COCHLEAR COILING AND LOW-FREQUENCY HEARING

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Surface gravity waves in a spiral channel can be used as an analogue for cochlear macromechanics (Manoussaki et al. [1]). We found that in a vertical-walled channel with uniform cross section, as a low-frequency wave propagates inward from larger to smaller spiral radii, the wave amplitude near the outside wall grows while the amplitude near the inside wall decreases. This relative amplitude change induces a radial tilt of the free surface, the magnitude of which increases in inverse proportion to the spiral radius. The tilt, which can be interpreted in terms of energy redistribution, can be explained by a "whispering gallery effect," can develop dynamically on the cochlear partition and, by contributing to the bending of apical stereocilia (Cai et al. [2]), can augment low-frequency hearing by as much as 20 dB. We therefore hypothesized that cochlear spiral radii ratios (largest/smallest) could account for interspecies differences in low-frequency hearing. Preliminary analyses of spiral parameters obtained from published data on mammalian species, as well as from histological sections and 3D CT scans of the cochleae of low-frequency baleen whales and high-frequency dolphins and porpoises, tend to support our hypothesis: species with good low-frequency hearing have larger spiral ratios than do those with poor low-frequency hearing.

1   Introduction

The search for the functional significance of cochlear coiling has attracted researchers in fields ranging from evolutionary biology and comparative physiology to auditory mechanics. Lieberstein [3] argued that coiling was an evolutionary adaptation required by small mammals to hear low-frequency sounds. This idea has been given some credence by West [4], who correlated features of cochlear coiling with behavioral audiograms in small ground-dwelling mammals. However, in studies of coiling by cochlear mechanicists, coiling effects have generally been found to be negligible. Huxley [5] provides a notable exception by suggesting that coiling can mechanically isolate adjacent sections along the cochlear partition and provide a sharper resonance effect.

2   Methods

2.1 Cochlear macromechanics

In Manoussaki et al. [1] we used the WKB method to study the propagation of surface gravity waves in a spiral vertical-walled channel of uniform cross section, so as to isolate the effect of curvature. We show that there is an analogy between surface gravity waves and the classical impedance formulation of cochlear mechanics when we neglect damping of both the surface gravity waves and the cochlear partition, since they have different dependencies on frequency. We restrict the frequency to be below the lowest characteristic frequency in the cochlear impedance model to enable the modeled cochlear wave to reach the apex. In the channel all waves will reach the apex; however, we must restrict input frequencies to values sufficiently low to suppress higher-order modes across the width of the channel. Under these conditions ρg (fluid density times gravity) plays the role of spring K and mass M on the cochlear partition, such that $\rho g = (K - M\omega^2)/2$. In this context the factor of 1/2 arises because of the reduction of two fluid layers in the cochlear model to one in the channel.

2.2 Ray Tracing

We simulated a spiral channel in which the paths of surface waves are represented by rays. The vertical sidewalls are modeled as ideal mirrors; that is, impinging rays undergo specular reflection at an angle equal to the angle of incidence relative to the normal to the sidewall. We calculated the paths of 100 equally spaced rays entering the outer turn of the channel, tangent to the walls. The rays are traced as they propagate toward the innermost point of the spiral, where the deviation from a uniform distribution gives a measure of energy-density redistribution across the channel.

2.3 Histology

Ears were fixed in 10% neutral buffered formalin and decalcified in 0.27 M ethylene-diamine-tetra-acetate (EDTA) containing 1% formalin. After decalcification, specimens were dehydrated in a graded series of ethanols from 50% through 100%, embedded in celloidin, and hardened. The celloidin-embedded tissue blocks were sectioned at 20 microns, and every tenth section was stained with hematoxylin and eosin and mounted on sealed glass slides for examination by light microscopy.

2.4 CT scans

Fresh, frozen, or formalin-fixed ears were examined using a Siemens Volume Zoom Helical CT scanner. Scan data were obtained at 0.5- to 1-mm increments with an ultra-high bone protocol and imaged at 0.1-mm slice thicknesses in coronal and transaxial planes. Three-dimensional views of the inner ear membranous labyrinth and associated neural canals were obtained by segmenting related X-ray attenuations.

