10. Linearity (Moore, 1989, pp. 10–11)

1. Before we learn about the peripheral auditory system, we need to know what is meant by the term *linearity*.

2. The auditory system is often modelled as a system consisting of a number of stages, each stage having an input and an output.

3. The input to a given stage is the output from the previous stage and the output of a particular stage provides the input to the next stage.

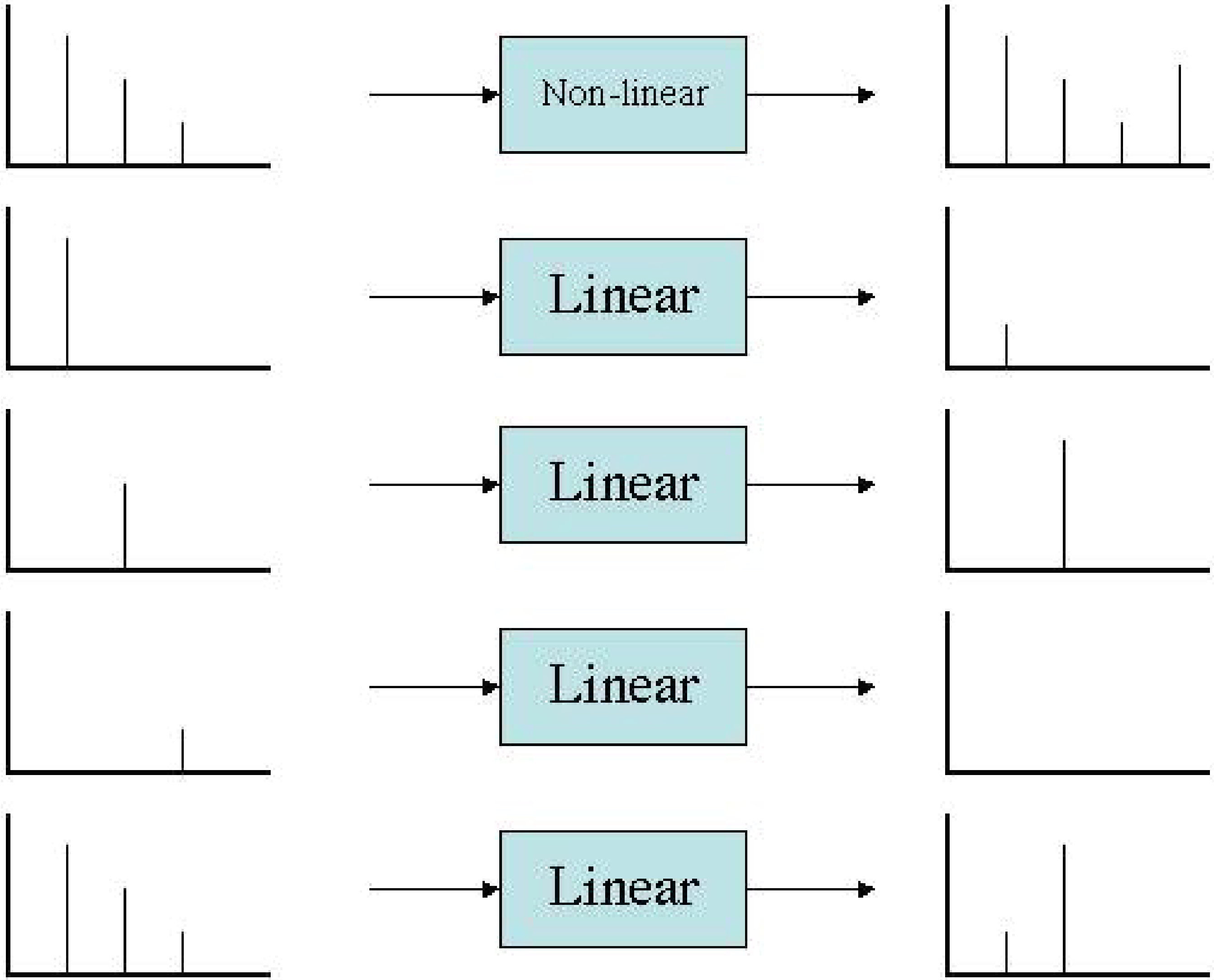
4. A given stage is said to be *linear* if it satisfies two conditions known as the conditions of *superposition* and *homogeneity*.

5. An input-output system is said to satisfy the condition of *superposition* if the output of the system for a number of independent inputs presented simultaneously is always equal to the sum of the outputs obtained when each input is presented in isolation.

6. For example, if X is the output of a system when the input is A and the system generates the output Y when the input is B, then the output when A and B are presented simultaneously will be $X + Y$ if the system is linear.

7. An input-output system is said to satisfy the condition of *homogeneity* if multiplying the magnitude of an input A by a factor k causes the magnitude of the output to be multiplied by k but otherwise causes no change in the output.

11. Linearity in acoustic systems



11. Linearity in acoustic systems

1. If the input to a linear system is a complex sound with Fourier components at a number of different frequencies, then the output of the system will not contain any components with frequencies that were not present in the input signal.

2. So if an acoustic system generates output containing frequencies that are not present in the input, then this is a sure sign that the system is non-linear.

3. This implies that if the input to a linear acoustic system is a sinusoidal simple tone, then the output of the system will be a sinusoidal simple tone with the same frequency as the input tone. The amplitude and phase of the output tone may, however, be different from those of the input tone.

