Question 1

Hearing loss can take various forms. For each of the instances described here, give a plausible account of the cause of the observed hearing loss in terms of a structure in the ear and the structure's function:

(a)The person shows a roughly 30dB loss in the minimum audible intensity for frequencies throughout the normal audible frequency range

(b) The person is effectively deaf to frequencies greater than about 3kHz, but shows nearly normal hearing for frequencies below this level

Question 2

Frequency has to do with the repetition pattern of a wave in time. One way it can be converted into a spatial measure is through the wavelength. This is not the way the basilar membrane encodes frequency as a spatial measure.

(a)Why does it not use wavelength?

(b)Could wavelength be used for any of the audible frequencies? Explain your answer.

Hint: assume audible range is 20-20.000Hz, sound speed in inner ear fluid 1500m/s, basilar membrane length 3.5cm

Place and temporal models of pitch perception

➢Place theory of pitch perception (reminder)

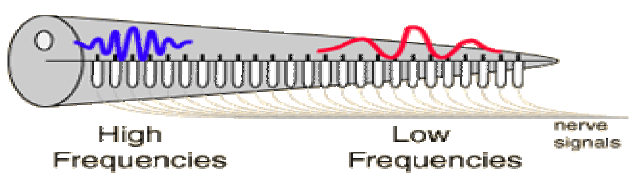
➢Neurons and their response

➢Neural decoding in Place theory

➢Phase locking – the basis of Temporal model of pitch perception

➢Neural decoding in Temporal model

Place theory



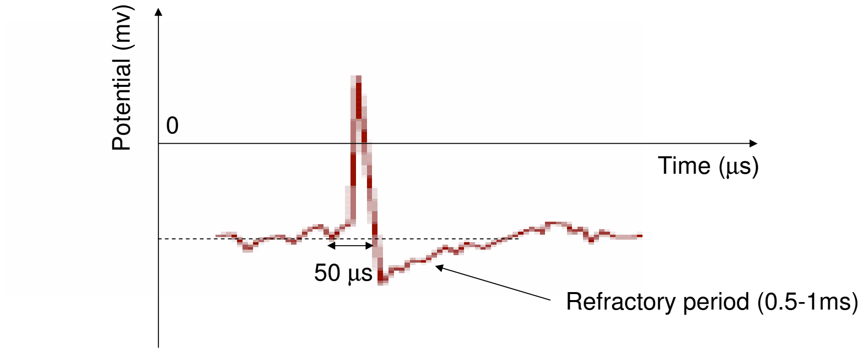
▪Basilar membrane (BM) is a mechanical frequency analyser

▪Each frequency component stimulates a resonant region along BM - place of maximum displacement is directly related to the tone frequency:
higher frequencies – closer to base **lower frequencies – closer to apex**

▪The hair cells "adjacent" to the resonant region are stimulated

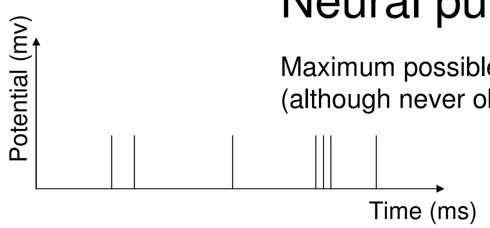
▪This results in the excitation in the nerve fibres (neurons) connected to the hair cells which carry the information from the cochlea further to the brain (approximately 32000 neurons in each auditory nerve)

Neural pulses (spikes)



Neural pulse train

Maximum possible firing rate - 1.000-2.000 spikes/s
(although never observed!)



