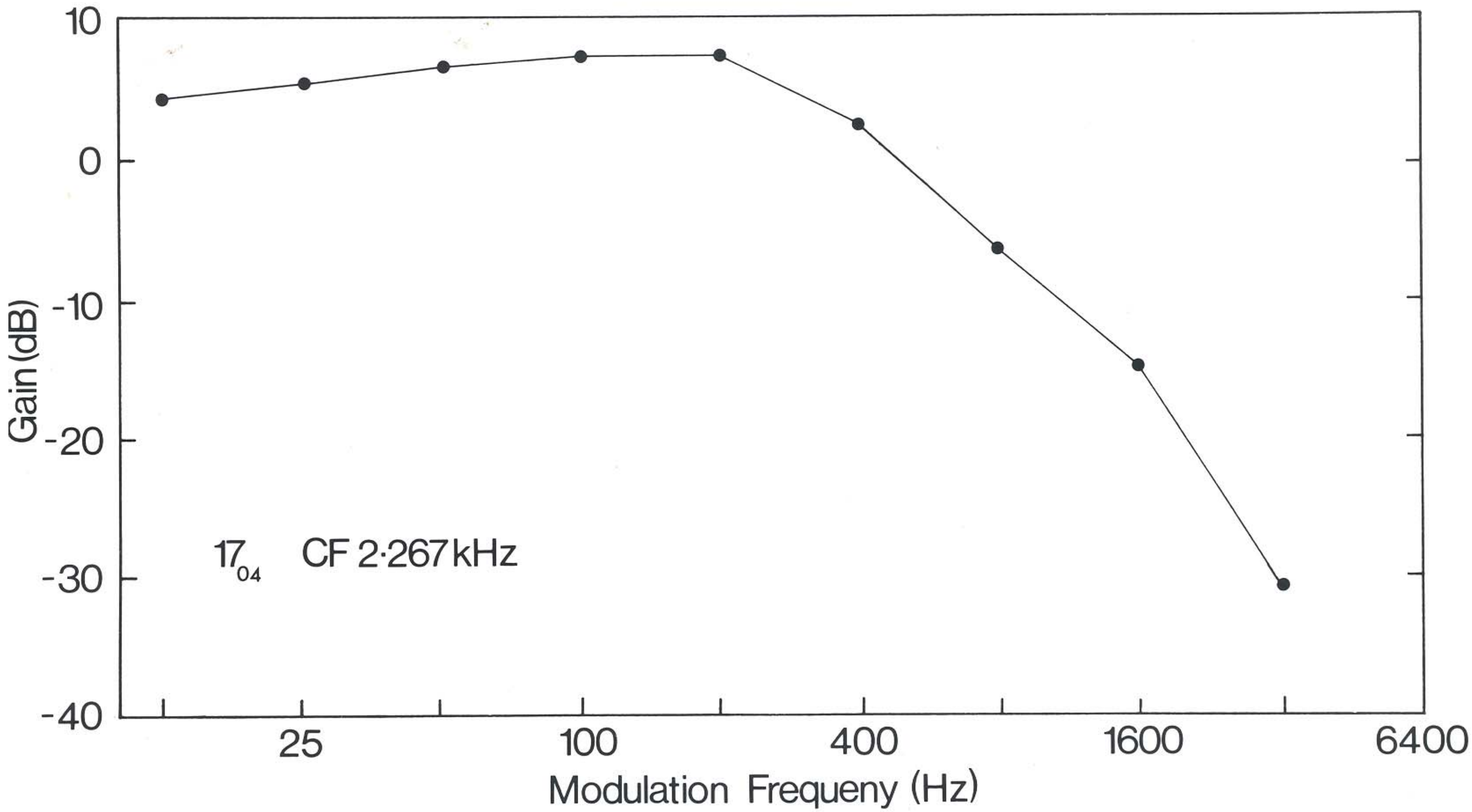
Amplitude
$f_c - m$
f_c
$f_c + m$
Frequency

Auditory nerve fibres follow the modulation of signals that fall within their response areas up to modulation frequencies determined by their bandwidth.