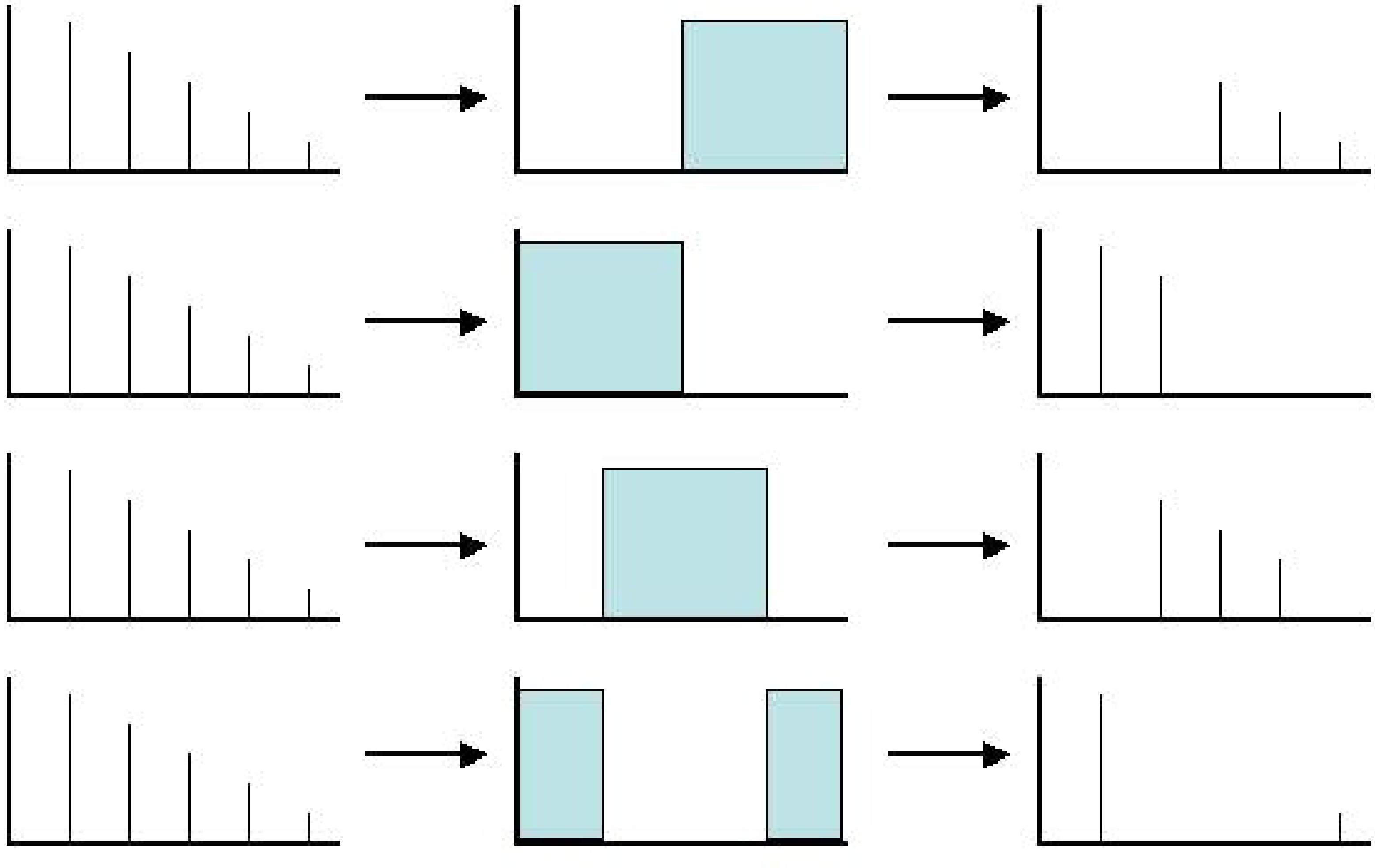
4. A linear system may respond differently to sinusoids of different frequencies, however. For example, it may reduce the amplitude to zero for any sinusoid with a frequency above a certain value.

5. This implies that if the input signal to a linear system is a complex tone containing Fourier components at various different frequencies, then the amplitudes of these Fourier components may not all be changed in the same way. If this happens, then the waveform of the output of the system will not be the same as the waveform of the input. For example, a square wave could be converted into a sinusoidal simple tone by a linear system that reduces to zero the amplitude of all frequencies above the fundamental of the square wave.

6. If an acoustic system is linear, then we can predict how it will respond to any complex sound provided we know how it responds to a sinusoidal input tone of any frequency. All we have to do is add together the responses of the system for all the sinusoidal Fourier components of the complex tone.

7. However, if an acoustic system is non-linear, then its response to a complex tone cannot in general be predicted from its responses to the individual Fourier components of the complex tone. This means that we cannot produce a precise model of a non-linear system simply by finding out how it responds to sinusoidal tones of different frequencies.

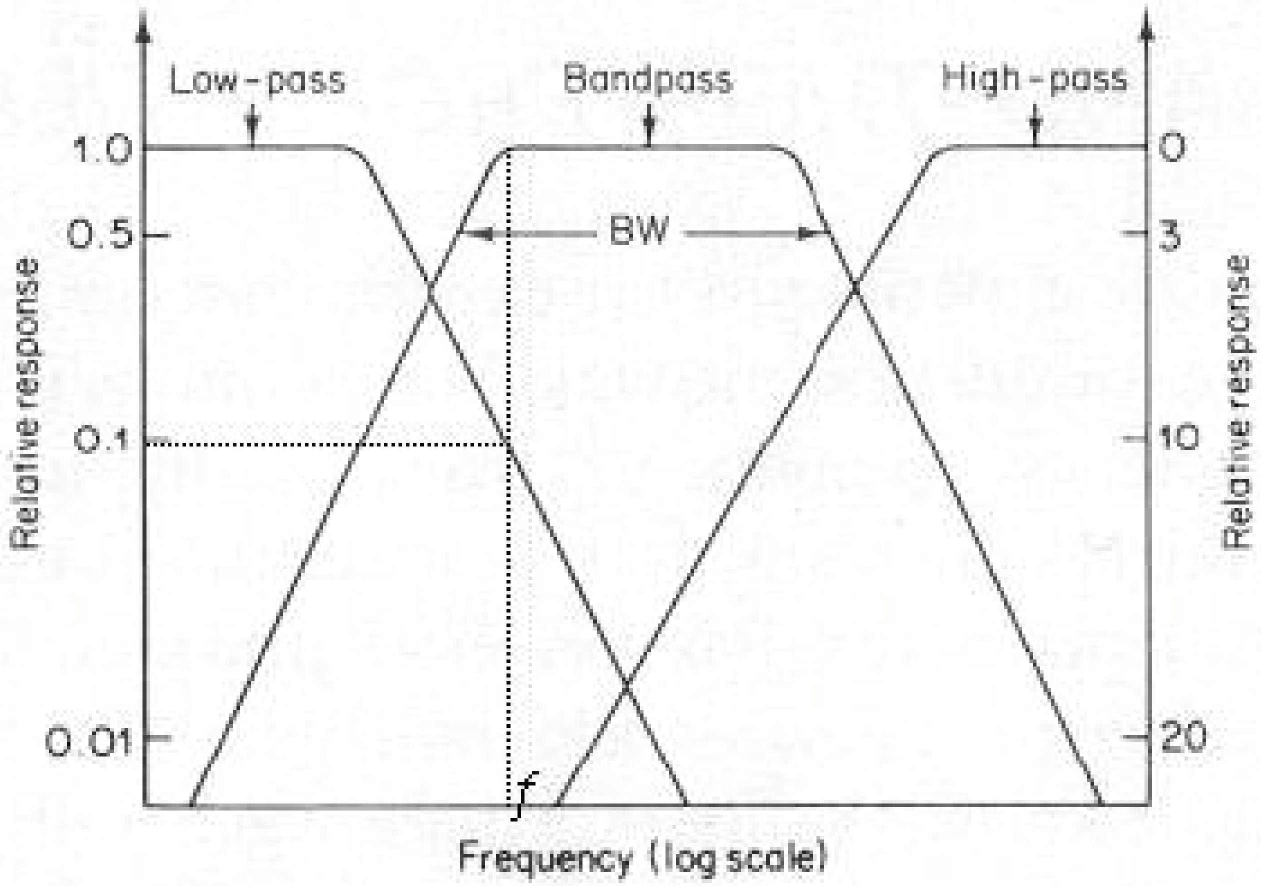
12. Filters and their properties (Moore, 1989, pp. 11–15; Roads, 1996, pp. 185–193)



