Helmholtz's piano strings:

reverberation of ripples on the tectorial membrane

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Abstract:

In 1857 Helmholtz proposed that the ear contained an array of sympathetic resonators, like piano strings, which served to give the ear its fine frequency discrimination. Since the discovery that most healthy human ears emit faint, pure tones (spontaneous otoacoustic emissions), it has been possible to view these narrowband signals as the continuous ringing of the resonant elements. But what are the elements? It is noteworthy that motile outer hair cells lie in a precise crystal-like array with their sensitive stereocilia in contact with the tectorial membrane, a gelatinous structure with an observed surface tension. This paper therefore speculates that ripples (surface tension waves) on the lower surface of the tectorial membrane propagate to and fro between neighbouring cells. This mechanism defines a surface acoustic wave (SAW) resonator, and relies on the outer hair cells directly sensing intracochlear fluid pressure through their cell bodies; in this way the theory revisits the resonance theory of hearing. The SAW resonator acts as a regenerative receiver of acoustic energy, a topology which was invoked in 1948 by Gold, who later drew the analogy to an 'underwater piano' to describe the cochlea's problem of how it could vibrate with high *Q* while immersed in fluid. The proposal also gives a physical description of the cochlear amplifier postulated by Davis in 1983. An active array of resonating cavities driven by outer hair cells can explain spontaneous emissions, the shape of the basilar membrane tuning curve, and evoked emissions, among others, and could relate strongly to music.

At levels above which the cochlear amplifier saturates, ripples on the tectorial membrane can still be identified, this time due to vibration of the tectorial membrane against the sharp vestibular lip. This second putative mechanism provides time delays between initiation of the ripple by acoustic pressure variations and its detection by the inner hair cells, and so represents an alternative way of interpreting the traveling wave.

Thus, by invoking two ways of generating ripples on the tectorial membrane, a comprehensive account of cochlear mechanics can be constructed, unifying a resonance theory (at low levels) with a traveling wave picture (at high levels).

PACS numbers: 43.64.Bt, 43.64.Kc

I. INTRODUCTION

To explain how the ear works, resonance theories of hearing — accommodating the ancient Greek idea that 'like is known by like' — have frequently been put forward. However, since Bauhin in 1605 formulated the first resonance idea on the basis of anatomy, the actual resonating elements have proved elusive (Wever, 1949). First it was air-filled cavities; later, minute strings. But even Helmholtz (Helmholtz, 1885), the major proponent of the resonance picture, found difficulty finding suitable candidates, at times favouring the arches of Corti, at others the transverse fibres of the basilar membrane. The problem is to find structures within the pea-sized cochlea that can resonate, like piano strings, over 3 decades of frequency. A high-frequency resonance at 20 000 Hz (the upper limit for human hearing) is easy to assign, but, as Helmholtz acknowledged, finding a structure that can resonate at 20 Hz (the lower limit) is difficult.

The fibres of the basilar membrane have continued to remain the favoured tuning elements, even though it is nigh impossible to make their combined stiffness and mass vary by the required 6 orders of magnitude (de Boer, 1980; Hubbard and Mountain, 1996; Naidu and Mountain, 1998). Moreover, these elements are closely coupled, so it is hard to understand how the high Q that the ear displays (150 at 2.5 kHz; Gold and Pumphrey, 1948) can arise. Nevertheless, it is this bank of graded resonators which auditory science has seen as the cause of the 'traveling wave', observed by Békésy (Békésy, 1960), that underlies the stimulation of inner hair cells and the generation of neural impulses.

It was just this problem of how the cochlea, immersed in fluid, could achieve the high Q's revealed by psychophysical experiments which led Gold and Pumphrey (1948) to declare that 'Previous theories of hearing are considered, and it is shown that only the resonance hypothesis of Helmholtz … is consistent with observation' (p. 462).

Gold (1948) went on to posit that some sort of 'regenerative receiver' must be at work in the cochlea, and indeed searched for objective evidence for it by placing a microphone in ears which, with loud sounds, had been caused to 'ring', a phenomenon that Gold saw as a clear indication of a regenerative receiver operating with excessive positive feedback. The experiment did not meet with success, but it didn't prevent at least two other later attempts to reinstate a resonance a theory of hearing: by Naftalin (Naftalin, 1963; 1965; 1970; 1981) and Huxley (Huxley, 1969). More recently, Dancer and colleagues (Dancer and Franke, 1989; Dancer *et al.*, 1997; Avan *et al.*, 1998; Magnan *et al.*, 1999) have suggested resonance but with no specific mechanism stated.

Some 30 years after Gold's work, his ideas received renewed attention when Kemp, with improved equipment, discovered that sound energy could be detected emerging from human ears when a sensitive microphone was placed in the ear canal (Kemp, 1978). The sound can be observed either as an answering echo to a stimulus or, more revealingly, occur spontaneously as a continuous faint ringing now called spontaneous otoacoustic emission or SOAE (for a review see Probst *et al.*, 1991).