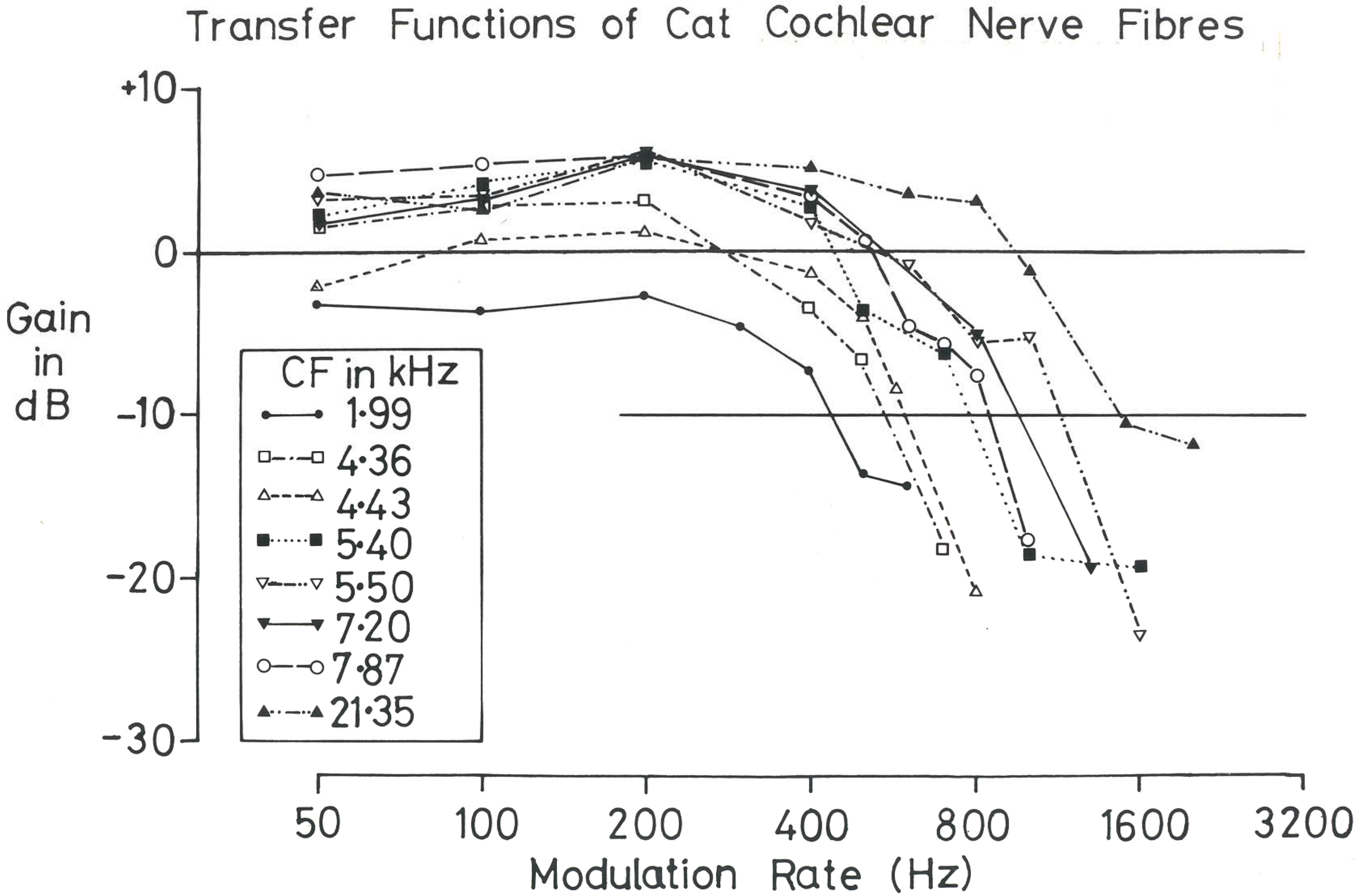


Palmer (1983)

Transfer function of a single auditory nerve fibre



Palmer (1983)