12. Filters and their properties (Moore, 1989, pp. 11–15; Roads, 1996, pp. 185–193)

1. One particularly important type of linear acoustic device is a *filter*.
2. When the input to a filter is a sinusoid, the output is a sinusoid with the same frequency and an amplitude that is either equal to or less than that of the input sinusoid.
3. The amount by which the amplitude of the input sinusoid is reduced or *attenuated* by a filter depends upon the frequency of the sinusoid.
4. There are four basic types of filter: highpass filters, bandpass filters, lowpass filters and bandstop filters.
5. A highpass filter removes all the Fourier components in the input sound whose frequencies are less than a certain cutoff frequency, and leaves unchanged all the components with frequencies above the cutoff frequency.
6. A lowpass filter removes all the Fourier components in the input sound whose frequencies are greater than a certain cutoff frequency, and leaves unchanged all the components with frequencies below the cutoff frequency.
7. A bandpass filter has two cutoff frequencies. It removes all components in the input with frequencies outside the range defined by these cutoff frequencies and leaves unchanged all components within this range. The frequency half way between the cutoff frequencies of a bandpass filter is called the *centre frequency*. The difference between the two cutoff frequencies of a bandpass filter is called the *bandwidth* of the filter.
8. A bandstop filter also has two cutoff frequencies but it does the opposite of a bandpass filter: it removes all the components in the input signal with frequencies between the cutoff frequencies and leaves unchanged all components with frequencies outside of the range defined by the cutoff frequencies.
9. The range of frequencies that are left unchanged by a filter is called the *passband* of the filter and the range of frequencies that are attenuated is called the *stopband*.
10. The concept of a bandpass filter is particularly important for understanding the function of the inner ear because one component of the inner ear, called the *basilar membrane*, is often likened to a bank of bandpass filters, each filter having a different centre frequency.

13. Real filters



13. Real filters

1. Ideally, a filter would reduce to zero the amplitude of all components with frequencies outside the passband. However, in practice it is not possible to build filters with perfectly sharp cutoff frequencies. Instead, there will be a range of frequencies around each cutoff within which the amplitudes of components are reduced but not eliminated completely.

2. This range of frequencies within which the power of the input is reduced but not completely eliminated is called the *transition band*.

3. We can describe the behaviour of a filter by using a graph called a *filter response curve* or *filter characteristic*. This figure here shows some typical characteristics for bandpass, lowpass and highpass filters.

4. The filter characteristic gives, for each frequency f on the horizontal axis, the ratio of the output power to the input power when the input is a sinusoid with frequency f. For example, when a sinusoid with the frequency f in the diagram is passed through this bandpass filter, it is left unchanged. However, when it is passed through this lowpass filter, its power is reduced to about $\frac{1}{10}$th of its original value—that is, its power is reduced by 10dB.

5. In an ideal filter with sharp cutoffs, the cutoff frequencies are clearly defined. In a real, non-ideal filter, the cutoff frequencies are usually defined to be those frequencies at which the power of the output is half the power of the input, or, equivalently, 3dB less than the power of the input. So for these filters here, the cutoff frequencies would be as marked in the diagram.

6. The bandwidth of a bandpass filter is equal to the difference between the cutoff frequencies. When these cutoff frequencies are defined to be the frequencies at which the power is reduced by 3dB, the bandwidth is called the -3 *dB bandwidth* or the *3 dB down bandwidth* or the *half-power bandwidth*. It is also often called simply the *3 dB bandwidth*.

7. When the filter response curve axes are both logarithmic as they are here, it is often the case that the filter characteristic is approximately a straight sloping line within the transition band, as shown in this diagram. We

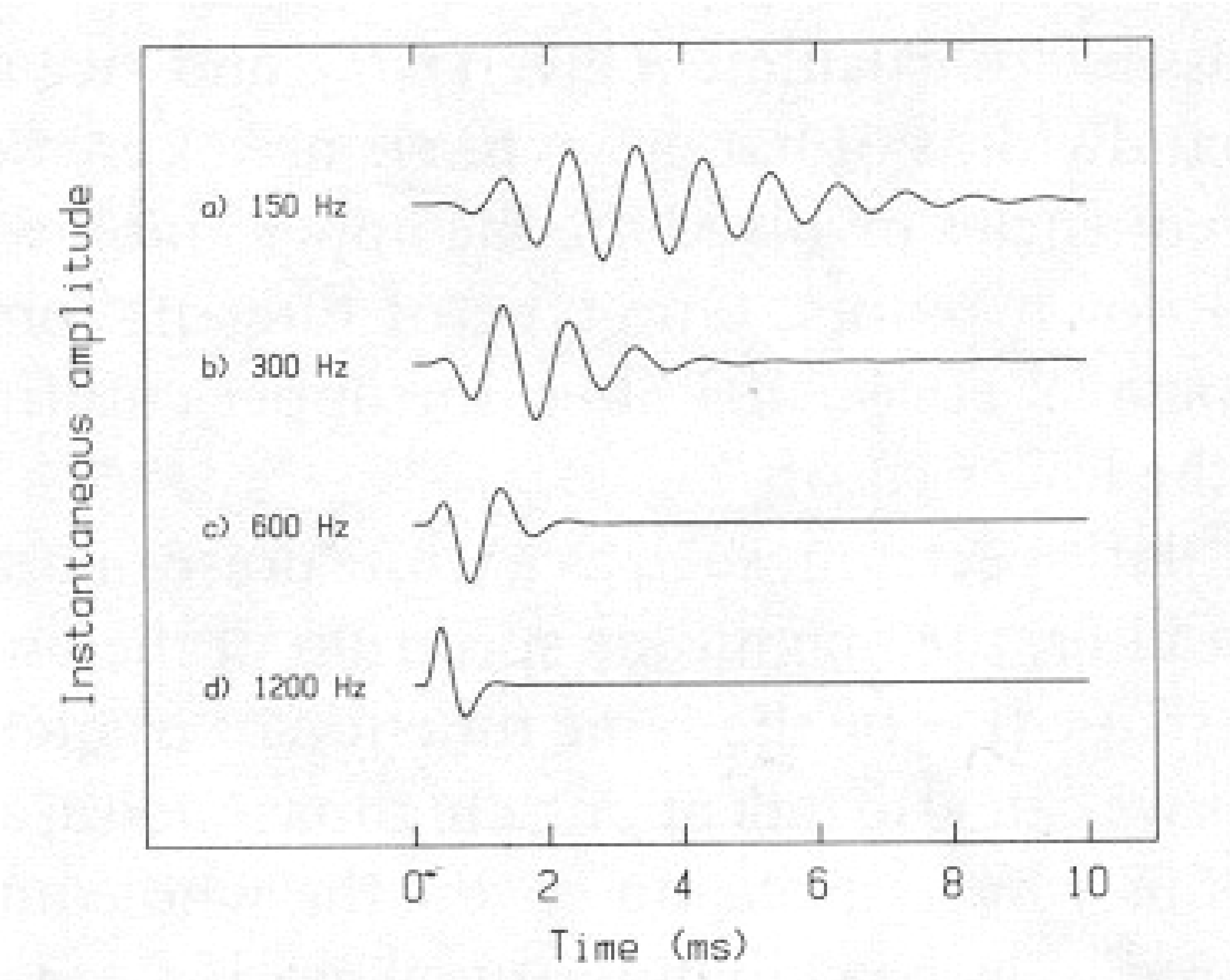
can therefore represent the sharpness of the cutoff frequencies of a filter by giving the slope of this line within the transition band.

