

## Why Are Tuning Curves Wider At The Top? Why Aren't The Edges Straight Vertical Lines?

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Tuning curves reflect movement on the basilar membrane. Essentially, each tuning curve shows how a particular neuron responds to a range of frequencies. A neuron will respond to a frequency if that frequency moves the basilar membrane enough in the place where its inner hair cell lives. So, the wider-at-the-top shape of tuning curves has to do with the shape of the traveling wave. To understand the shape of the traveling wave, we need to talk about the impedance gradient of the membrane (i.e., the decrease in stiffness and increase in mass as we go from base to apex).

Any stimulation of the cochlea (e.g., through pressure at the oval window from the stapes or pressure from bone conduction transmitted through the petrous bone) hits the entire cochlea at the same time (the speed of sound in fluid is ~1400 m/s and the basilar membrane is ~35 mm), but we get a traveling pressure wave because the round window is more compliant than the oval window, and because of the impedance gradient along the membrane. The energy moves through the basilar membrane at an optimal place where the impedance is lowest for that frequency. Near the base, the membrane may be too stiff to move much for that frequency (high stiffness reactance), but as we all know, the stiffness reactance decreases, and the mass reactance increases from base to apex. It changes gradually. Movement builds up slowly for any frequency as the total reactance decreases, reaching a peak at zero reactance (resonance) where the impedance is purely resistive. This is the point where the stiffness and mass are optimal for that frequency. As we move farther along the membrane, the system will be mass dominated (which involves the membrane and surrounding fluids), and the wave will die very quickly. So the gradual change in stiffness and mass creates the gentle slope of the traveling wave, which is reflected in the slopes of the tuning curves.

The impedance gradient also explains why the wave seems to 'travel' from the base to the apex. This is due to phase angle shifts with impedance change and increasing delays towards the apex. Said most simply, stiff systems move faster, and massive systems move slower (i.e., increased mass involves inertia that resists acceleration).

But this is only part of the answer. The impedance gradient only explains the shape of the traveling wave for higher-level sounds, because the active system mechanically sharpens and amplifies the movement pattern for softer sounds. The reason that tuning curves have sharp tips at the base and increasing width for higher levels is mostly due to the decreased contribution from the active system for higher-level inputs. The active system significantly sharpens the displacement pattern (and thus the tuning curve) from what we would get if this was simply an impedance gradient issue. Tuning curves are just measures of neural threshold for a range of frequencies, so the wideness of the curves at higher levels just reflects broader displacement patterns, i.e., less sharpening. Impedance plays an important role, but without the active system, the stiffness/mass

gradient would give us much shallower (roughly bowl-shaped) tuning curves rather than the nice pointy (roughly V-shaped) tuning curves we get.

To get a tuning curve that was very narrow across a wide range range of levels (i.e., one with straight vertical lines), you would need to have a basilar membrane displacement pattern that was almost a spike, which is probably not an easy or possible thing to accomplish with a membrane, even with a strong active system.