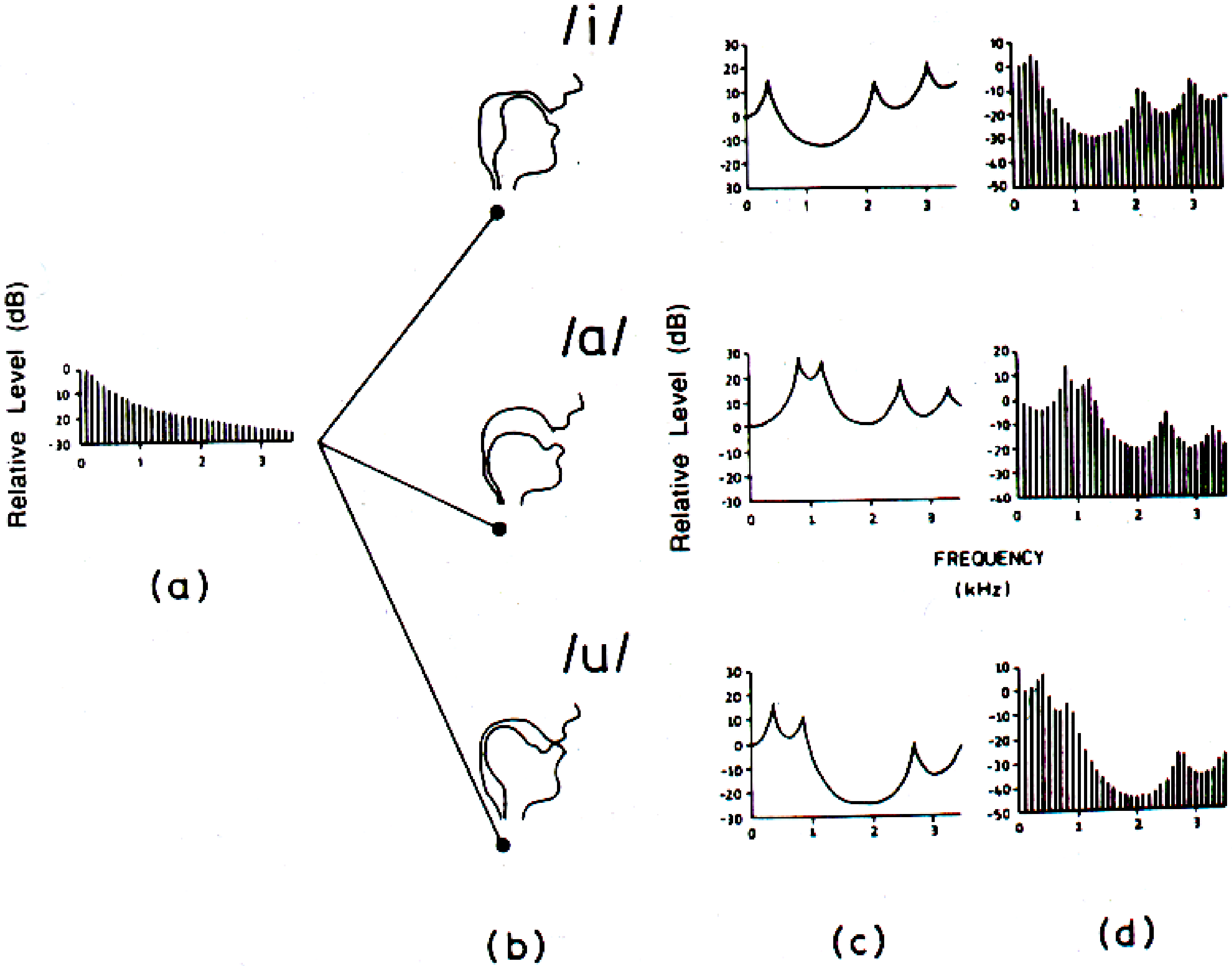


Palmer and Evans

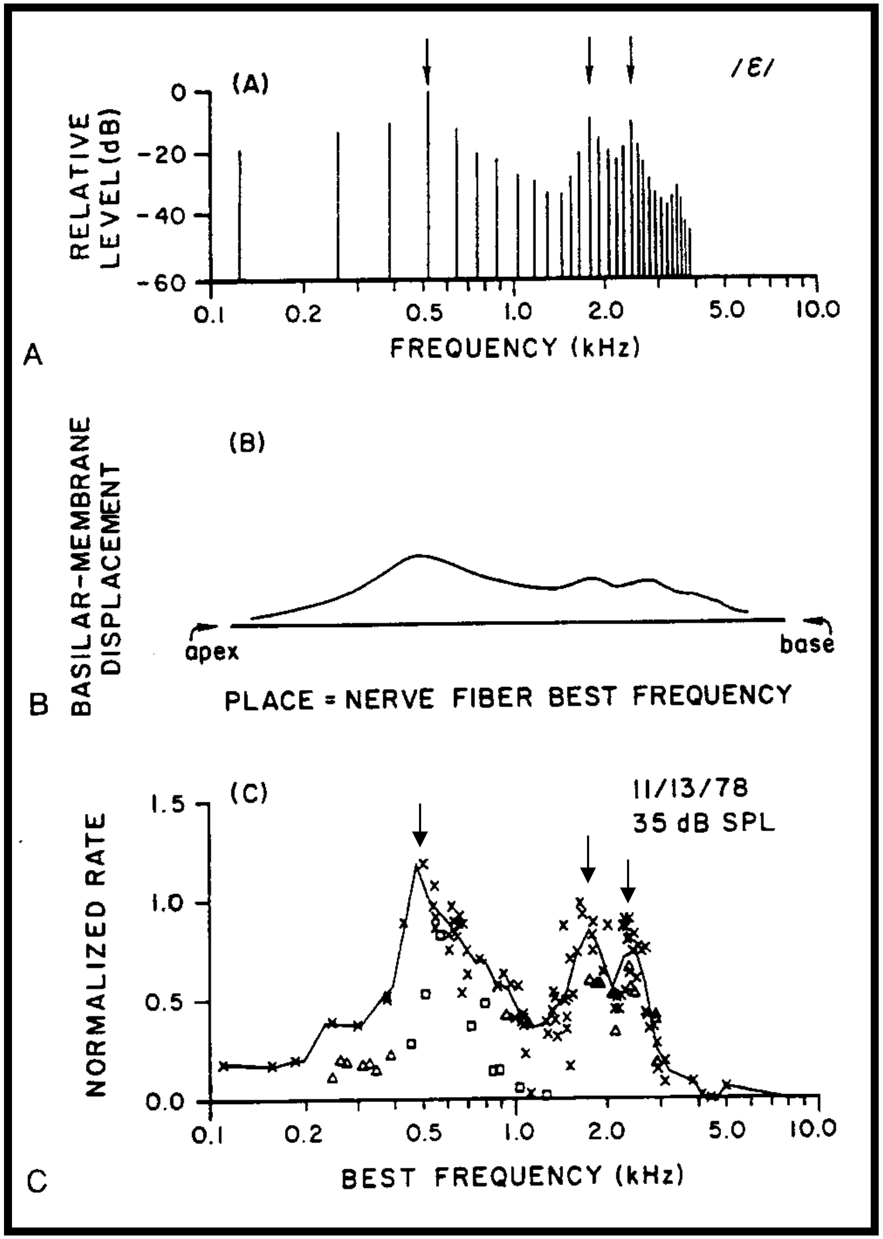
Complex Stimuli