8. On this graph, equal distances along the vertical axis correspond to equal level changes in dB and equal distances along the horizontal axis correspond to equal frequency *ratios*.

9. To express the slope of this line, we therefore have to choose a particular frequency ratio as the unit for the horizontal axis and the commonest ratio to choose is 2:1, that is, an octave.

10. The sharpness of the cutoff frequencies of a filter is therefore usually represented by the slope of the filter characteristic within the transition band, expressed in dB/octave. For example, if a lowpass filter has a slope of 24 dB/octave, this means that the ratio of the input to output power outside the passband decreases by 24 dB each time the frequency is doubled.

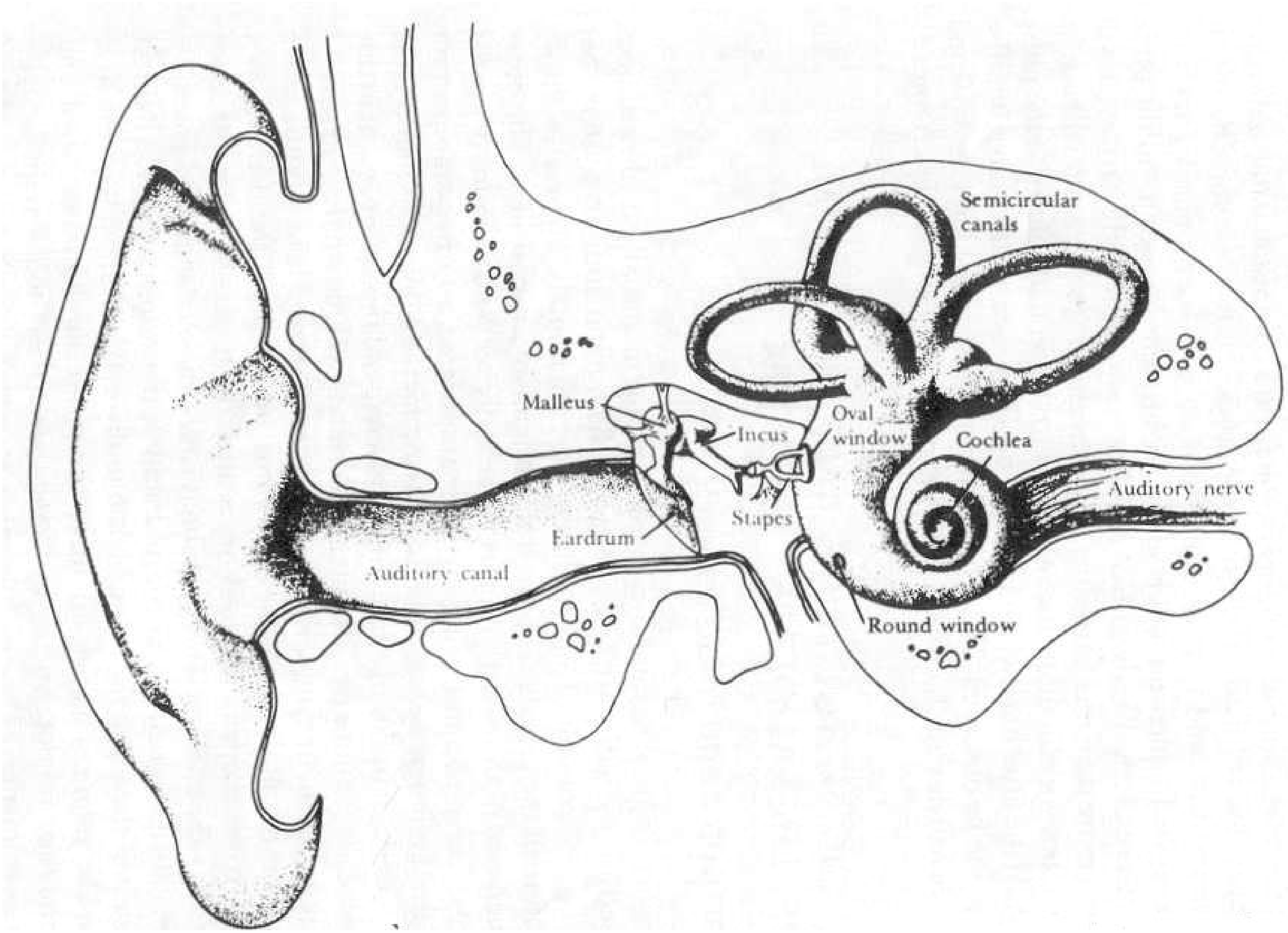
14. Impulse response



14. Impulse response

1. If we pass a signal with a flat spectrum such as a white noise or a click through a filter, then the spectrum of the output signal will be the same shape as the filter characteristic.
2. If we alter the spectrum of a sound by filtering it, this will cause a corresponding alteration in the waveform of the sound and a change in the way it is perceived.
3. For example, if we pass white noise through a narrow bandpass filter, then the waveform of the output will resemble a sinusoid with fluctuating amplitude. The output sound will have a pitch that is similar to that of a sinusoid with a frequency equal to the centre frequency of the filter.
4. If we pass a brief click or *impulse* through a filter then the output is called the *impulse response* of the filter and because the Fourier spectrum of the impulse is flat, the Fourier spectrum of the output will have the same shape as the filter characteristic.
5. This figure shows the waveforms of the impulse responses obtained from four different bandpass filters. Each filter has a centre frequency at 1000Hz but they all have different bandwidths.
6. For the narrowest filter, the output resembles a sinusoidal tone burst at the centre frequency of the filter that rises and then falls in amplitude. This is called a ‘ringing response’.
7. As the filter bandwidth increases, the oscillations in the impulse response become less regular, the duration of the response gets shorter and the output becomes more and more like the input click.
8. This demonstrates that if you use a bank of bandpass filters to perform a Fourier-like analysis of an input signal, then if you use very narrow filters in order to get high frequency resolution, you lose the ability to respond quickly to a changing input signal because the responses of the filters will last a long time. On the other hand, if you use wide filters, then you will have better time resolution but the frequency resolution will be reduced.

