Illustrations of Lighthill's 1992 Equations for the Two-Dimensional Fluid Motion and Associated Viscous Dissipation within the Cochlea

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Abstract. Given the negligible longitudinal stiffness coupling within the cochlear partition, it is generally accepted that the cochlear fluid is the dominant medium of energy transport within the cochlear travelling wave. It is therefore important to be aware of its motion and viscous dissipation when considering the energy flux within it. In 1992, James Lighthill published analytically derived equations for the two-dimensional fluid motion and energy dissipation associated with the cochlear travelling wave (J. Lighthill, J. Fluid Mech. **239**, 551–606, Appendix A). This paper attempts to graphically illustrate their meaning.

INTRODUCTION

While Lighthill's 1981 publication on the energy flux in the cochlea[1] is probably his best known paper in our field, his paper about acoustic streaming in the cochlea[2] remained largely ignored, although its A*ppendix A* contains a most detailed analytical descriptions of the two-dimensional particle trajectories and viscous energy dissipation in the cochlear fluid, which have been recently confirmed numerically by finite element simulation[3]. Although Lighthill asserts that his descriptions are even accurate enough to quantify the cochlear fluid motion at short wavelengths, with fluid motion supposedly being locally two-dimensional, his equations for the two-dimensional case do certainly describe qualitative phenomena, which apply also to the real three-dimensional cochlea. This paper attempts to illustrate and describe these phenomena and to highlight some fluid dynamic principles within the cochlea. While many of these descriptions may be obvious to the expert, they might be less so to researchers who focus on analyzing the motion of the solid basilar membrane (BM) only.

FLUID PARTICLE TRAJECTORIES AND PRESSURE FIELD

Figure 1 illustrates the fluid particle trajectories and the pressure filed adjacent to a travelling wave (TW) along the BM up to a fluid depth of +/- 155 μm. Note however that all of Lighthill's analytical equations assume an indefinite fluid depth (i.e. no cochlear wall). Given the wavenumber k and BM velocity amplitude V at longitudinal position x, the velocity components of the fluid particles in longitudinal (u) and transversal (v) direction at the distance y from the BM were derived by Lighthill as:

$$u = iAe^{i(\omega t-kx)}(e^{-ky} - e^{-Ky}), \qquad v = Ae^{i(\omega t-kx)}(e^{-ky} - kK^{-1}e^{-Ky}), \tag{1}$$

where A and K satisfy the equations

$$A(1 - kK^{-1}) = V, \qquad K^2 = k^2 + i\omega\upsilon^{-1}. \tag{2}$$

The parameter $\upsilon=\mu/\rho$ is the kinematic viscosity, with μ being the dynamic viscosity and ρ the density of the fluid (of water in the present figures).

In order to illustrate the principle meaning of these equations, BM amplitude in all figures is kept constant (4 μm) along the TW and the abscissa is labeled with wavelength rather than distance along the BM. The wavelength ranges logarithmically from 1000 μm to 100 μm. Figure 2 shows the corresponding progressive phase accumulation to slightly more than 2 cycles, which corresponds roughly to the measurements made by Ren et al.[4] in the gerbil cochlea, obtained within a 600-μm long region along the BM with a 16 kHz stimulation at 10 dB SPL. The wavelength at the