3. Speech: vowel sounds

Generation of vowel sounds

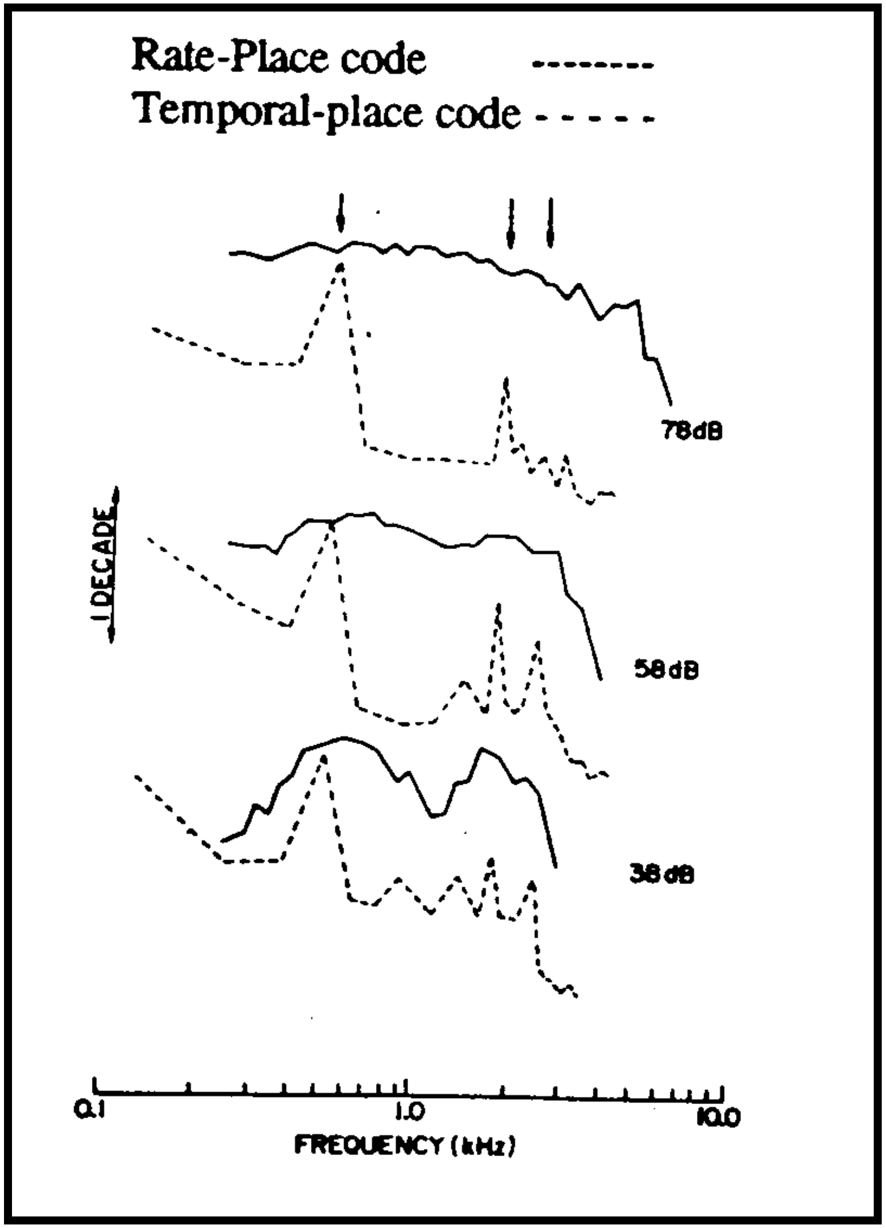


Moore