15. The peripheral auditory system



15. The peripheral auditory system

1. This figure shows the human peripheral auditory system.
2. Conventionally, this system is divided into the outer, middle and inner ear [SHOW ON DIAGRAM].
3. The outer ear consists of the *pinna* which is the bit that protrudes from the side of the head, and the ear canal or *auditory meatus*.
4. The human pinna actually has a quite significant effect on the incoming sound, particularly at high frequencies, and contributes to our ability to localize sounds—that is, tell where they are coming from.
5. In other mammals such as dogs, for example, the pinna is much more well developed and can be directed towards the sound source. This can be used to amplify quieter sounds by 'funnelling' more of the sound energy down into the ear. You can experience this amplification effect yourself by cupping your hands over your ears so that the opening is directed towards a sound source.
6. The incoming sound travels down the auditory meatus and causes the eardrum or *tympanic membrane* to vibrate.
7. The tympanic membrane is the interface between the outer ear and the middle ear. The vibrations of the tympanic membrane are transmitted through the middle ear by three small bones, called the *auditory ossicles*, to a membrane-covered opening in the bony wall of the inner ear. This opening is called the *oval window*.
8. The three ossicles are called the *malleus* (or hammer), the *incus* (or anvil) and the *stapes* (or stirrup). The lightest of these is the stapes and it is this bone which makes contact with the oval window. The auditory ossicles are the smallest bones in the human body.
9. The oval window is the interface between the middle ear and the inner ear. The inner ear consists of a fluid-filled, spiral-shaped structure called the cochlea.
10. The middle ear seems to have evolved to ensure that the vibrations of the tympanic membrane are efficiently transmitted to the fluids inside the cochlea.

11. If the sound were to impinge directly onto the oval window, then most of it would be reflected back because the fluids in the cochlea are much more dense than the air—we say that the *acoustical impedance* of the fluids in the cochlea is much greater than that of the air.

12. The force exerted on the tympanic membrane is equal to the pressure times the area. This force is transmitted by the auditory ossicles onto the oval window. However, the area of the oval window is roughly 1/25th of the area of the tympanic membrane, so all the force on the tympanic membrane is concentrated onto the much smaller area of the oval window. If this were the whole story, then the pressure on the oval window would be 25 times that on the tympanic membrane. But it is not the whole story because the auditory ossicles act as a system of levers that approximately doubles this pressure.

13. So the pressure on the oval window is about 50 times the pressure on the tympanic membrane, but the distance moved by the stapes is only about half that of the tympanic membrane.

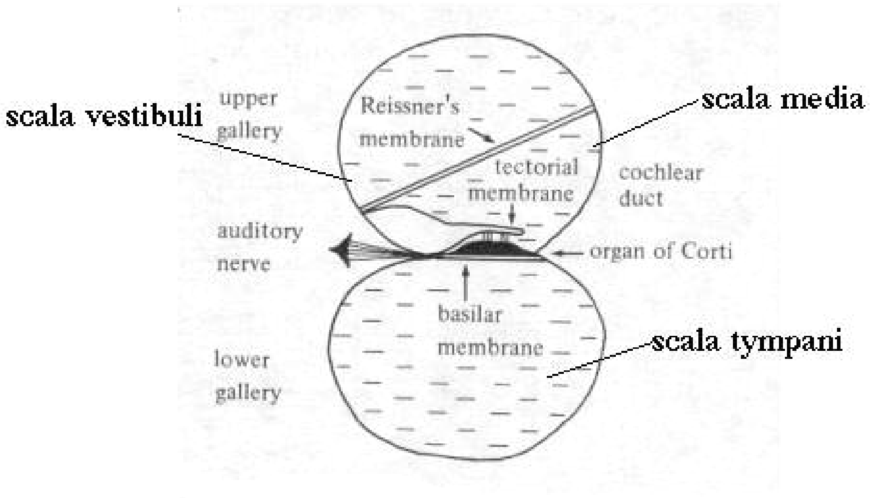
14. Recall that the loudness of a sound is related to its intensity which is proportional to the square of the pressure amplitude. If the pressure at the oval window is 50 times that at the tympanic membrane, then the intensity is multiplied by 2500 times by the middle ear. In other words, the middle ear increases the sound pressure level by over 30 dB. This extra intensity ensures that a much larger fraction of the sound energy is transmitted to the inner ear.

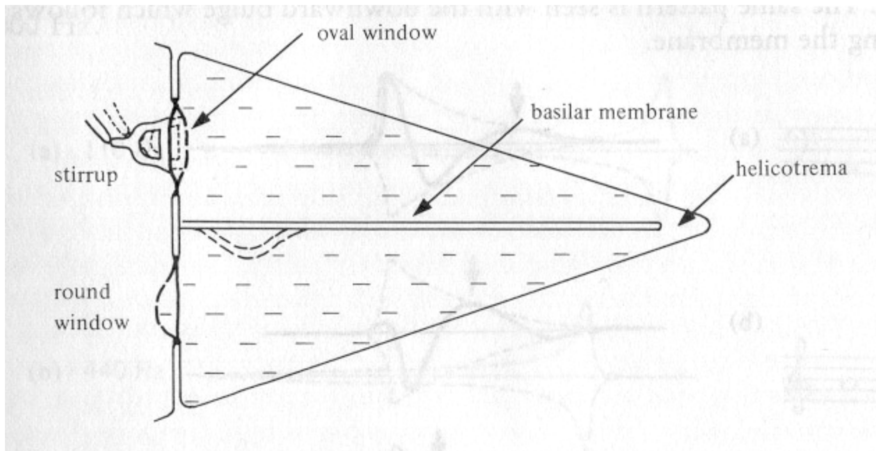
15. When the middle ear is exposed to very loud sounds at frequencies below about 1000Hz, a muscle attached to the stapes automatically draws the bone slightly away from the oval window. This is called the *middle ear reflex* or the *acoustic reflex* (Morgan and Dirks, 1975).

16. This reflex seems to have evolved in order to protect the inner ear from sudden loud noises. However, as the reflex takes about 1/10 second to act, it cannot protect the inner ear from very sudden noises such as a gunshot.

17. It has also been suggested that the middle ear reflex has evolved because it reduces the audibility of one's own speech—it has been shown that the reflex is activated just before vocalization.