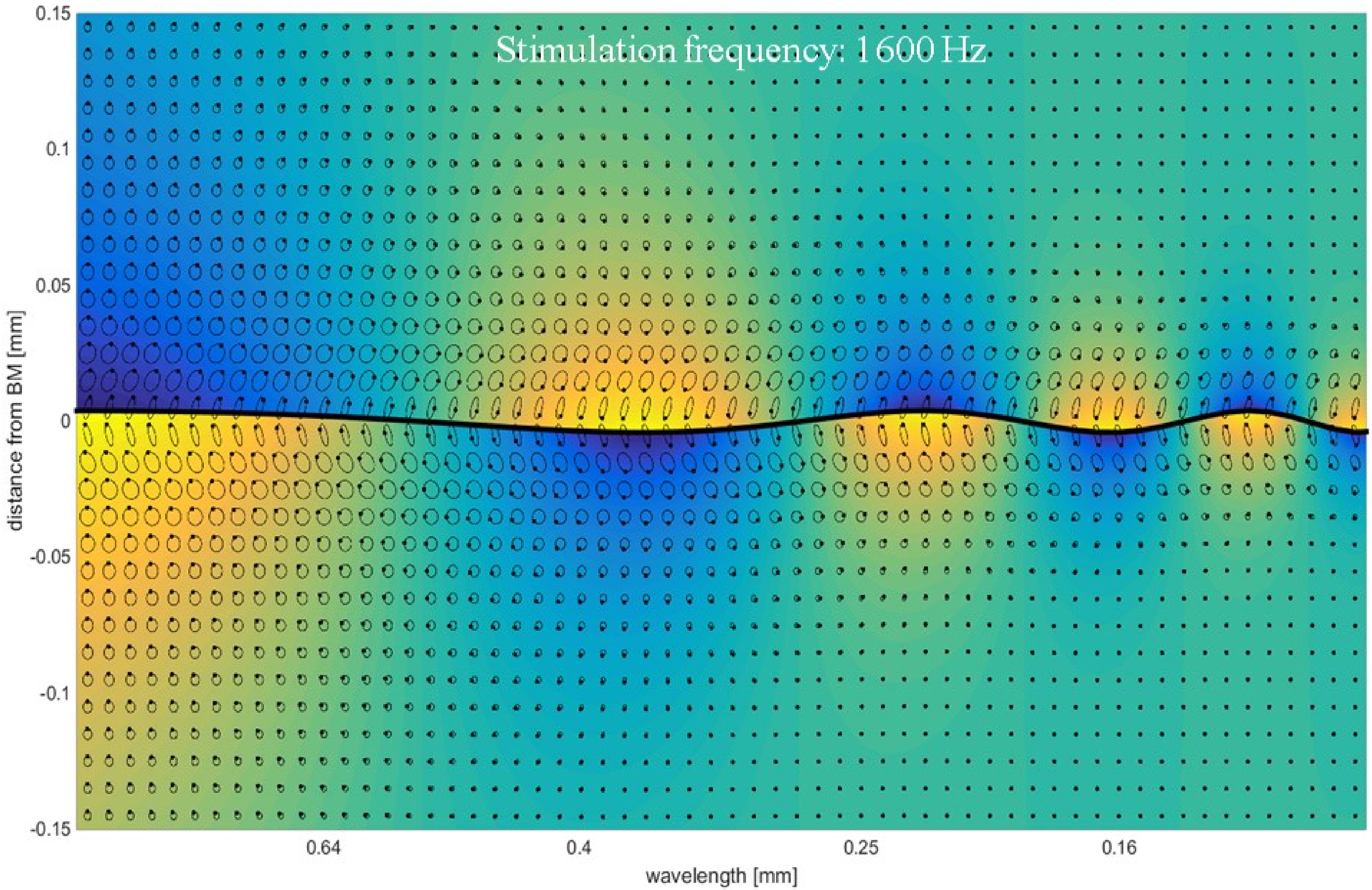

FIGURE 1. Particle trajectories within the fluid adjacent to a traveling wave along the basilar membrane. Dots on the trajectories show the particle positions of at the instant of the shown pressure field (positive pressure is yellow, negative pressure is blue). Note that the BM displacement amplitude is constant 4 µm along its entire length. The wavelengths given along the abscissa correspond roughly to the 600-µm peak region of a realistic cochlear travelling wave[4].

TW peak was approximately 260 μm in their measurement. Note however, that a stimulation frequency of 1.6 kHz was chosen for Fig. 1 so that the effects of a reasonably thick viscous boundary layer can be visualized. Its thickness decreases with the square root of frequency.

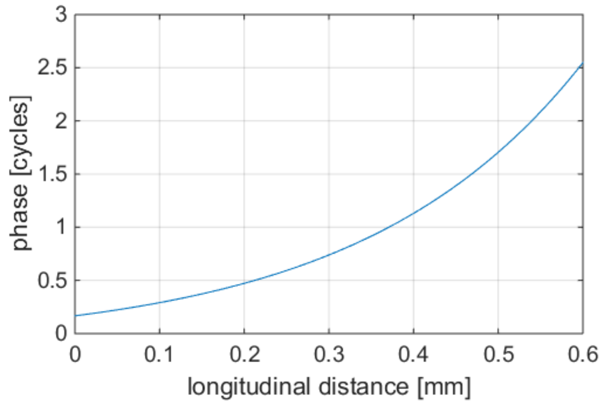

FIGURE 2. Unwrapped phase of the TW corresponding to the wavelength shortening shown in Fig.1.