Since Kemp's seminal discovery, the ear could be viewed as an active device, not a passive detector, and the motile properties of outer hair cells soon identified them as the locus of some sort of 'cochlear amplifier' (Davis, 1983), although how these cells perform this function is still the focus of much current investigation. Energetic activity of OHCs can be observed at frequencies of more than 20 kHz (Dallos and Evans, 1995) and SOAEs have been recorded as high as 63 kHz (in a bat; Kössl and Frank, 1995). This paper puts forward a physical model that brings together all these disparate features.

It is suggested that, at low sound pressure levels (below about 60 to 80 dB SPL), the resonant elements comprise adjacent outer hair cells reverberating with each other via capillary waves (ripples) on the tectorial membrane. These elements resonate sympathetically with incoming sound energy and, because they are discrete, high *Q*'s can be achieved. A good analogy of this process is that of the surface acoustic wave (SAW) resonator found in solid-state electronics. A companion paper (Bell, 2001) provides a more detailed description of how the cochlear elements work together to create a SAW resonator; most of this paper is concerned with the ramifications of such a configuration for cochlear mechanics, and it is shown that the model provides a good account of observed cochlear behaviour.

At sound levels above 60 to 80 dB SPL, when the resonance mechanism and its associated cochlear amplifier have saturated, it is suggested that ripples are still central to cochlear mechanics, but they arise from a second mechanism. This time it is hypothesised that ripples are generated at the vestibular lip by movement against the tectorial membrane, which, because of its acoustic impedance, is caused to move to and fro by sound pressure on either side of it. This implies that ripples are launched simultaneously along the length of the cochlea and propagate towards the inner hair cells, where they arrive after a time interval equal to several wavelengths of the slow-propagating ripples.

Thus, a complete cochlear mechanics is assembled comprising two complementary mechanisms in which capillary waves are a novel and central element. The lower-level mechanism represents a resonance picture of the cochlea, but the second one – involving a progressive delay in wavefronts launched simultaneously at all points along the vestibular lip and arriving at the inner hair cells after propagation delays – represents a traveling wave. In other words, this paper reinterprets the classical traveling wave as the outcome of slow-propagating capillary waves instead of resulting from hydromechanical eddies as normally thought. In this way, the two major theories of hearing, the resonance and traveling wave pictures, can be reconciled. They are both correct, but operate at different sound pressure levels.

II. CONSTRUCTION OF A PHYSICAL MODEL OF THE COCHLEAR AMPLIFIER

The reverberation hypothesis calls on a particular feature of OHCs that has been overlooked: in all higher animals, including humans, OHCs lie in three or more rows in geometric alignment with their neighbours. Examination of published micrographs shows that the geometry is typically closely defined, much like that of a thin slice of crystal lattice, with regular alignments of hair cells in defined directions (**Fig. 1**).

The essence of the theory is that resonant cavities can form between lines of outer hair cells. Since OHCs are mechanical sensors/actuators, a wave disturbance in the gel of the tectorial membrane (in which the OHC stereocilia are embedded) can undergo successive amplification and reflection between the rows. This constitutes a surface acoustic wave resonator in which the stereocilia, connected to fast molecular motors in the hair-cell body, pump in acoustic energy.

A good analogy is the familiar solid-state surface acoustic wave (SAW) resonator which employs regularly placed electrodes on the surface of a crystalline material to generate (relatively slow) electromechanical ripples that resonate between the electrodes, giving stable frequencies in the megahertz range (Bell and Li, 1976). The companion paper elaborates on this analogy and points to evidence in the literature supporting this proposed mechanism.

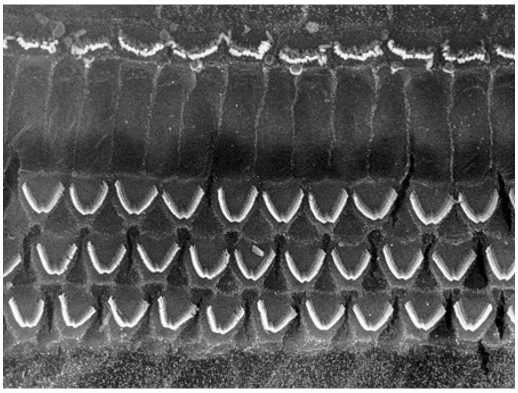

FIG. 1. Geometrical arrangement of the hair cells of a rabbit, showing three rows of outer hair cells and one row of inner hair cells. Observe the regular face-centered orthorhombic arrangement of the OHCs. [SEM courtesy of Allen Counter and the Karolinska Institutet and used with the permission of Elsevier Science Ltd. Reprinted from Counter, S. A., Borg, E., and Löfqvist, L. (1991), "Acoustic trauma in extracranial magnetic brain stimulation", Electroencephalography Clin. Neurophys. 78, 173–184.]