16. The inner ear

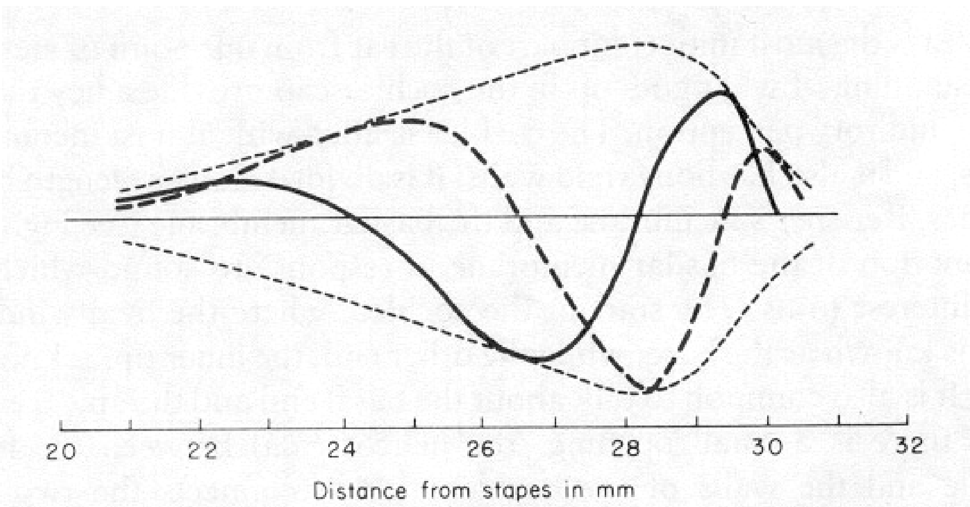


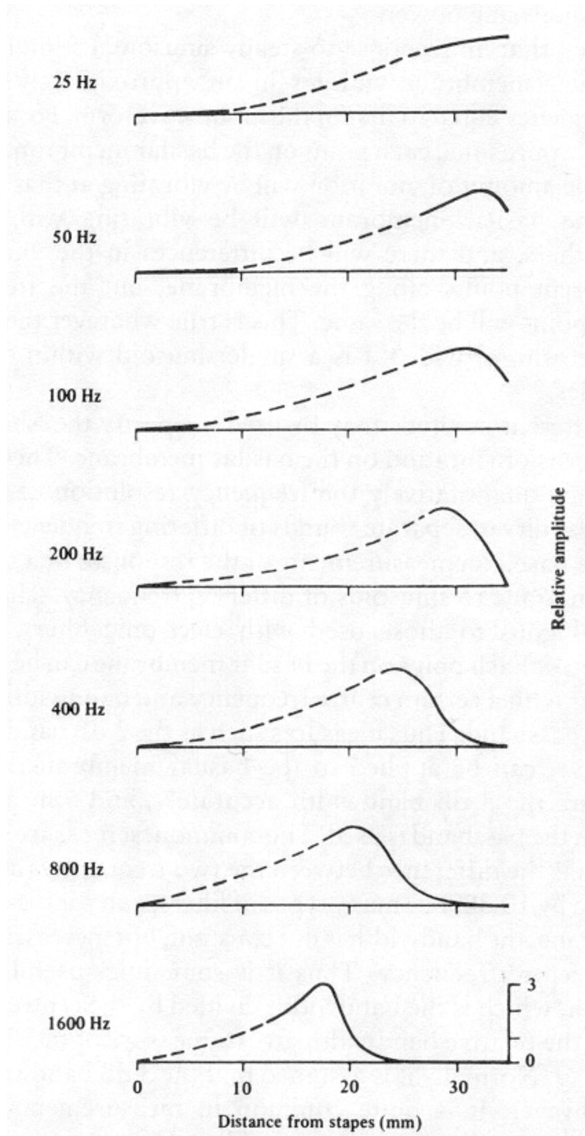


16. The inner ear

1. The sound is transmitted by the middle ear into the inner ear via the oval window.
2. The inner ear consists of the *cochlea* which is a spiral-shaped tube with bony walls filled with incompressible fluid.
3. When we take a cross-section across the cochlea, we see that it is divided into three chambers by two membranes that run almost all the way along the tube, as shown in this diagram.
4. The oval window opens into the top chamber which is called the *scala vestibuli* or *upper gallery.*
5. The scala vestibuli is separated from the middle chamber by a very thin membrane called Reissner's membrane.
6. The middle chamber is called the *scala media* or *cochlear duct* and this chamber is separated from the lowest of the three chambers by a rather more substantial membrane called the *basilar membrane.*
7. The lowest of the three chambers is called the *scala tympani* or the *lower gallery.*
8. The end of the cochlea where the oval window is situated is called the *base* or *basal end* and the opposite end of the cochlea is called the *apex* or *apical end.*
9. At the basal end of the scala vestibuli (the upper gallery), we find the oval window and at the basal end of the scala tympani (the lower gallery), we find another membrane covered opening called the *round window.*
10. At the apical end of the cochlea, the scala vestibuli and the scala tympani meet and the gap through which they communicate is called the *helicotrema.*
11. When the stapes is pushed inward against the oval window by an incoming sound, this displaces some of the fluid in the scala vestibuli and, because the basilar membrane is not rigid, it is pushed downward at the basal end. This in turn displaces fluid in the scala tympani which pushes the round window outward.