Best seen at larger wavelength, the fluid particle trajectories are circular outside the viscous boundary layer, like in a fluid surface wave. However, while fluid particle at the surface of a such wave can freely move in wave direction, the fluid particles at the boundary to the solid BM comply with the "non-slip condition" and move only transversally with the BM (given the BM itself has no longitudinal deformation). This would be equivalent to putting a thin solid, but compliant sheet on the fluid surface. The viscosity of the fluid hinders longitudinal flow also in the layers adjacent to the BM, the so-called Stokes boundary layers, resulting in rather elliptic than perfectly circular trajectories. It is clear that the transversal component of these trajectories are reflecting the displacement of the BM, i.e., the fluid motion adjacent to the BM is dominantly longitudinal when this motion considered relative to the BM. Consequently, the radius of the trajectories starts at the BM with the amplitude of the BM displacement and decreases exponentially with distance to it (except within the boundary layer, where the decrease in transversal fluid motion is shallower and the longitudinal component is even increasing at first due to the non-slip condition). This decay in fluid motion with distance from the BM becomes visibly steeper as the wavelength shortens and so does the pressure field which drives the motion. It must therefore likewise decay exponentially with distance from the BM (see experimental data by Olsen[5]). The dot on each trajectory in Fig. 1 indicates the particle position at the instant of the shown pressure field. The impedance of the BM is dominated by its stiffness and the BM is therefore proportionally displaced to the pressure difference either side of it. Just outside the boundary layer, where the particle trajectories become circular, it is best to observe that the fluid particles have their largest longitudinal displacement at the location of the largest pressure gradient (green areas between pressure maxima and minima), where they experiences their maximum longitudinal acceleration. The fluid reaches its maximum velocity in wave direction while in a pressure maximum. (Note that fluid particle trajectories are anticlockwise above and clockwise below the BM.) The observation that pressure and velocity component in the wave direction are in phase are evidence for energy transport within the cochlear fluids. Given the negligible longitudinal stiffness coupling within the BM, it is generally accepted that the fluid is the dominant medium of energy transport within the cochlea, and it is therefore incorrect to describe the cochlear TW as a purely transversal wave.

VISCOUS DISSIPATION

The main point made by Lighthill in his appendix is that the overall dissipation along the TW is greater than just the dissipation in a Stokes boundary layer, especially if its wavelength shortens and becomes comparable to the boundary layer thickness. Under such conditions, the viscous dissipation due to the deformation of the fluid elements in the irrotational motion field becomes substantial. This deformation is illustrated by the grid in Fig. 3, and best