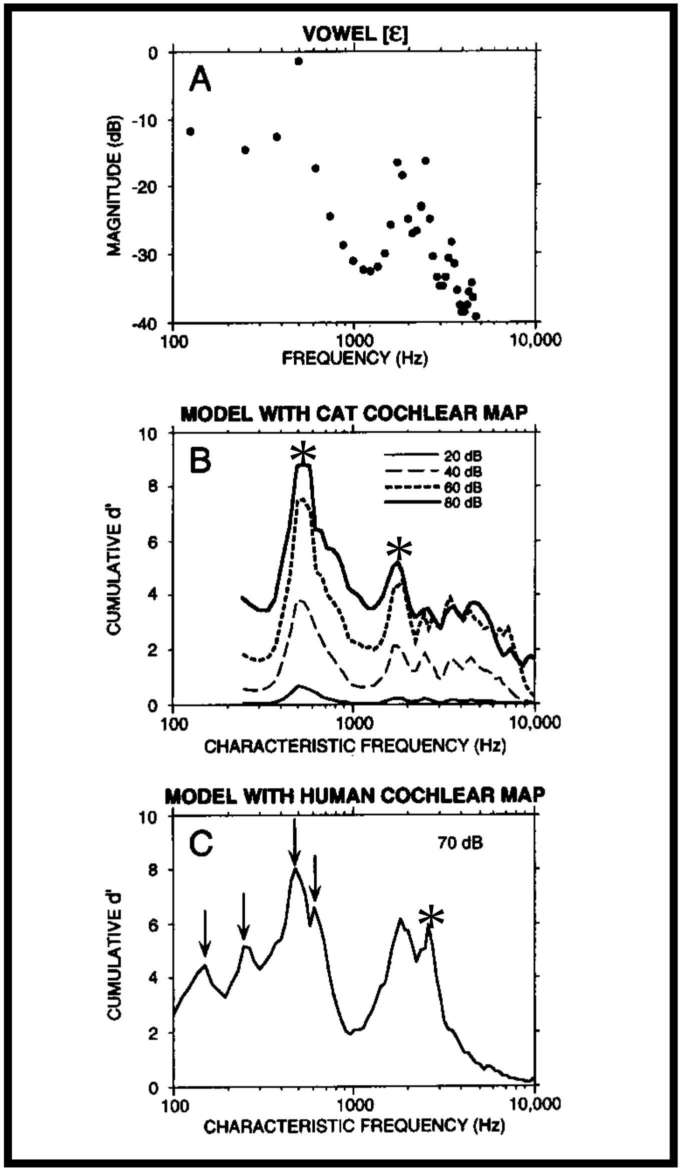
At low sound levels steady-state vowels are well represented in the mean discharge rate.