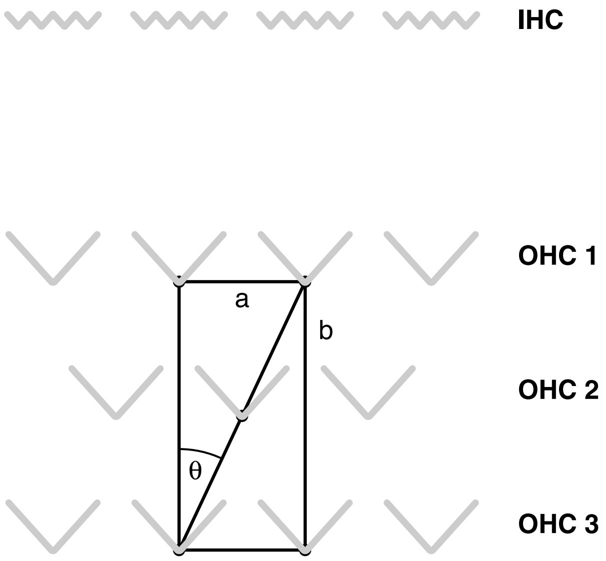

FIG. 2. Schematic arrangement of hair cell geometry, showing longitudinal distance, *a*, between OHCs (along the length of the cochlea), and distance *b* between the first and third rows. The diagonal appears at an angle θ given by arctan *a*/*b*.

Developing the idea of a resonant cavity between facing stereocilia, active resonators may form not only at right angles to the OHC rows but also at defined oblique angles – notably at about 19°, 35°, 46°, 54°, 60°… to the radial direction – where successive alignments of two or three hair cells occur. Herein is the genesis of the cochlea's typical tuning curve, of sets of spontaneous emissions, and perhaps, of musical ratios.

In this sense, Helmholtz was right: there are piano strings in the ear, but they are smaller and less conspicuous than he imagined. In fact, without appreciating the integral role of the tectorial membrane – called a 'peculiar' elastic membrane by Helmholtz – the resonating elements are virtually invisible. In considering Helmholtz's piano-string model, Gold (1987) asks "how can a tiny structure of little strings immersed in liquid be so sharply tuned?" (p. 154). He draws an analogy to an underwater piano and points out that only by adding a positive feedback system to each string could such a device be made to work. This is what the current hypothesis does.

A. Geometry of the OHC lattice

When micrographs of the organ of Corti, as shown in Fig. 1, are examined, one is immediately struck by the regular parallel rows of OHCs (three or more) which run from the base, or high-frequency end, of the spiral cochlea to its apex, where low frequencies are detected. Not only is the inter-row spacing precisely defined (typically 15 μm in humans, but continuously graded from 10 μm at the base to 25 μm at the apex), but so too is the longitudinal spacing, usually 8–12 μm (Fig. 92 of Bredberg, 1968). Cochlear geometry is fixed by birth, and stays constant throughout life (p.13 of Bredberg, 1968), just like frequencies of SOAEs (Burns, 1999).

The typical OHC geometry of Fig. 1 is drawn schematically in **Fig. 2**, where we see that five adjoining cells can be grouped into a 'face-centered orthorhombic' unit cell with spacing a in the longitudinal direction and spacing b in the radial direction (between OHC rows 1 and 3), an arrangement defining a diagonal at θ degrees to the radial.

Measurement of a wide variety of published micrographs and maps of hair cell positions (cochleograms) shows that a/b centers around 0.35, so that θ, numerically arctan a/b, is usually about 20°. For humans, of 17 such examples, 12 returned a value of 20 ± 3° (**Table 1**). For a range of other vertebrate species (29 examples), more than half (16 cases) gave a value in this range (data not shown, but see Appendix 1b from footnote 1). Narrow angles derive from apical regions and wide ones from basal locations (Zhou and Pickles, 1996); the median appears to represent the important mid-frequency region where, in humans, speech is detected and SOAEs are most prevalent (Probst *et al.*, 1991).

The most common angle of about 20° means that the diagonal is (1/cos20°) times the length of the perpendicular, or 1.06. That number is a key one, for it is also the favoured ratio between neighbouring spontaneous emissions (e.g., Braun, 1997). The suggestion, taken up later, is that these two directions represent adjacent reverberating cavities.

B. Generation of ripples on the tectorial membrane

The tectorial membrane (TM), a gelatinous acellular matrix permeated with fibres (Steel, 1983), occupies a central place next to the hair cells of many animal ears; in contemporary hearing theory its role has been to deflect the stereocilia, through shear between the tectorial and basilar membranes, when the latter moves up and down from acoustic pressure across the partition (Allen, 1980). Hardesty (1908) described the TM as “most inconceivably delicate and flexible”, adding that “the readiness with which it bends when touched or even agitated is beyond description” (p. 117). Like a number of his fellow hearing scientists of the time, Hardesty believed that the tectorial membrane was a far more likely candidate for the frequency-resolving element in the cochlea than the basilar membrane, and the reasons are forcefully set out in this classic paper; it also contains superb detailed drawings of the tectorial membrane. This present communication conjectures that the special role of the tectorial membrane is as a medium supporting the propagation of slow surface waves, thereby allowing microscopic distances to be tuned to acoustic frequencies.

