Peter van Hengel, Dick Lyon and other contributors, my apologies for the late response to your contributions to this topic.

However in my opinion this subject is still far away from a satisfactory result. And I prefer to give you a clear and well overthought reaction.

Therefore let me first give you a comment on Peter's following reaction to Matt Flax:

** One small comment to your statement that there are only forward traveling waves. I think much of the confusion stems from the fact that the observed motion of the cochlear partition is often referred to as the traveling wave. In actual fact this is only a 'reflection' of the actual wave which is traveling in the fluid. The fluid supports waves traveling in both directions, but the unique properties of the cochlea cause only the appearance of a forward traveling on the cochlear partition.**

Yes indeed that is the explanation for the 'traveling wave hypothesis' within the common paradigm. And if you want to explain a reported apparently observed 'traveling wave' over the basilar membrane, running from the base – near the round window – to the apex – near the helicotrema, with a mathematical model designed by you, of course it is legitimate to try this.

However in the background of all the exercises there remains to be incorporated a constraint that cannot be ignored or disobeyed: the basics of such mathematical models must be in full agreement with the general rules and laws of physics.

I seriously hope that the AUDITORY List members agree with me that there doesn't exist – beside general physics – a special cochlear physics theory with its own laws and rules, which are different from and occasionally even at variance with the general ones. If not, we can end our discussion right away, because we then can only agree that we fundamentally disagree.

But let me comment on Peter's statement about the observed basilar membrane traveling wave:

In actual fact this is only a 'reflection' of the actual wave which is traveling in the fluid.

I really must remind you to the fact that a mechanical vibration – and the sound stimulus is such a vibration – in a fluid, or in this case water like perilymph, will always propagate with the speed of sound, which has typically here the value of 1500 m/s.
That is just one of those constraints dictated by general physics. And with the equation that counts for the relation between sound velocity, frequency and wavelength we simply can calculate that for a 1000 Hz stimulus the corresponding wavelength in the perilymph is 1.5 meter. So approximately equal to 50 times the length of the active partition of the basilar membrane.
That is the only reason why the round window is moving in opposite direction related to the oval window. A widely reported always observed phenomenon in experiments.

And under the existing conditions in the cochlea there is no physics ground for so-called 'slow waves' with wavelengths even in the order of fractions of a millimeter. With the same equation for the relation between wave propagation velocity, frequency and wavelength as is used for the 'fast' running waves here above.

Just because such a slow wave demands the propagation of a row of successively higher and lower pressure areas with sizes in the order of those wavelengths and even smaller. And that is impossible in general physics. The incompressibility of the perilymph fluid makes this impossible.

It cannot be that a mathematical wish for explaining the existence of a hypothesized traveling wave with a small wavelength prescribes that physics has to offer the possibility for such a slow wave. Just because the general physics rule prescribes that wave propagation velocity equals frequency times wavelength.

And therefore the only possibility that remains is that under the incompressibility constraint the entire perilymph fluid column between oval window – helicotrema – round window is moving as a whole, while it is stimulated by a mechanical vibration of the stirrup.

Peter you further stated:
The fluid supports waves traveling in both directions, but the unique properties of the cochlea cause only the appearance of a forward traveling on the cochlear partition.

If we look closer to the basilar membrane properties, we observe that there exists a frequency-place related distributed resonance capability. With a subdivision that has a logarithmical scale from apex to base. High resonance frequencies near the base and low resonance frequencies near the apex.

Actually this unique property is the cause that a stimulus, that is equally present all over the length of the basilar membrane, evokes phase related movements which appear as a ‘wave’ that is always running from base to apex.
And it is this ‘wave’ phenomenon that is erroneously interpreted as the ‘traveling wave’ that transfers the sound stimulus.

And of course the perilymph fluid can be stimulated from both sides. Wever and Lawrence have reported that already in 1950. They reported that stimulating either the oval window or the round window results in identical cochlear potentials.
But that doesn’t imply that there have to run traveling waves in both directions.
We can only draw the conclusion that a perilymph push-pull caused by a sound stimulus isn’t dependent on the pathway that is chosen.