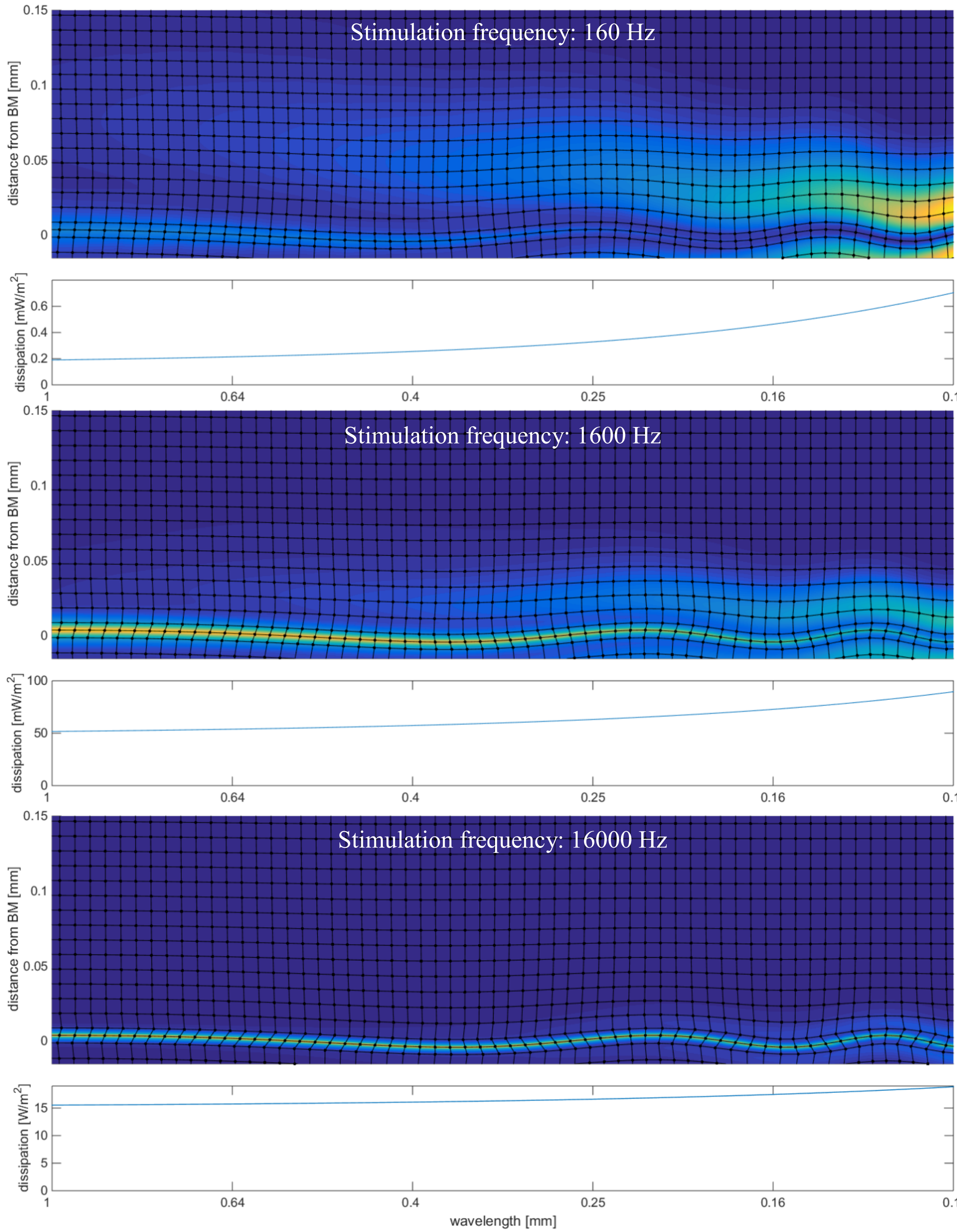

FIGURE 3. Illustration of energy dissipation within the fluid motion field for 3 stimulation frequencies. The grid illustrates the deformation of the fluid elements causing the energy dissipation. The panels below show the integral of dissipation rate along the entire fluid columns (infinitively long) as a function of wavelength. Note the constant BM displacement of 4 μm.

visible in the panel with 160 Hz stimulation frequency. Because the velocity field decays rather rapidly at short wavelength the velocity gradient in y-direction creates considerable shear in the irrotational motion field, whichbecomes comparable and can even exceed that within the boundary layer. The decrease in wavelength is also causing an increase in transversal shear motion. This leads to an increase in overall dissipation rate as the wavelength shortens (Fig. 3, lower panels). (Keep in mind that the BM amplitude is kept here constant along the TW.) Nevertheless, Lighthill pointed out that the overall loss is considerably smaller than the simple sum of the viscous dissipation in the irrotational flow and in the boundary layer. His analytic derivation shows negative cross terms in the quadratic equations (appearing in the middle), which offset the irrotational field losses (first term) and boundary layer losses (last term):

$$2\mu|A|^2k^2\left\{2e^{-2ky} - Re\left[(2 + k^{-1}K + kK^{-1})e^{-(k+K)y}\right] + \left(1 + \frac{1}{4}|k^{-1}K + kK^{-1}|^2\right)|e^{-2Ky}|\right\} \tag{3}$$

The effect of the cross terms can be easiest seen in Fig. 3 at stimulation frequency 160 Hz: The fluid elements just above and below the BM are tilted according to the slope of the BM displacement pattern, so that at wavelengths shorter than 250 μm the dissipation-causing shear movement in the boundary layer is almost completely absent. At longer wavelengths (250 μm to 400 μm), or at higher stimulation frequencies (see panel with 1600 Hz stimulation frequency), the maximum offsetting effect of the tilt occurs further away from the BM, causing an area of lower dissipation between the distinct dissipation areas in the boundary layer and the external irrotational field.

When comparing the areas of dissipation across the three stimulation frequencies, it becomes clear that the impact of the irroational flow is larger at low frequencies when the boundary layer is thicker. Accordingly, also the increase in overall dissipation rate with shortening wavelength, shown in the panels below the dissipation areas, is most dramatic at the lowest stimulation frequency. (Note that the dramatic increase in the scale of dissipation rate with frequency increase is here due to the fact that the BM displacement amplitude is kept constant across all three frequencies, which means that the BM velocity increases also in ten-fold steps. Because viscous dissipation growth with velocity squared, this alone leads to a hundred-fold increase in dissipation rate with each frequency step.)