The two outermost rows of OHCs are like the partially reflecting surfaces of a Fabry-Perot etalon, except in this acoustic analogue they are active and can supply energy upon reflection. It is proposed that, in general terms, OHC can detect a surface wave traveling in the TM, so that when a wave reaches an OHC the cell changes polarization, alters its length accordingly, and executes an active return to its equilibrium point, in the process reflecting and amplifying the disturbance (see companion paper for details). The process repeats as the wave travels back and forth between the rows, creating continuous oscillation. In other words, there is a resonant cavity between the rows, a cavity that behaves like a pipe open at both ends and sounding in its whole-wavelength mode. The companion paper shows how the three rows of active outer hair cells, in conjunction with the gel of the tectorial membrane, operate like a surface acoustic wave resonator, similar to its solid-state counterpart but operating in the audio range. A SAW resonator is able to amplify a wave disturbance between its outermost sensors, and, if it is presumed that the OHC are in fact pressure sensors capable of responding directly to intracochlear pressure, the result is a physical description of a cochlear amplifier. This amplifier acts as a regenerative receiver of acoustic pressure in the cochlea, answering Gold's specification for how the cochlea might detect low-level acoustic signals.

C. Propagation of ripples

Length changes of OHCs mean there are corresponding up-and-down movements of the TM, and this calls for the TM to support some form of transverse wave with a vertical component. Various modes of wave propagation in a gel (a polymer swollen with fluid) are possible, depending on the gel's particular internal properties (Heinrich *et al.*, 1988; Onuki, 1993), and the physics of this as applied to the TM require further study. However, given the TM's high water content and extreme flexibility (Naftalin, 1970), the simplest model is one involving familiar capillary waves, like ripples on the surface of water, in which surface tension provides the restoring force (Tonndorf, 1973). No measurements of surface tension of the tectorial membrane are available, although there are a number of observations that indicate it has considerable surface tension. Hardesty (1908) noted of fresh material that "its quality of adhesiveness is phenomenal. It is so subject to surface tension that, it matters not how clean the needle point may be, to touch the membrane is to have it stick… Scraps of debris and shreds of tissue will adhere to it" (p. 117). Olson (1998) noted that a probe inserted near the basilar membrane experienced significant surface tension effects, enough to interfere with precise positioning of the probe. Surface tension is a phenomenon based on electrostatic attraction, and it is appropriate that the tectorial membrane is composed of proteoglycans, which have a high negative charge density (Slepecky, 1996).

It is thus posited that ripples propagate isotropically across the surface of the TM in response to sound-induced movement of the OHCs. The speed of propagation, c, of a capillary wave is related to the surface tension, T, by

$$c = (2\pi T/\lambda\rho)^{½}$$

where λ is the wavelength and ρ is the density (Lighthill, 1978). Ripples are dispersive, with the speed increasing as the wavelength decreases. On the surface of water, for example, the speed is 0.86 m sec^{-1} at 1 kHz and only 0.36 m sec^{-1} at 100 Hz. Note that these are about 4 orders of magnitude less than the velocity of a compressional wave in water, some 1500 m sec^{-1}. As the companion paper notes, a characteristic of solid-state SAW resonators is that the speed of the Rayleigh wave on the surface of the device is typically 5 orders of magnitude less than the speed of the excitatory signals in its electrical leads, a wavelength compression of particular value in signal processing applications such as convolution.

Capillary waves have just the right properties for the cochlear resonators: a very low propagation speed which, in order to tune the bank of resonating cavities, decreases steadily from base to apex. Calculating values, if a cavity 30 μm long is to oscillate in its whole-wavelength mode at 1 kHz, a propagation speed of 30 μm per ms would be required; that is, 30 mm sec^{-1}. Although lower than the speed of ripples on the water–air interface, this value is reasonable for a water–gel interface and could occur if the surface tension between the TM and the endolymph were about 4 μN m^{-1}. At higher frequencies nearer the base, say 10 kHz, the necessary speed would be faster, typically 20 μm per 100 μs, or 200 mm sec^{-1}, and calling for a T of 130 μN m^{-1}; whereas near the apex, say 0.1 kHz, the requisite speed would fall to 50 μm per 10 ms, or 5 mm sec^{-1}, and T would need to be 0.2 μN m^{-1}.

Because of the dispersive behaviour of ripples, the SAW model calls for a ratio of only about 600:1 in the values of surface tension between base and apex. This is a much smaller ratio, and could well be easier to achieve physically, than the ratio of 10^4 or more required in conventional traveling wave theory for the stiffness ratio of the basilar membrane between base and apex (Naidu and Mountain, 1998). Potentially, the surface tension ratio could be as low as 200:1 because of the way in which the characteristic frequency (CF) at low frequencies appears to be set by using long cavities at oblique angles (see section III-A).

Another advantage of dealing with short-wavelength capillary waves is that their curvature is correspondingly high, vastly easing the stereocilia's task of detecting angular deflections. It is worth noting that the cuticular plate can tilt through some 14° (Zenner *et al.*, 1988), an impossibly large angle for dealing with deflections of the basilar membrane, but an angle of curvature within the realms of possibility for high-amplitude ripples on the TM.