Peter, you made the remark:
** If one wants to observe the reverse traveling waves in the cochlea it is necessary to measure fluid velocity, which I believe is not yet possible.**

No indeed. A direct measurement of velocity inside the cochlea is known as extremely difficult. So far every attempt fails, mostly because of the intolerable disturbances of the properties in the location that has to be examined. This makes the experimental results unreliable. And non-invasive measurements still show not enough details of fluid movements.

But from what really happens there we nevertheless can still make a reliable imagination, which is simply based on physics and the physiological properties and parameters which exist in the cochlea.

Let us make an inventory of them.

The physiological structure data:

- The walls of the cochlear envelope are extremely rigid. Hardly compliant to not compliant at all. So bone conduction based on deformation of that envelope is not possible.
- The cochlea shaped cavity is subdivided into the perilymph filled duct, which is folded at the apex and which parts are the scala vestibuli between oval window and apex and the scala tympani between apex and round window.
- In between these two scalae the third one – scala media – is located, filled with endolymph.
- The partition between scala vestibuli and scala media is formed by the Reissner membrane. This membrane is extremely thin, but on all available electron microscope pictures it is observed as straight, except for Ménière cochlea, where it is curved into the direction of the scala vestibuli. This membrane has compliance.
- The partition between the scala tympani and the scala media is formed by the basilar membrane. This membrane has substantially more volume, while both the inner and the outer hair cells are embedded in it. This membrane has a place located frequency dependent compliance. It can be observed as a resonance device.
- The hair bundles of the outer hair cells are at their top connected with the tectorial membrane, a rim structure that is completely located in the scala media and connected with the bony envelope of the cochlea.
- At every location along the cochlear partition the cross sections of scala tympani and scala vestibuli are practically equal in size. In average the channel diameter is 0.3 mm.
- There exists a tapered shape in the perilymph duct, larger at the base to smaller at the apex.
- The maximal deflections of the oval window and the round window are estimated to be in the order of a few micrometers.
- Deflections of the basilar membrane also do not exceed a few micrometers. Otherwise the hair bundles of the outer hair cells would be damaged due to overstressing.

The involved material quantities:

- The perilymph fluid in the scala vestibuli and scala tympani as well as the endolymph fluid in the scala media has a density equal to that of water. So 1000 kg/m^3.
- Both fluids are incompressible and have a low viscosity, comparable with water. This can be considered in practice as ‘viscous free’.
- The propagation velocity of acoustic vibrations in the perilymph is 1500 m/s.

Cardinal fluid dynamics numbers:

- The main criterion for non-turbulent fluid flow in the cochlea is the Reynolds number. Calculation in case of the highest hearable frequency stimulus of a 20 kHz vibration with an amplitude of 1 micrometer with a dynamic viscosity coefficient equal to that of water: 0.001 Ns/m^2 gives for this Reynolds number a value of 36. For vibrations with lower frequencies and with similar amplitudes this Reynolds number is proportionally lower.

Hence the Reynolds number is for all situations far below the boundary of 2000, the value that counts for upper boundary of the laminar flow conditions. And therefore the perilymph flow inside the cochlea is definitely non-turbulent.

All these aspects together result in the fact that it is allowed to consider the perilymph movement inside the cochlea as a periodic movement that can be theoretically expressed by the non-stationary Bernoulli equation. Just as I have done in the attached PDF in my message to the AUDITORY List of Saturday, October 1, 2011.

For those of you who think that I misuse the Navier-Stokes theory in the case of the cochlear fluid dynamics I can point to the following elucidating introductory explanation placed on-line on the Internet by the Academic Medical Center of Amsterdam that I cite here:

> -- The Navier-Stokes equations are a set of equations that describe the motion of fluids (liquids and gases, and even solids of geological sizes and time-scales). These equations establish that changes in momentum (acceleration) of the particles of a fluid are simply the product of changes in pressure and dissipative viscous forces (friction) acting inside the fluid. These viscous forces originate in molecular interactions and dictate how sticky (viscous) a fluid is. Thus, the Navier-Stokes equations are a dynamical statement of the balance of forces acting at any given region of the fluid.
>
> They are one of the most useful sets of equations because they describe the physics of a large number of phenomena of academic and economic interest. They are useful to model weather, ocean currents (climate), water flow in a pipe, motion of stars inside a galaxy, flow around a wing of an aircraft. They are also used in the design of aircraft and cars, the study of blood flow, the design of power stations, the analysis of the effects of pollution, etc.
>
> The Navier-Stokes equations are partial differential equations which describe the motion of a fluid, so they focus on the rates of change or fluxes of these quantities. In mathematical terms these rates correspond to their derivatives. Thus, the Navier-Stokes for the simplest case of an ideal fluid (i.e. incompressible) with zero viscosity states that acceleration (the rate of change of velocity) is proportional to the derivative of internal pressure. Poiseuille’s Law and Bernoulli’s equation are special cases of 1D Navier-Stokes.
>
> The fluid motion is described in 3-D space, and densities and viscosities may be different for the 3 dimensions, may vary in space and time. Since the flow can be laminar as well as turbulent, the mathematics to describe the system is highly complex.
>
> In practice only the simplest cases can be solved and their exact solution is known. These cases often involve non turbulent flow in steady state (flow does not change with time) in which the viscosity of the fluid is large or its velocity is small (small Reynolds number).
>
> For more complex situations, solution of the Navier-Stokes equations must be found with the help of numeric computer models, here called computational fluid dynamics. Even though turbulence is an everyday experience it is extremely hard to find solutions for this class of problems. Often analytic solutions cannot be found.

> Reducing the models to 1D, as is often done in fluid dynamics of blood vessels, makes the problem handsome. --

[See also: http://onderwijs1.amc.nl/medfysica/compendiumDT.htm edited by N. A. M. Schellart 2005]

After studying my PDF that I sent to the List on October 1 2011, you can see for yourself that I have derived the analytical solution for the non-stationary non-viscous incompressible time dependent wiggle-waggle movements directed along the core of the perilymph duct. Because in that case the reduction of the complex set of Navier-Stokes equations to the non-stationary Bernoulli equation is fully permitted.

And this finally results in the fact that everywhere inside the perilymph duct the evoked pressure variations are proportional to the sound energy stimulus.

This means that by resonance in the basilar membrane, i.e. the frequency-place related distributed resonance capability, the stimulus can evoke simultaneously all the frequency contributions of the sound energy signal, including the exact phase relation for each contribution, which will be sent to the auditory cortex.
Further details I will give in my answers to the comments of Dick Lyon here below.

Finally Peter you reacted to Matt Flax with:

** Model calculations clearly show the reverse traveling wave and produce results in accordance with data on OAEs (see e.g. the work of Mauermann et al or Epp et al). **

Yes that is based on the ‘transmission line model’. And of course that will present a reverse traveling wave. The entire model that is used is based on the hypothesis that there must exist and consequently must be explained a traveling wave whatsoever.

However that is the cardinal subject of difference between your statements and mine.
In my concept, based on the Bernoulli solution, there still exists a ‘wavy motion’ on the basilar membrane, but that is the result of phase dependent behavior.
Locations with higher resonance frequencies react in phase with the frequency stimulus; at resonance locus this motion is 90 degrees behind in phase; locations with lower resonance frequencies react 180 degrees retarded in phase.
And because higher resonance frequencies are found near the round window, while lower resonance frequencies are found near the helicotrema the ‘wave’ always runs from base to apex. And as Tianying Ren et al. also experimentally detected: there doesn’t exist a reversed traveling wave.

And now my reactions to the comments of Dick Lyon:

Dick you remarked:
** Willem, your approach in which "the flow behaves as a parallel streaming oriented along the core of the perilymph duct" and in which "there exists only a contribution in the x-direction" is what might be called a "non-compliant membrane" approximation.**

In strict theoretical terms you could name it as such, but in practice it means that the movements of the incompressible viscous-free perilymph, in the direction perpendicular to the core of the perilymph duct, are negligibly small compared to the movement in the core direction.