Spontaneous firing rates of neurons

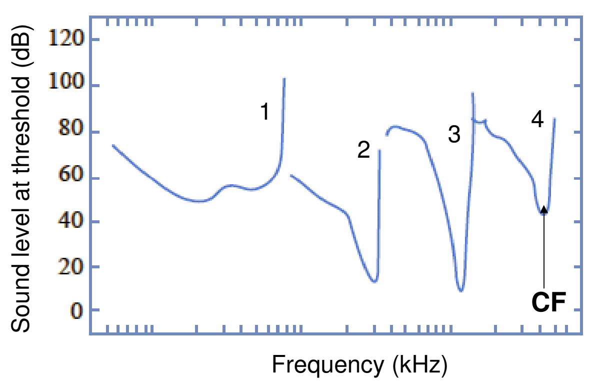
Neurons fire even in the absence of stimulus
(spontaneous firing):

61% - high spontaneous firing rate (18-250 spikes/s)
23% - medium spontaneous firing rate (0.5-18 spikes/s)
16% - low spontaneous firing rate (<0.5 spikes/s)

General rule: the **higher** the spontaneous rate the **lower** the neuron's threshold, i.e. sound level at which neuron's activity is different from that in the absence of stimulus

Frequency selectivity of neurons and place theory

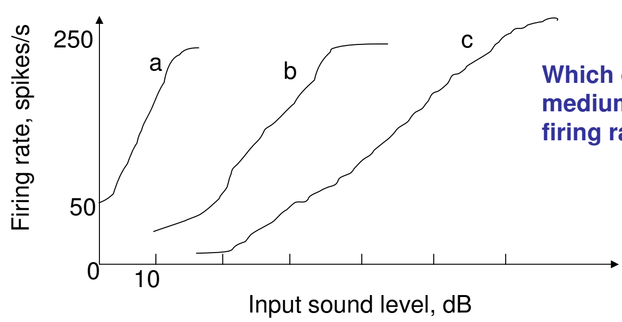
Tuning curves - each curve shows threshold level vs frequency for one neuron



CF=characteristic frequency
frequency at which the threshold level is the lowest

Place theory: neural tuning is a function of the neuron's "place" on the basilar membrane (i.e. neuron 1 is closer to apex, than neuron 4)

Firing rate as a function of intensity at a fixed frequency (CF)



Which of neurons (a,b,c) has low, medium and high spontaneous firing range?

Floor (threshold) level: sound level below which neurons fire spontaneously

Saturation level: sound level above which neuron no longer responds to the increase in sound level

Dynamic range: the range of sound levels between threshold and saturation levels.

?How do these characteristics depend on neuron's spontaneous rate?

Neural decoding in Place theory

1. Neurons can be only in two states: on and off (stimulus level above and below threshold)

2. Single neuron response is partly determined by its “place” on the basilar membrane

3. Each frequency of input sound generates a characteristic pattern activity (binary array)over the entire range of neurons in the auditory nerve.

4. This pattern is “read” by the brain (we don’t exactly know how!) and information about input sound parameters is returned.

? Count the number of possible patterns assuming 32000 neurons in each auditory nerve

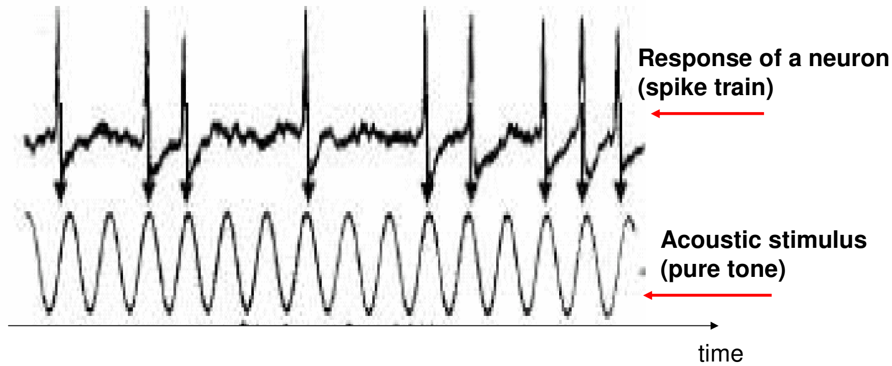
So far only the changes in firing rate of a neuron in response to acoustic stimulus were described.

However the information about the stimulus frequency is also carried in the **temporal patterning** of the neural spikes.