Although this hypothesis calls for small values of surface tension, such values are easier to achieve than uncommonly large ones. Indeed, it would be surprising if there were no surface tension between TM and endolymph, particularly since the environment is electrically charged. The outer hair cells themselves possess surface tension by virtue of charge accumulation associated with their membrane potential (see companion paper). Membrane potential is under the control of efferent-liberated transmitters (Guinan, 1996), and so the requisite grading in surface tension between base and apex could be achieved through regulation of membrane potentials. A major purpose of the extensive efferent supply is therefore, it is supposed, to regulate the cochlear tuning map.

The simplest form of the ripple hypothesis is one having isotropic wave propagation. In this connection, the surface of the TM is covered with a thin amorphous layer in which the OHC stereocilia are embedded (see Fig. 3 of Kimura, 1966) and it is conjectured that it is this isotropic medium in which the capillary waves propagate. One property of capillary waves is high attenuation at acoustic frequencies, but this should not be a problem when dealing with distances measured in micrometres. No attenuation could in fact lead to interference problems (see Section V-C), and exponential attenuation, with a space constant of 10 μm, is factored into a model of cochlear tuning described below. Some measurements of the physical properties of the tectorial membrane are given in Abnet and Freeman (2000), although no surface tension measurements were made (however, one potentially relevant property of the isolated mouse TM which was measured was a space constant of 27 μm for longitudinal attenuation of tangentially imposed vibration and a corresponding figure of 21 μm in the radial direction).

It is possible that other wave propagation modes are involved, either separately or in conjunction with surface tension (see, for example, p. 495 of Békésy, 1960). A flexural wave mode, for example, could be considered, but its speed varies only as the square root of the frequency (Fletcher, 1992), so that a 1000-fold variation in frequency leads to just a 32-times variation in speed. Membrane thickness is another significant variable, increasing by about 6-fold from apex to base (Hardesty, 1908). However, for purposes of cavity tuning, this factor is in the wrong direction for a flexural wave: for a constant shear modulus, such a wave would increase in speed as the square root of the thickness (Fletcher, 1992), indicating that some other wave mode, perhaps relying on transmission along the embedded fibres of the TM, may be involved. It cannot be ruled out that the TM belongs to the class of peculiar gels – the so-called 'ringing gels' (Radiman *et al.*, 1994) – that possess an inherently resonant internal structure which rings like a bell when struck. The frequency here depends on the size, shape, and water content of the sample, and it is thought that the ringing results from resonance of a periodic membrane made up of a viscoelastic fluid and a very weak elastic solid which couple to a shear mode at the surface to produce sound.

It is worth noting that stereociliar length and OHC length grow progressively from base to apex (Pujol *et al.*, 1992), which no doubt assist in cavity tuning and impedance matching. Isolated OHCs respond directly to oscillating acoustic pressure in a tuned manner (Brundin *et al.*, 1989), although this tuning is broad and it could result from the vibration of free-standing stereocilia.

III. IMPLICATIONS FOR COCHLEAR MECHANICS

A. Cavities in several directions and the cochlear tuning curve

So far, a resonant cavity involving reverberation of wave energy between OHC1 and OHC3 has been postulated. However, the same process that creates reverberation at right angles to the rows could also work for hair cells that are obliquely disposed, as shown in **Fig. 3**, creating a series of resonators L_0, L_1, L_2, L_3, L_4, L_5, …

A well-known observation from the literature (e.g., Braun, 1997) is that neighbouring SOAEs exhibit a favoured ratio in their frequency spacing of close to 1.06, or very nearly a semitone. (This finding often appears in a different guise in the literature where it is expressed as 0.4 Bark, where 1 Bark is a psychophysical unit chosen to represent a critical band in the ear's frequency discrimination.) Analysis of data from Russell (1992) confirms that the most favoured nearest-neighbour ratio is at about 1.06, as shown in **Fig. 4**. The ratio appears as its reciprocal in the figure as the peak at 0.94–0.95 where, to show longer-range relationships, SOAE frequencies are expressed as a ratio to the highest occurring emission in an ear.