Sachs and Young, (1979)



At first sight, the fine temporal pattern of the discharge seems to retain information about the formants of vowels better than just the mean discharge rate.

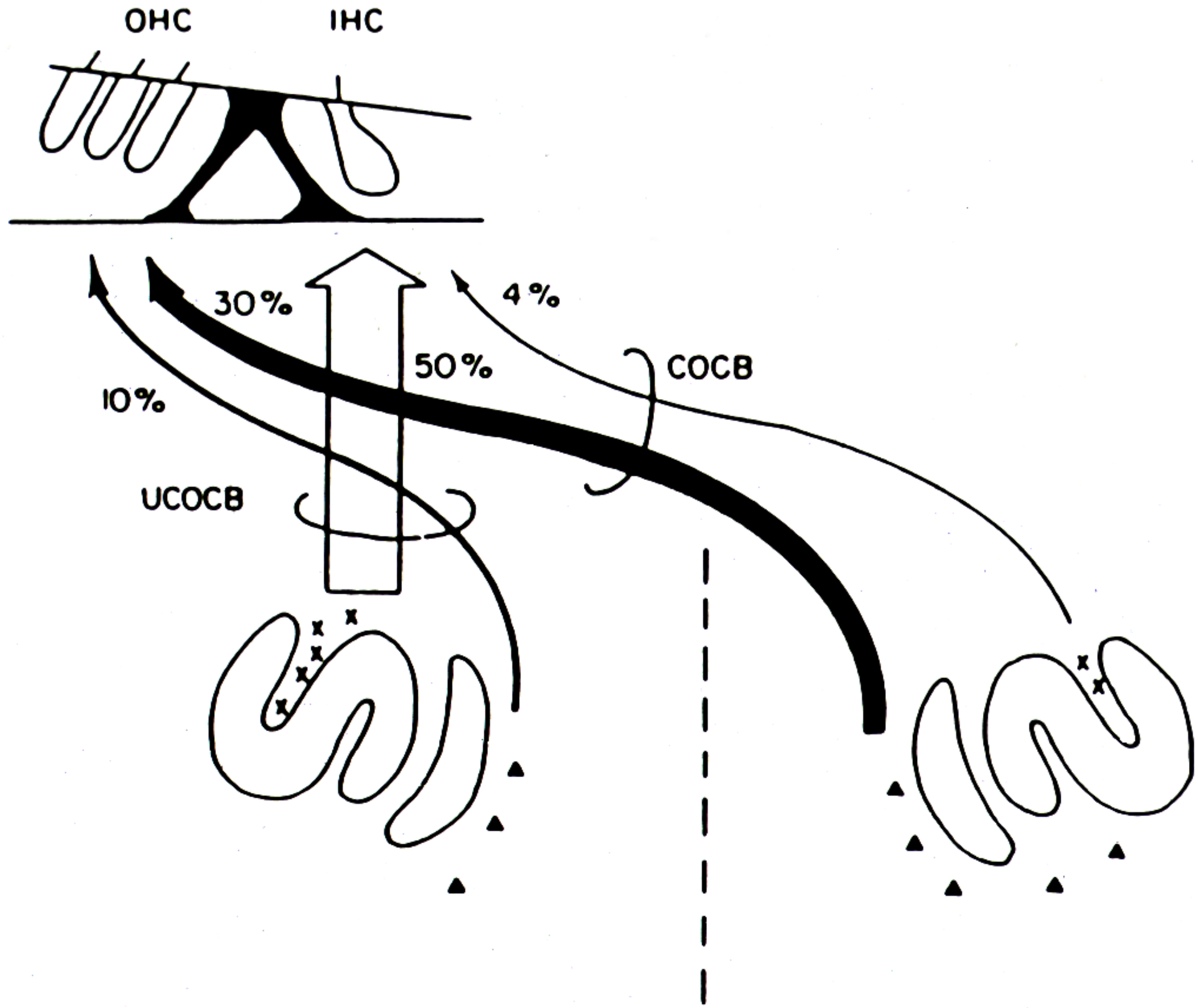
Sachs, Young and Colleagues