17. Patterns of vibration on the basilar membrane



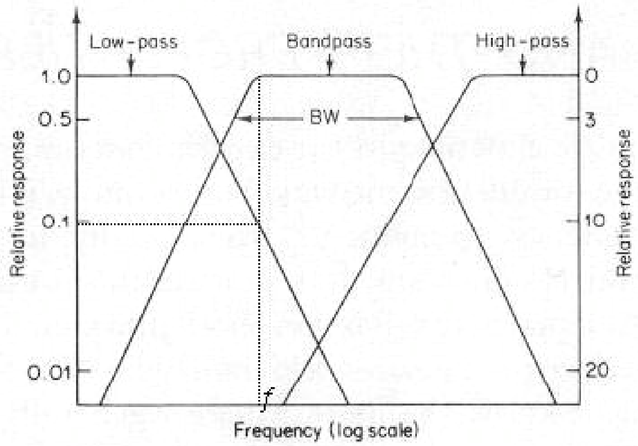


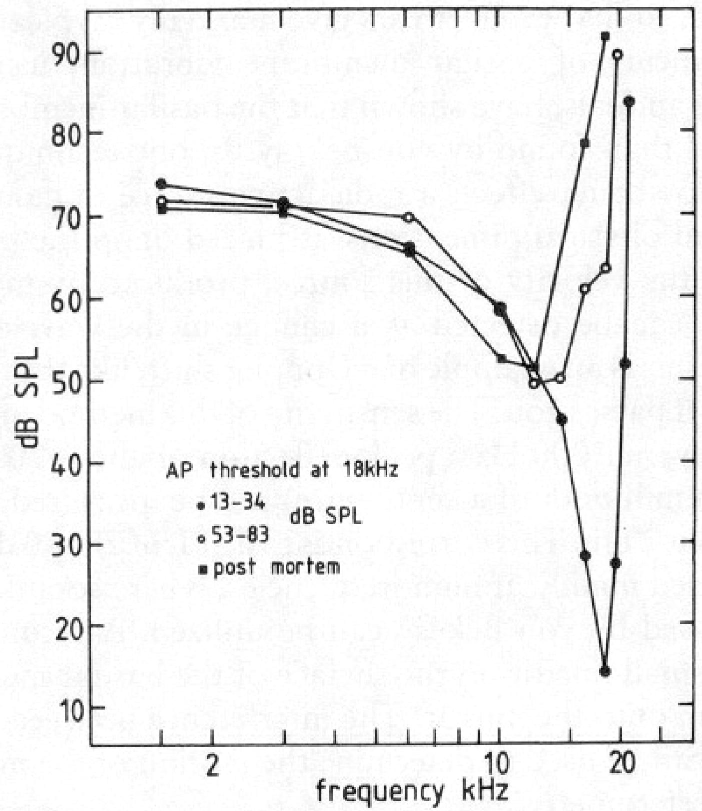
17. Patterns of vibration on the basilar membrane

1. We all know that if we have a length of string and we sharply flick one end of it in a vertical direction, then this causes a wave to travel down the string.
2. Exactly the same thing happens in the basilar membrane. The displacement in the basilar membrane caused by the inward motion of the stapes is transmitted along the basilar membrane just like the impulse is transmitted along a string.
3. Now, the linear density of a string or rope is roughly constant throughout its length. So when the disturbance is transmitted along it, the wavelength of the disturbance remains roughly the same and the amplitude diminishes gradually as the energy is dissipated.
4. However, the basilar membrane does not have a homogeneous structure like a string. Instead, it is rather narrow and stiff at the basal end and gets wider and more flexible the nearer you get to the apical end.
5. So when the cochlea responds to a sinusoidal stimulus, the wavelength and amplitude of the wave in the basilar membrane change as it travels along it. The wavelength gets shorter and the amplitude gradually increases until it reaches a certain point on the basilar membrane, after which it rapidly decrases.
6. This diagram shows the shape of the basilar membrane at two different instants in time when it is stimulated by a 200Hz sinusoid. This dotted curved line shows the track or locus of the points of maximum displacement in the wave. As you can see, the amplitude increases gradually up to a point and then falls rapidly after that point. This dotted line is called the *amplitude envelope* of the basilar membrane response.
7. Because the basilar membrane gets wider and more flexible, the nearer you get to the apex, the point on the basilar membrane at which the maximum amplitude occurs (i.e., the peak of the amplitude envelope) depends on the frequency of the stimulus.
8. When the stimulus has a high frequency, the peak of the amplitude envelope is near to the base where the basilar membrane is narrow and stiff. When the stimulus has a low frequency, the peak of the amplitude envelope is nearer to the apex where the basilar membrane is wide and flexible.

9. This diagram here from von Békésy (1960) shows the amplitude envelope of the basilar membrane response for sinusoidal stimuli of various frequencies.
10. Note that, whatever the stimulus frequency, the disturbance on the basilar membrane does not travel much further after the amplitude has peaked.
11. Since the point on the basilar membrane at which the maximum displacement occurs varies with frequency, the basilar membrane effectively separates out the sinusoidal components in the stimulus. In other words, it performs a crude form of Fourier analysis.
12. When the stimulus is a steady sinusoidal simple tone, every point on the basilar membrane responds by vibrating up and down in an approximately sinusoidal manner at the same frequency as the stimulus.
13. However, points on the basilar membrane further away from the oval window will show a phase lag behind those points nearer the oval window.
14. Also, because the width and flexibility of the basilar membrane increase the nearer you get to the apex, each point on the membrane will have its own unique resonant frequency. The closer this resonant frequency is to that of the stimulus, the greater the amplitude with which that point will vibrate.

18. Frequency resolution of the basilar membrane





- *Relative bandwidth* of a bandpass filter is the ratio of the bandwidth to the centre frequency.
- Q is a measure of the sharpness of the tuning of a bandpass filter. It is the reciprocal of the relative bandwidth (i.e., ratio of centre frequency to bandwidth).

18. Frequency resolution of the basilar membrane

1. We've seen that the basilar membrane performs a sort of Fourier analysis on the stimulus. That is, it separates out the sinusoidal components in the stimulus. But what is the *frequency resolution* of the basilar membrane? That is, how close must two simple tones be in frequency before the basilar membrane is unable to distinguish between them?

2. We measure this by assuming that each point on the basilar membrane behaves a bit like a bandpass filter, with a particular centre frequency, a bandwidth and a sloping transition band at the upper and lower cutoff frequencies.

3. It is often hard to measure the -3 dB bandwidth accurately for a point on the basilar membrane, so the -10 dB bandwidth is usually used instead in this case. The -10 dB bandwidth is the difference between the two frequencies at which the power of the output of a filter is 10 dB less than the power of the input.

4. The -10 dB bandwidth is not the same for all points on the basilar membrane. However, the ratio of the bandwidth to the centre frequency *is* roughly the same for most points on the basilar membrane.

5. The ratio of the bandwidth of a bandpass filter to its centre frequency is called its *relative bandwidth* and the reciprocal of the relative bandwidth—that is, the ratio of the centre frequency to the bandwidth—gives a measure of how 'sharply' tuned the filter is to its centre frequency. This measure of sharpness of tuning is called Q when the bandwidth is the -3 dB bandwidth. However, in the case of the basilar membrance, the bandwidth measured is the -10 dB bandwidth and, in this case, the measure of sharpness is denoted by Q_{10dB}.

6. Most of the early work on the response of the basilar membrane was done by von Békésy (1928, 1942, 1960). He measured the response of the basilar membrane to very loud sinusoids (about 140 dB SPL) at fairly low frequencies in recently deceased humans, using a microscope with stroboscopic illumination to measure the vibration amplitude.

7. For the range of frequencies that von Békésy measured, the relative bandwidth was about 0.6. That is, the bandwidth at each point was about 60% of the centre frequency. This relative bandwidth is far too wide to explain our ability to 'hear out' the partials in a complex tone. It is also too wide to explain the fact that individual neurons in the auditory nerve only respond to a very narrow range of frequencies—that is, they are very sharply tuned.

8. Moore (1989, p. 21) suggests that this discrepancy is due to two factors. First, the basilar membrane is now believed to be non-linear. This means that one cannot necessarily predict how it will respond to quiet sounds by examining how it responds to very loud ones like those that von Békésy used in his experiments. Second, in more recent experiments on animals, it has been shown that the response of the basilar membrane is *physiologically vulnerable*—that is, it changes depending on how healthy the subject is. So the response of the basilar membrane in human cadavers is going to be significantly different from its response in healthy living subjects.