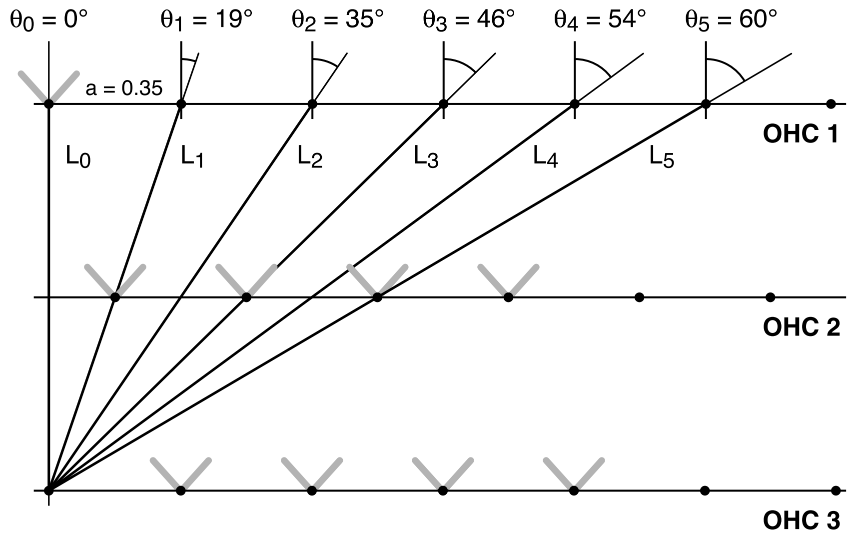

FIG. 3. Geometry of outer hair cell array, elaborated from Fig. 1 with *a* = 0.35 and *b* = 1, showing multiple oblique alignments of hair cells. We obtain a set of alignments at angles θ_0, θ_1, θ_2, θ_3, θ_4, θ_5… with lengths L_0, L_1, L_2, L_3, L_4, L_5, …

The angles shown produce cavity lengths of 1.00, 1.06, 1.22, 1.44, 1.71, 2.00, … which would have corresponding frequencies of 1.00, 0.94, 0.82, 0.69, 0.59, 0.50, …

It is noteworthy that L_1:L_0 is 1.06, close to a semitone and equal to the most common ratio between SOAEs, and that L_5:L_0 is 2:1 (an octave).

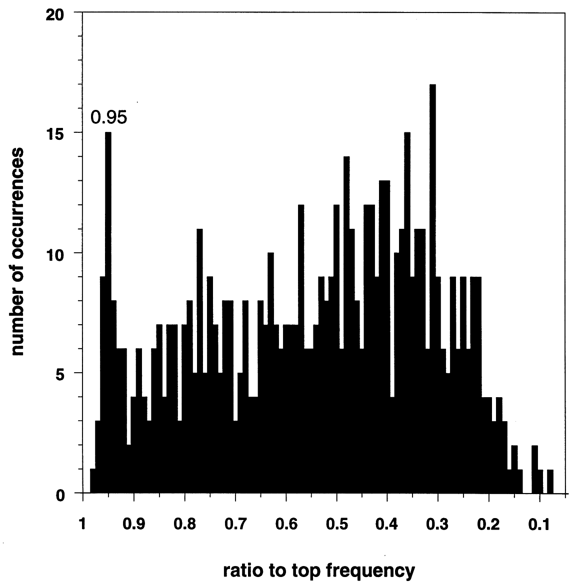

FIG. 4. Most prevalent spacing of neighbouring SOAEs is at a ratio close to 1.06, a well-known finding in the literature (e.g., Braun, 1997) and shown here by the analysis of the data of Russell (1992). The ratio appears here as its reciprocal as the peak at 0.94–0.95 where, to show longer-range relationships, SOAE frequencies are expressed as a ratio to the highest occurring emission in an ear.

In terms of reverberant cavities, a resonance frequency one semitone lower will occur if the cavity is made 1.06 times longer. Considering a radial cavity L_0 to have a resonance frequency f, then its neighbouring L_1 cavity will have a frequency $f/1.06$ if it occurs at an angle of 19.4° (1/cos19.4° = 1.06), an angle consistent with the 20° angle recurring in Table 1. Closer examination of nearest neighbour ratios (footnote 1) reveals an average interval of 1.06 with a range from 1.03–1.08, corresponding to oblique angles of 14° and 22° respectively and covering much of the range seen in Table 1. It is therefore posited that the observed favoured ratio of 1.06 between SOAEs reflects the simultaneous excitation of these two cavities.

For a pair of SOAEs f_0 and f_1 with approximate semitone spacing and relative frequencies 1.00 and r_1 ($=f_1/f_0$), simple trigonometry gives $\theta_1 = \arccos r_1$. Subsequent frequencies in the set will then occur at $r_n = \cos \theta_n = \cos(\arctan(n \tan\theta_1))$, where n is 2, 3, 4, 5, …]. Similarly, if $L_3 = 2.0$, then $L_1 = 1.15$ and $\theta = 30^\circ$. This paper suggests it is significant that when the fifth oblique is at 60°, ($L_5 = 2.0$, an octave), the first oblique is at 19.1° (a semitone); therefore, it is possible to explain angles near 14° from recognizing that when the *seventh* oblique is at 60°, the first oblique is at 13.9°.

Neighbouring hair cells, acting like a phased array of transmitters/receivers, co-operatively generate a strong coherent wavefront. However, the strength of the first oblique mode, L_1, and the other odd-numbered alignments, is augmented because they have a middle row hair cell (in OHC 2) acting in antiphase to OHC1 and 3, which helps in wavefront propagation (Bell, 2001).