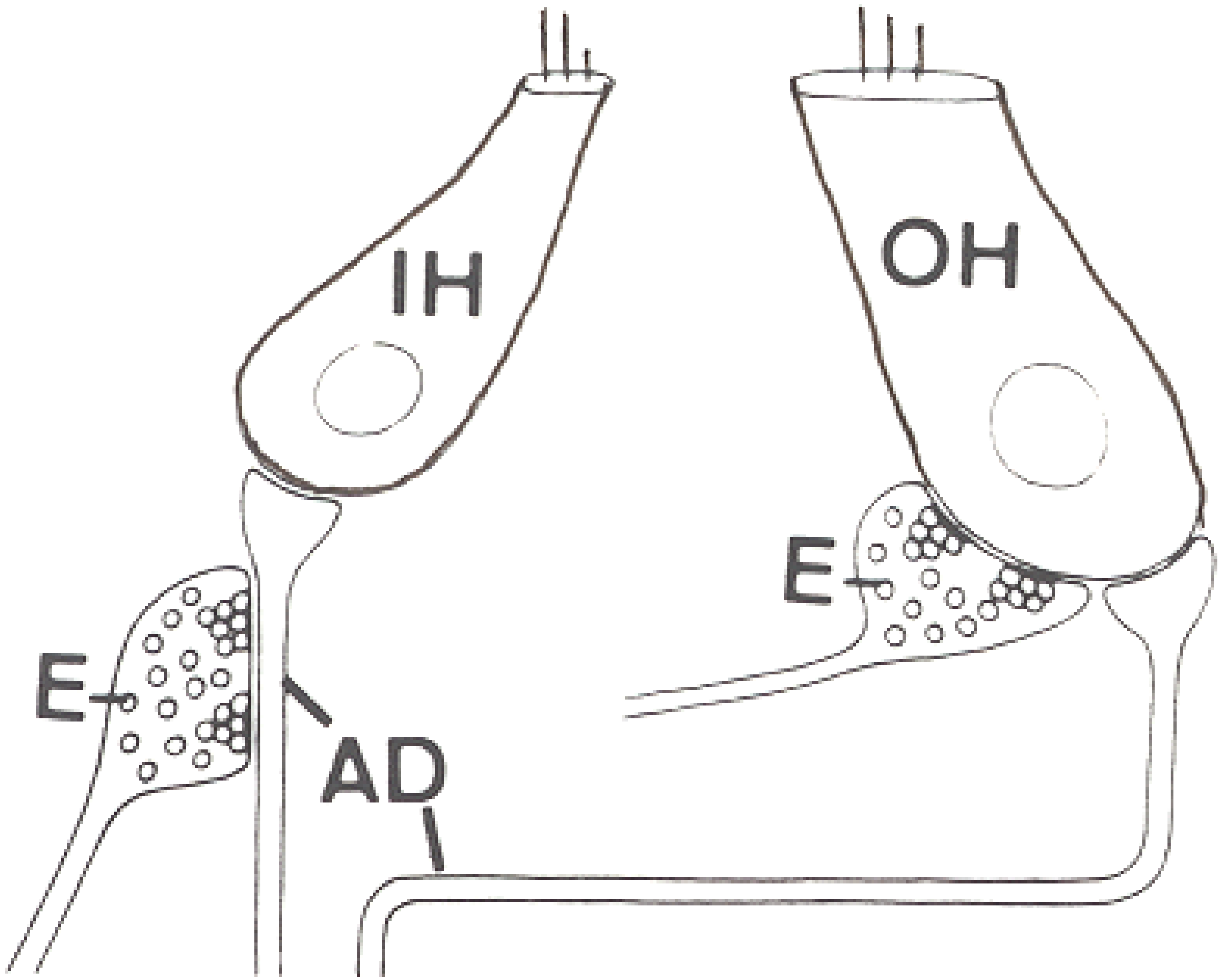
Theoretical computations, based on optimally weighting the different spontaneous rate populations, reveal that mean rate alone may contain sufficient information even at high sound levels.