DISCUSSION

The reduction in depth of the fluid velocity field, illustrated in Figs. 1, is evidence that the TW carries less and less energy relative to the BM amplitude (here kept constant) as it travels and its wavelength shortens[6,7]. Lighthill argues that the increasing dissipation relative to this already decreasing energy with the shortening of the cochlear TW is the reason for the dramatic decrease in its amplitude past its peak[1,2]. This amplitude decrease is evident in the astonishingly steep slope of the BM tuning curve above the characteristic frequency, which can exceed 100 dB/octave[4,7], and is almost as steep even in passive cochleae[8,9]. It is however puzzling that this dissipation increase is more pronounced at low-frequencies, whereas cochlear tuning has been universally shown to be sharper at high- frequency stimulation. Still, future numerical simulations with various stimulation frequencies might reveal that the frequency-dependency of the viscous dissipation described by Lighthill might be compensated by other effects as the TW travels within a realistic three-dimensional finite-element model.

ACKNOWLEDGMENTS

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COMMENTS AND DISCUSSION

Julien Meaud: This is a nice manuscript – illustrating the theoretical equations from Lighthill. I do agree that looking at the fluid mechanics, rather than just the basilar membrane, is useful.

1) I am wondering about what part of the motion trajectory is due to fluid viscosity. It would be interesting to analyze what happens when the viscosity goes to zero.
2) The fluid pressure looks very similar to what is observed with an inviscid model – in a 2D model the pressure decays exponentially away from the basilar membrane, at a rate related to the wavelength of the traveling wave. It would be interesting to relate these theoretical results to experimental findings – Lisa Olson has measured the fluid pressure in a series of paper and has observed that the pressure decays exponentially from the BM (see for example Olson, 1999, Nature 402).
3) While I agree that fluid coupling is the main source of longitudinal coupling, there are other sources of coupling that are non-negligible (including the basilar membrane, but also the phalangeal process, the tectorial membrane…)

Reply:

1) Without viscosity, the fluid trajectories would be circular in this "deep channel" analysis (i.e. no cochlear walls). The non-slip condition of the fluid particles at the cochlear partition causes in combination with the viscosity the elliptic trajectories near the partition, indicating a "shear-resistance" within the fluid that inhibits fluid oscillations in longitudinal direction. (Note that the vertical component of the trajectory reflects just the up-and-down movement of the partition.). This resistive impedance, in addition to the mass reactance, causes also a slight phase lag, with the result that the elliptic trajectories are slightly tilted.
   Reduction of viscosity causes this "boundary layer" of elliptic trajectories to become thinner (similar to the effect of increasing the stimulation frequency). With zero viscosity, this layer would be infinitesimal thin.
2) The pressure was not mathematically analyzed by Lighthill, and was here just approximated for illustrative purposes as exponentially decaying in accordance with the exponentially decaying velocity field. It should therefore not be compared quantitatively with the details of experimental data.
3) I agree with you that longitudinal coupling within the cochlear partition is not negligible. It might even be level dependent and underlie cochlear nonlinearities.

Questions and Answers after the Podium Presentation

Q1: If you move away from the basilar membrane, one would expect a variation in the longitudinal component of the fluid velocity due to the non-slip condition at the basilar membrane. Why is there also a variation in the transverse component?

A1: The vertical component of the trajectory just reflects the up-and-down movement of the basilar membrane. Relative to the basilar membrane, the fluid particles simply slides longitudinally along it. The vertical flow component imposed by the basilar membrane movement is diverted in longitudinal flow so that it decays exponentially with distance from the basilar membrane. The fact that the trajectories remain circular shows that both, vertical and longitudinal of the velocity field decay equally with distance from the basilar membrane.

Q2: Just to be clear, the membrane motion is imposed in these simulations and generates the pressure. But the pressure does not react back on the basilar membrane. Is this correct?

A2: The simulations are based only on the velocity equations provided by Lighthill, which do not include pressure as a variable. In other words, Lighthill makes the point that the velocity field is fully defined by wavenumber, frequency, and kinematic viscosity. The pressure is only added in these figures here for illustrative purposes, and is derived from the velocity field based on the assumption that the pressure gradient accelerates the fluid. The viscous impedance of the fluid was thereby ignored.

Q3: One should note that the non-slip condition is not universally happening. You can have a partial slip. You should not think non-slip is a universal law.

A3: Indeed, I did assume that non-slip is the condition applicable at all fluid-solid boundary. I will keep your comment in mind and look into it more carefully. Thanks!