Examination of published micrographs, particularly the map of stereocilia positions for almost the entire cochleas of rhesus monkeys (Lonsbury-Martin *et al.*, 1988), sometimes reveals a very well defined oblique. Examples are shown in **Fig. 5**. These, and others like it,

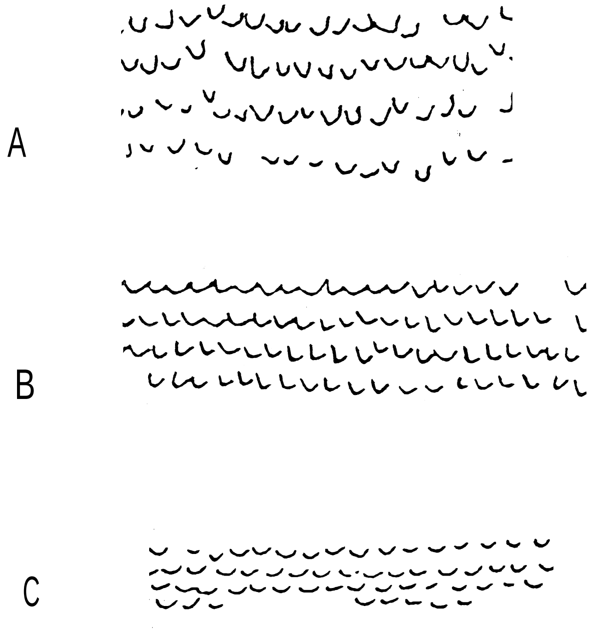

FIG. 5. Maps of stereociliar positions for three different frequencies of a monkey cochlea (same scale; from Lonsbury-Martin *et al.*, 1988), showing progressive change in unit cell geometry and arm orientation. **A**: region about 20% from apex, with CF near 100 Hz; **B**: about 38% from the apex, CF about 500 Hz; **C**: about 80% from apex, CF about 16 kHz. In A, a/b is 0.34, giving a θ_1 of 19°; in B it is 0.29 (16°); and in C it is 0.64 (33°). Note that at low frequencies, the arms enclose acute angles and pick out oblique cavities, so that the strongest resonator (CF) may be a long (low-frequency) cavity. At high frequencies, the arms enclose obtuse angles, and CF will derive from a short cavity. Observe also that row spacing at high frequencies is shorter than at low, and that when a fourth-row cell is present it is placed to emphasise an oblique cavity. The significance of oblique cavities lies in the way they contribute low-frequency resonance to the partition, and this relates to the shape of the tuning curve (which is derived as the sum of all the active resonators at a point) as illustrated in Fig. 8.

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show the tendency for stereociliar arms to define certain oblique directions (that is, the arms sit at right angles to the axis of the cavity), and sometimes a fourth row hair cell appears to augment this direction. Occasionally, the whole hair cell geometry appears sheared from orthorhombic to rhombic to emphasise an oblique mode, although this could arise as a preparation artifact.

Inspection of the rabbit cochlea in Fig. 1 indicates that the stereociliar arms are well placed to define the third and fourth oblique modes. That is, they are placed perpendicular to these cavities (which slant some 52° and 59° from the perpendicular).

If the first oblique mode (L_1 or L_{-1}) were stronger than the L_0 mode (because of the above factors), and an emission were associated with the former, then the tip of its suppression tuning curve might be expected to be ½–1 semitone higher, and be more sensitive, than at the emission frequency, and this has been observed (Bargones and Burns, 1988; Abdala *et al.*, 1996).

Significantly, multiple tips and notches are regularly seen in suppression tuning curves (Nuttall *et al.*, 1997; Bargones and Burns, 1988; Powers *et al.*, 1995), appearing on the low-frequency or high-frequency slope (or both) depending, it is suggested, on whether the SOAE arises from L_0 or from an oblique resonator (see Appendix 3 from footnote 1).

Of particular interest, if the response of all the resonators is summed, the result is the typical response curve of a point on the cochlear partition. That is, take a single high-Q resonator at L_0 with slopes of 100 dB/octave and add to it the response of the other associated cavities. Assume that the strength of a linear propagating wave front falls off, by attenuation, as a simple exponential and is further weakened, because of circular expansion, by a $1/r^2$ factor. It is known that capillary waves are strongly attenuated at high frequencies

(Lighthill, 1978). Longer resonators will therefore make successively weaker contributions at frequencies the inverse of their length. In this model, the effect of OHC2 has been ignored for the sake of simplicity. The summation, shown in **Fig. 6,** exhibits a sharply tuned tip flanked by a very steep high-frequency slope and a more gently sloping, although somewhat notched, low-frequency tail. This curve resembles the psychophysical (de Boer, 1980) and mechanical (Nuttall *et al.*, 1997) tuning curve of the cochlea. In particular, it explains the notches that are commonly seen.

Perhaps one of the clearest instances of a tuning curve in which the contributions of the individual resonators can be seen is a laser-beam investigation of the guinea pig cochlea (Nuttall *et al.*, 1997). In this study, tiny glass beads were placed on the basilar membrane and their movement detected with a laser doppler velocimeter. The core of that work, shown in **Fig. 7** here, shows the response of a bead to broad-band noise, and it is clear that the typical shape of the cochlea's mechanical response is generated. Note the distinct peaks, reproducible between the 80 and 90 dB curves. The frequency of the peaks marked is consistent with oblique alignments of hair cells derived from a rhombic geometry with a/b of 0.383 and a tilt of 4 degrees. These positions represent alignments in which response to imposed sound is enhanced. Observe the simple integer ratio between L_1 and L_3 (2:3) and between L_1 and L_{-5} (1:2).