2.5 Spiral parameters

The calculation of the ratio of maximum to minimum radii of a cochlea is very sensitive to the location of its center. To facilitate comparisons across species, it is necessary to establish an objective, repeatable method for determining the mathematical center of the cochlear spiral. Using mid-modiolar CT sections to estimate the basilar membrane (BM) position relative to the scalae media-vestibuli margins, we first traced and extracted the *x-y-* coordinates of the border of the BM on a top orthogonal image of the 3D CT scan. We made an initial guess of the center by fitting a circle to a small number of points at the spiral apex, and used this guess as the center of a grid of coordinates generated to represent possible best-fit centers. For each point in this grid, we computed R and θ along the length of the traced curve, and we fit the data to a nonlinear spiral model of the form

$$R(\theta) = R_0 \left(\exp(-\beta\theta) - a\theta - b\theta^\lambda \right).$$

The mean squared error was determined for each fit, and the grid point that minimized the error was selected as the computational center. The estimated BM location curve and the computed center were then overlaid on the image of the cochlea, from which we determined the ratio of the maximum and minimum distances to the best-fit center.

Results

3.1 Cochlear macromechanics: surface gravity-wave analogue

In a straight channel, or in one of constant curvature, we expect waves to propagate uniformly without change. However, Manoussaki et al. [1] found a surprising result when the channel has non-uniform curvature: for waves propagating in a direction of increasing curvature (decreasing radius of curvature), the amplitude on the outside wall amplifies, while the amplitude on the inside wall decreases. This results in an increasing radial tilt of the free surface (Fig.1). Thus the increase in curvature seems to induce a passive mechanical amplification of tilt while preserving the constancy of energy flow along the cross section of the channel or cochlear duct. Manoussaki et al. [1] found a simple relation that quantifies the radial tilt: $\Delta\eta \propto 1/R_m$, where the difference in wave amplitude on the outside and inside walls is $\Delta\eta$, and R_m is the distance from the center of the spiral to the midline of the channel or cochlear partition. Thus if R_m decreases by a factor of 10 from base to apex, as it does in some species (Table 1), the tilt increases by a factor of ten. If this tilt is a signal that can be sensed by the neurosensory cells in the cochlear partition, curvature in this species could account for a passive amplification of 20 dB. In a separate study of the effect of curvature on cochlear micromechanics, Cai et al. [2] showed that the tilt effect persists in a model with structural elements in the organ

of Corti and a circular cross section: curvature significantly improves the shearing efficiency of apical outer hair cell stereocilia bundles. These results lead us to the hypothesis that cochlear curvature improves low-frequency hearing sensitivity, and that mammalian species with good low-frequency hearing should have higher maximum/minimum spiral radii ratios than those with poor low-frequency hearing sensitivity.
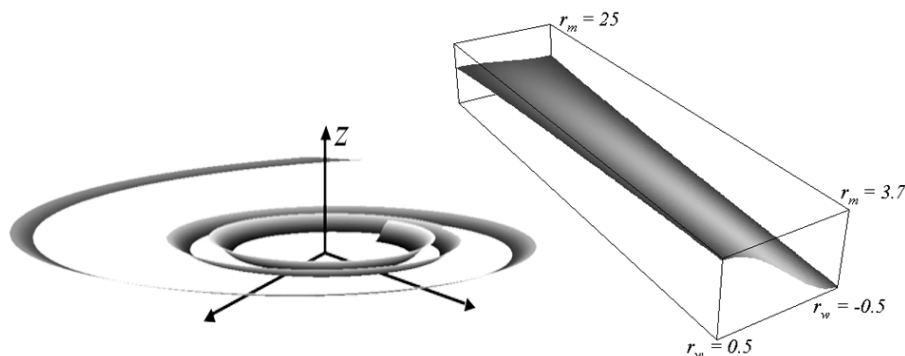

Figure 1. Radial tilt of the wave amplitude. On the left, the the wave amplitude is shown for the spiral channel. On the right the same is shown graphically in a straight box to illustrate the amplification of tilt more clearly. The outside wall is denoted by $r_w = 0.5$, and the inside wall is at $r_w = -0.5$. The wave enters the channel at $r_m = 25$, and travels inward to $r_m = 3.7$.