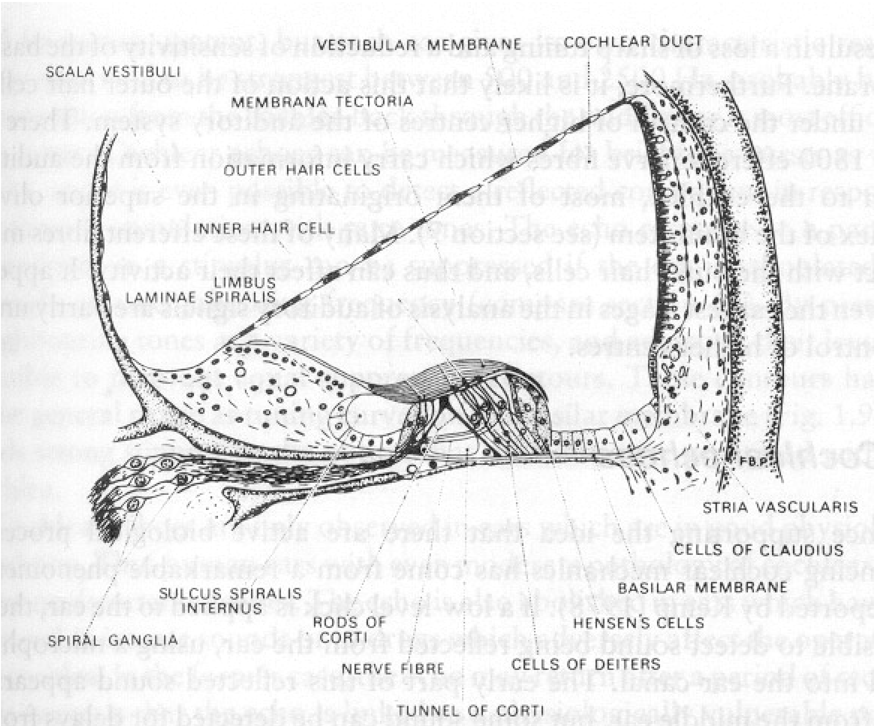
9. More recent experiments carried out on living animals have shown that the living basilar membrane is tuned much more sharply than suggested by von Békésy's experiments.

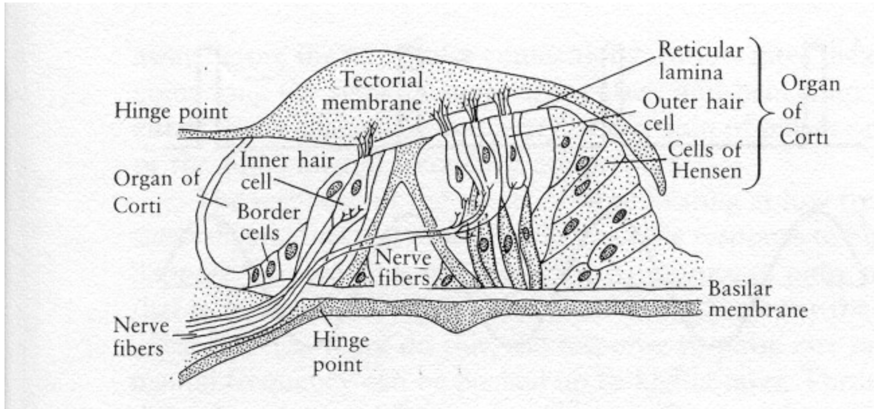
10. For example, this graph here shows the least sound level required to cause a constant velocity of motion at a particular point on the basilar membrane as a function of frequency. As you can see, at the start of the experiment when the animal was still healthy, only a very low sound level was required to cause a response at the best frequency. However, as the condition of the animal deteriorated, the tuning becomes less and less sharp.

11. So recent experiments seem to show that in normal healthy ears, each point on the basilar membrane is sharply tuned and behaves like a narrow bandpass filter with a value of Q_{10dB} in the range 3–10 (i.e., with a bandwidth between 1/10th and 1/3 of the centre frequency).

12. It also seems that this sharpness of tuning is the result of *active* processes—that is, the cochlea does not just send signals *to* the brain, it also receives signals *from* higher brain centres that affect the way that it responds to sounds.

19. The transduction process and the hair cells





19. The transduction process and the hair cells

1. We've seen that the basilar membrane acts as a sort of Fourier analyser with a limited resolving power.
2. In the last few minutes I'm just going to talk briefly about how the spectral information obtained by the basilar membrane is conveyed from the cochlea into the auditory nerve and then to the brain.
3. This diagram here is a more detailed cross section of the cochlea.
4. As you can see, just above the basilar membrane is a gelatinous structure called the *tectorial membrane*. And between the tectorial membrane and the basilar membrane there are some special cells called *hair cells*. The hair cells and tectorial membrane form part of a structure called the *organ of Corti*.
5. This diagram shows the organ of Corti in more detail.
6. The hair cells are divided into two groups by an arch called the *tunnel of Corti*. The group of hair cells nearer the outside of the cochlea are called the *outer hair cells* and those on the inside of the tunnel of Corti are called the *inner hair cells*.
7. In humans, the outer hair cells are organized into five rows, running along the basilar membrane and the inner hair cells are arranged as a single row. In total there are about 25000 outer hair cells, each with about 140 hairs protruding from it and about 3500 inner hair cells, each with about 40 hairs.
8. The hairs on the outer hair cells actually make contact with the tectorial membrane but the inner hair cells probably do not.
9. The tectorial membrane is effectively fixed or 'hinged' at its inner edge so that when the basilar membrane moves up and down, the tectorial membrane slides over it with a shearing motion, causing the hairs on the hair cells to be displaced.
10. This causes the inner hair cells to fire and send signals up the auditory nerve to the brain.

11. It seems that most of the afferent neurons that connect to the cochlea (that is, the ones that carry signals to the brain) are connected to the *inner* hair cells, each hair cell being contacted by about 20 neurons. So it seems to be the *inner* hair cells that are concerned with conveying information about the incoming sound to the brain.

12. Most of the 1800 or so efferent neurons that connect to the cochlea (that is, the ones that carry information from the brain to the cochlea) connect to the outer hair cells and it seems that signals carried in these neurons can cause the outer hair cells to change their length and shape, consequently affecting the way that the basilar membrane responds to sounds (see Pickles, 1988).

13. In experiments where subjects have been dosed with drugs that only affect the outer hair cells, it has been shown that this leads to a reduction of sensitivity in the basilar membrane—that is, each point on the basilar membrane becomes less sharply tuned and responds to a wider bandwidth of frequencies.

14. This shows that active processes involving signals being sent from the brain down to the outer hair cells contribute to the sharpness of the response of the basilar membrane.

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