You commented also with:
** Generally, the BM is interpreted as being variably compliant (and the RM very compliant), such that there is some velocity (and pressure variation) ortogonal to the x dimension, which corresponds to BM displacement. **

Regarding the first part of it, the compliance of the membranes, I agree with you. And I have also used this frequency dependent 'compliance' of the basilar membrane in my description of the evoked movements in this membrane due to a sinusoidal sound stimulus.
It results in a DC deflection all over the basilar membrane due to the 'time average of the sound energy signal' and the locally evoked AC or frequency dependent deflection at the corresponding resonance locus with a doubled frequency. And it results in an all over the Reissner membrane existing combination of a DC deflection towards the scala vestibuli and an AC deflection with a doubled frequency.

It isn't a basilar membrane movement due to an 'overpressure' caused by an increase in pressure inside the perilymph. That is in essence the specific behavior of a potential flow – like this Bernoulli flow actually is – where the decrease in internal pressure [delta p] is proportional to the decrease in potential energy [E potential], while the kinetic energy [E kinetic] of the entire perilymph mass [m] in the flow tube increases proportionally to the fluid velocity [v] squared. Thereby potential energy and kinetic energy in the potential flow remain always in balance.

You commented:
** If you assume no BM displacement, then of course you have no traveling wave. **

Nowhere in my explanation have I stated that basilar membrane mobility doesn't exist.

Of course there exist basilar membrane displacements. But their influences on the local cross section of the perilymph duct are rudimentary.

And for clarity let us make an indicative calculation:
The average diameter of the perilymph duct is 0.3 mm. And let us assume the cross section to be circular. Then the size of the surface can be calculated as 0.0706 square mm. The local deflection of the basilar membrane cannot be much larger than a few micrometers. Otherwise the hair bundles of the outer hair cells would be overstretched or even disrupted.
The width of the basilar membrane is approximately 0.1 mm. If that is displaced 1 micrometer over its entire width, the corresponding surface of that cross section is 0.0001 square mm.

This means that the cross section at the place of the membrane deflection is relatively 1.4 pro mille decreased. So you cannot maintain that this will have a serious influence on the main fluid movements in the core direction of the perilymph duct.

You commented further:
** The BM (or the whole of scala media in your approximation) separates the two parts of the folded duct in which you have a longitudinal pressure gradient, so there will be a substantial

pressure difference across it, from the far-apart x locations (except near the apex where it folds). **

I am sorry that I have to tell you, but with this statement you show that you do not really understand the general mechanism of the potential flow.

And I can explain this at best with the example of a straight tube in which a (periodic) potential flow exists. For this flow condition the fluid in the tube is incompressible and non-viscous and the flow isn't turbulent, which means 'rotation free'.
Since there doesn't exist internal laminar friction [the fluid isn't viscous] it will 'stream' along the core direction of the tube everywhere with the same velocity.
In that case the (non-stationary) Bernoulli equation is valid and the internal pressure in the tube is everywhere the same and given by the well-known Bernoulli relation. The decrease in internal pressure in the fluid is equal to half the density of the fluid multiplied with the square of the fluid velocity. In case of the non-stationary Bernoulli flow, the involved velocity in this equation is then a function of time.

If we insert pressure sensors at two places along the tube in its wall, each of the pressure sensors will detect a decrease in pressure proportional to the square of the fluid velocity – in full accordance with the Bernoulli equation.
However, if we try to measure the pressure difference between the two locations, we will find zero as the result. That is logic because the fluid velocities in both cross sections are equal.

However, if we want to measure the fluid velocity in the tube, we can use the solution found by Venturi. Then we have to place in the tube an intersection in which the cross section along the length of that partition gradually and fluently decreases from the tube cross section to a minimum value and then fluently increases again to the size of the original tube cross section. And let us place this Venturi tube in-between the two original pressure sensors.

If we insert now in the wall of the narrowest cross section of that Venturi tube a third pressure sensor, we will measure there an extra decrease in pressure related to the other two pressure sensors.