3.2   Mechanism of radial tilt: the whispering gallery effect

What then is a simple, intuitive explanation of both the free surface tilt and its amplification as the wave propagates towards the spiral center? Concerning first the tilt itself, we can adopt the geometric optics argument that Rayleigh [6] used to explain the phenomenon of the Whispering Gallery in London's St. Paul's Cathedral, where whispers travel large distances along a curved wall. Rayleigh showed that a pencil of rays emanating from a source toward a nearby concave boundary, would, after any number of reflections, be confined near the boundary. In other words, disturbances tend to cling to a concave boundary. The same line of reasoning can be used to demonstrate that disturbances are dispersed by a convex boundary. In the present problem of surface gravity waves propagating in a curved, vertical-walled channel, the concave boundary is the outer wall, the convex boundary is the inner wall, and the source of disturbances is the walls themselves. Any redistribution of rays shows the redistribution of energy density across the channel. Wave energy density is related to wave amplitude, so that wave energy redistribution results in a radial tilt of the free surface, increasing from inside to the outside (Manoussaki et al. [1]). This is illustrated in the geometric ray tracing of Fig. 2, in which rays entering the channel at the outer opening (arrows) cling to the outer wall as they propagate to the center.
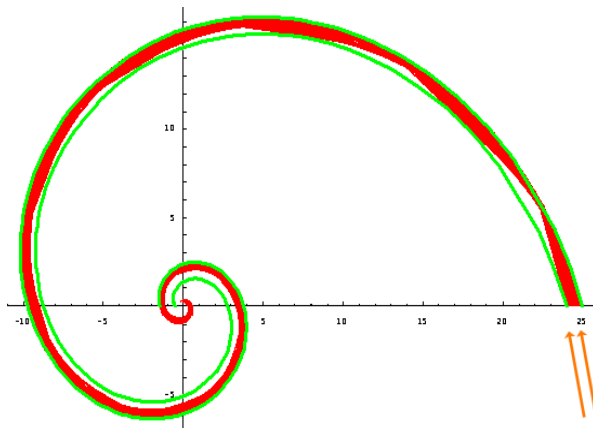
Figure 2. Ray tracing analysis shows that spiral walls redistribute rays toward the outer wall at the center of the spiral. This illustrates the whispering gallery effect.

3.3 Analyses of cochlear spirals for different species

Table 1. Radii ratios and low-frequency thresholds. Spiral center estimated from inner turn of von Békésy's cochlear partition spiral diagrams [7]. Low-frequency hearing thresholds are from West [4].

species	man	cow	elephant	guinea pig	rat	mouse
Rmax/Rmin	10	10	7.5	7.4	4.3	4.0
Hz	30	20	15	40	400	800

Table 2. Radii ratios and low-frequency thresholds for some marine mammals. Spiral centers were estimated from complete spiral fits to Ketten's basilar membrane spiral diagrams that were reconstructed from histological sections [8]. Low-frequency hearing thresholds are from Ketten [8].

species	humpback whale	bottlenose dolphin	harbor porpoise
Rmax/Rmin	8.3	5.5	2.6
Hz	20	200	500

Table 3. Radii ratios and low-frequency thresholds for some marine mammals. Spiral centers were estimated from spiral fits to curves estimating the location of the basilar membrane on the orthogonal projections of the CT scans based on mid-modiolar CT sections. Low-frequency hearing thresholds are from Ketten [8].