This forms the basis of the

Temporal model of pitch perception

Phase locking in auditory neurons (1)

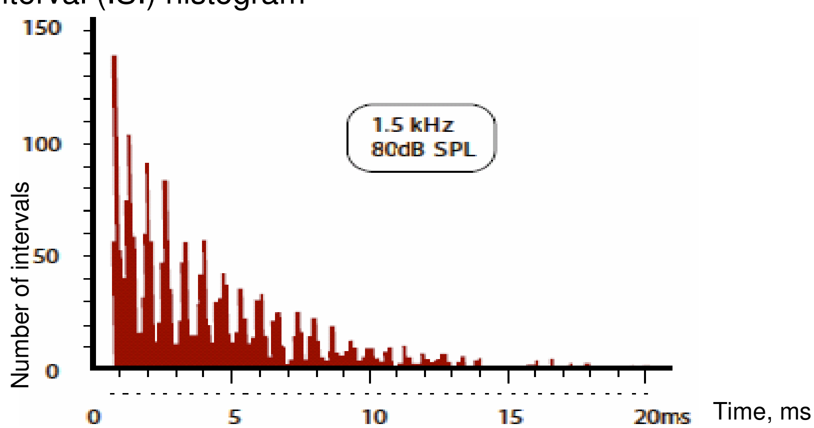


- **Neuron does not necessarily fire on every cycle of the stimulus**
- **But when it fires this occurs roughly at the same phase of the waveform each time**

? Explain this from the point of view of basilar membrane vibrations

Phase locking in auditory neurons (2)

Another way to demonstrate phase locking is to plot an inter spike interval (ISI) histogram



Interval between dots – period of the wave.
Maximum of each mode on the histogram coincides (approximately!) with one of the dots. Time intervals between modes equal to an integer number of periods

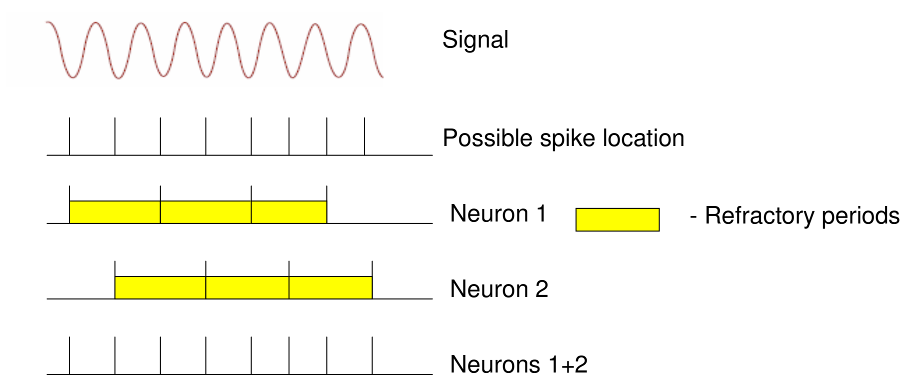
Neural decoding in Temporal model

- Each neuron that responds to a tone carries information about tone frequency in its temporal pattern of firing (due to phase locking).
- The task of the nervous system is to estimate the time intervals between the modes of ISI histogram and extract the sound period (computationally simpler task than reading binary arrays!)
- The large number of practically identical neurons carrying similar information provides the needed large sample size of spike intervals.

? What do you think might cause a problem for the mechanism to work at high frequencies?

Volley theory

It seems difficult to apply the Temporal model to high frequency pitch perception due to neuron's refractoriness. This is the possible way to overcome the difficulty:



Upper frequency limit of the phase locking

•Determined by **a precision with which the initiation of the nerve impulse is linked to a particular phase of the stimulus** (NOT REFRACTORINESS) and is 4-5kHZ . Refractoriness would give 1-2kHz

•At frequencies higher than that the variability in the instant of the initiation of nerve impulse becomes comparable with the wave period

The spikes “smeared out” over the whole period of the waveform instead of occurring at particular phase.

Place or Temporal model?

Probably both…

Some of the psychoacoustic phenomena can be explained using Place model.
To explain others the Temporal model has to be applied.

Further reading

- BCJ Moore The introduction to the psychology of hearing. Chapter 6
- RD Luce Sound and hearing: a conceptual introduction. Part 3 Chapter 4
- JG Roederer The physics and psychophysics of music. pp.50-66