Delgutte, (1996)

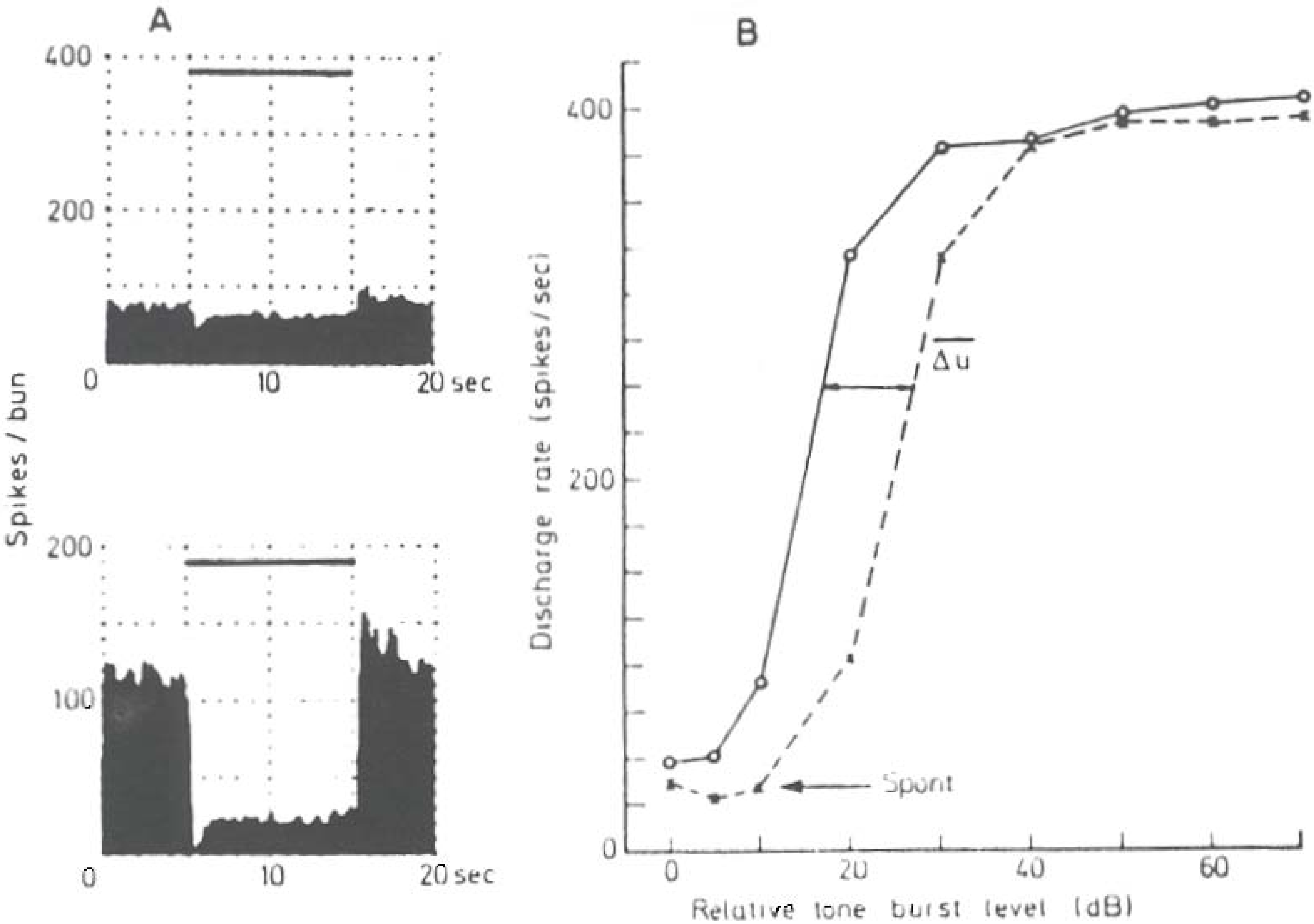
Descending pathways to the cochlea



Warr (1978), Warr and Guinan (1979)



Spoendlin (1971)



Wiederhold and Kiang (1971)

Function of the descending or centrifugal innervation

- Protection from acoustic trauma
- Involvement in selective attention
- Detection of complex signal in noise
- Control of the mechanical state of the cochlea