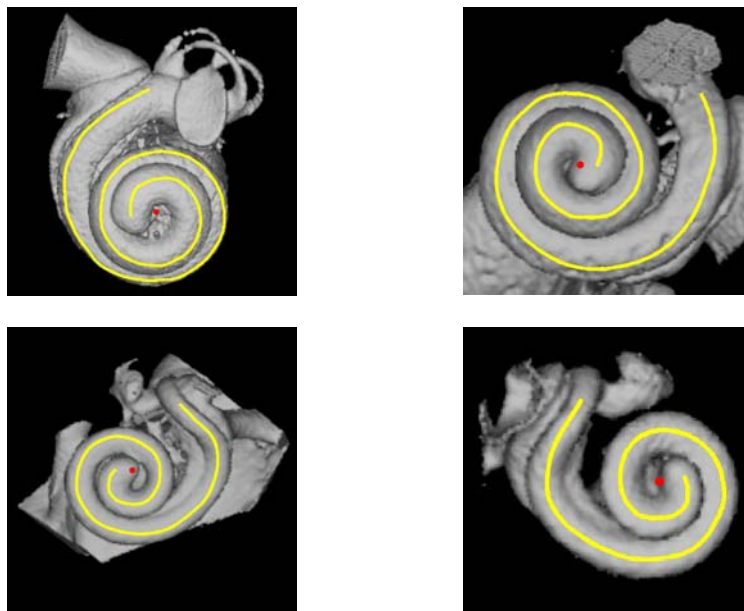| species	blue whale	Northern right	bottlenose dolphin	harbor porpoise
Rmax/Rmin	4.8	8.1	5.0	4.5
Hz	12	15	200	500

Figure 3. Top orthogonal projections of CT scans. Upper left, blue whale; upper right, Northern right whale; lower left, bottlenose dolphin; lower right, harbor porpoise. Estimated BM location from mid-modiolar sections (yellow curve); best-fit spiral center (red dot). Radii ratios are given in Table 3.
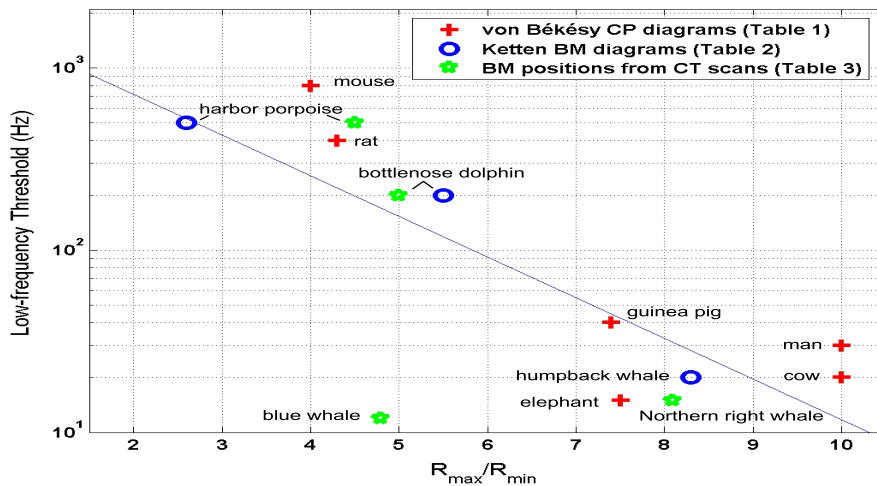

Figure 4. Semi-log plot of Rmax/Rmin vs low–frequency hearing threshold.

3 Discussion

The idea that cochlear curvature was an adaptation by mammals to improve low-frequency hearing sensitivity is given more credence in this present work. We have elucidated a physical principle of radial redistribution of wave-energy density by the spiral geometry, which can be interpreted as a whispering gallery effect. The principle is demonstrated three ways: a) radial tilt of a surface gravity wave analogue of cochlear macromechanics; b) improved apical outer hair cell bundle bending efficiency due to curvature in a complex wave propagation model that includes the organ of Corti and tectorial membrane; and c) an elementary ray tracing analysis in a spiral channel. The effect grows in proportion to the ratio of maximum to minimum spiral radii. This leads to the hypothesis that the larger this ratio, the lower the low-frequency threshold of a particular species. Tables 1-3 and Fig. 4 demonstrate the trends, which generally support the hypothesis, using three different methods of data analysis. Further work is required to understand differences in estimated radii ratios of the same species using different methods. The obvious deviation of the blue whale seen in Fig. 4 begs further investigation. Also, the spiral radius ratio is not the sole determinant of the frequency hearing sensitivity, and clearly more work is required to establish the roles of different factors.

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