The now measurable pressure difference between the Venturi pressure sensor and the pressure sensor either 'up-streams' or 'down-streams' is proportional to the fluid velocity in the tube multiplied with the total of the square of the ratio between tube cross section and Venturi cross section minus 1.

Hence there exists a lower pressure in the Venturi tube, but equal pressures on both sides of the Venturi tube.

And remark that in principle the Venturi tube in the potential flow isn't forming an obstacle in that flow. Otherwise there would exist a pressure difference between locations on both sides of the Venturi tube.

Now we can make one further step: we can smoothly fold the tube in the Venturi partition in such a way that the narrowest cross section also forms the 'elbow' in the folded tube. [let us name that the helicotrema].

Hence – contrary to what you suggested in your comment – under the potential flow conditions inside the cochlea there doesn't exist a longitudinal pressure gradient, which evokes a substantial pressure difference across the helicotrema.

Finally we can place in-between the two parts of the tube [scala vestibuli and scala tympani] a third one [the scala media] that forms an intersection of the two other ones.

As long as the cross sections of both perilymph ducts at some place x away from the base [oval and round window] are identical, the evoked pressures on both sides of the scala media will be directed outwards and equal. Exactly as is shown in Fig. 3 on page 22 of our booklet 'Applying Physics Makes Auditory Sense'.

The movements shown in several animations on the Internet, where the stapes activation creates 'waves' of higher frequency stimulus contributions which leave the core flow in the scala vestibuli and let the Reissner membrane and the basilar membrane simultaneously vibrate at a location nearer to the base, while from that location in the scala tympani a reverse 'wave' propagates toward the round window, is based on a hypothesis for which I cannot find a sound physics principle.

[See for instance: http://www.blackwellpublishing.com/matthews/ear.html]

Dick, you commented also:
** If you allow the pressure across the BM to deflect it, as we usually do with membrane compliance, you get a very different analysis, based on the same physics but different mechanical approximations. In this analysis, the v-squared pressure differences due to Bernoulli's law are generally very small compared to the pressure differences accelerating the fluid within the short wavelength of the traveling wave, so are neglected. **

Let me first calculate what pressure decrease will be evoked in front of the basilar membrane by a stimulus of 1000 Hz which let the oval window deflect with an amplitude of 2 micrometer.

With the density of perilymph [1000 kg/m^3] the maximum pressure decrease will be 72 mPa. Not really a low value.

Another fact is that we also have to cope with the problem that the pressure differences accelerating the fluid within the short wavelength of the traveling wave – that would exist indeed in the 'transmission line' hypothesis and in the companying mathematical model, which calculates these hypothesized effects – have no physics ground to exist in the wiggle-waggle movements of the perilymph.

Finally you commented:
** Which approximation is better? Probably the one that yields a traveling wave like the one seen in direct mechanical measurements, I think.**

Already years ago I corresponded with Tianying Ren, the man who did this kind of mechanical measurements. On his request because those measurements did not fit well within the ruling traveling wave paradigm. Actually they were flawed in that time by the auditory peers.

In 2008 De Boer et al. also reported that there were serious doubts about the hypothesized existence of reversed traveling waves. Only forward 'waves' on the basilar membrane could be observed. He also suggested that in the first place there must be found an explanation that can dispose this newly arisen anomaly.

The observed 'wave phenomena' on the basilar membrane resemble the forms that are shown in the following animations, which can be downloaded from the Internet:

http://lab.rockefeller.edu/hudspeth/graphicalSimulations

or:

http://www.youtube.com/watch?v=dyenMluFaUw

These simulated animations also resemble very well with the phase wave phenomena which I have calculated and which I have presented in brief in our booklet for one sinusoidal stimulus. The traveling wave you refer to in your comment here above is by far not an accomplished fact.

Therefore I hope you will agree with me that the best theoretical description of the functioning of our hearing sense is the one that is in the first place in agreement with physics, describes and explains the experimental findings very well even in detail, can cope with the existing anomalies, and can predict correctly in detail new and until now unknown hearing and auditory perception phenomena.

And I am convinced that under these requirements our hearing paradigm is a very serious candidate.

Kind regards,

Pim Heerens