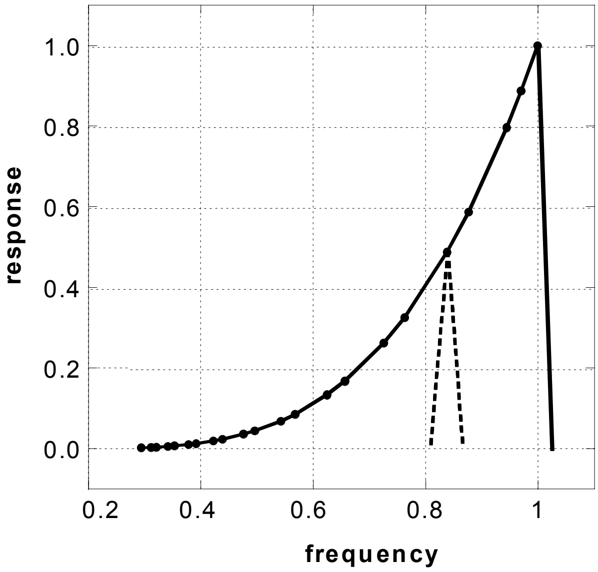

FIG. 6. Summing the response of each of the cochlear resonators produces, using simple assumptions, a curve that resembles the mechanical response of the cochlear partition (and, inverted, the typical cochlear neural threshold curve). Here, each resonator L_0, L_1, L_2, L_3, …L_{11} of a set similar to that in Fig. 2 (a=0.3, b=1, tilt of 2.9°) is arbitrarily assigned a *Q* of 50 derived from multiple reflections between hair cells (the small tilt is introduced to make leftward and rightward facing resonators of slightly different length so that the data points to not superimpose; a 3° tilt is observed in Fig. 39 of Bredberg, 1968). Each member of the set (•) produces a peaked response (like that shown dotted for one representative member; peaks like these can be found whenever multiple reflections give rise to standing waves, such as in organ pipes or plucked strings). The L_0 resonator is assigned a response of 1 at a relative frequency of 1; other longer resonators act at progressively lower frequencies corresponding to the inverse of the cavity length (that is, the X-axis is simply the inverse of the cavity length). The Y-axis response is given as $k \exp(-L)*(1/L^2)$, where *k* is a normalising factor (2.73) and *L* is the cavity length. The exponential term is a simple expression of attenuation of capillary waves with distance as they travel between one outer hair cell and its partner. The amplifying ability of the hair cell is, for simplicity, taken as constant (that is, independent of the particular resonator in which it acts), meaning that the orientation of the stereociliar arm with respect to the resonator axis is ignored. The negative exponential provides a space constant of about 10 µm, which may be compared to a value of 21–27 µm found by Abnet and Freeman (2000) for vibration attenuation of an isolated tectorial membrane. The second term is introduced to represent circular expansion of the wavefront. The final response envelope is shown as the full curve. Note that notches will inevitably occur between the points – as is frequently observed in cochlear responses and in Fig. 7. Given the simplifying assumptions used, there is excellent agreement with Fig. 7, particularly the general shape of the curve and the range of frequencies that contribute to it.

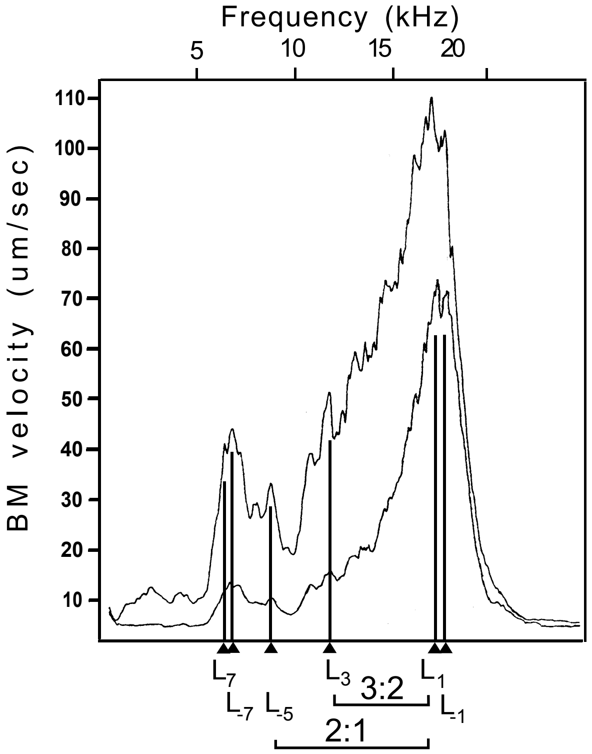

FIG. 7. Peaks in the mechanical response of a guinea pig cochlea match the expected response from an outer hair cell array with $a/b = 0.383$ and tilt of 4°, a value consistent with measurements of micrographs. The response of glass beads to wide-band noise was measured with a laser doppler velocimeter (Nuttall et al., 1997). Note the general reproducibility of peaks, marked with vertical lines, between stimulation at 90 dB SPL (top curve) and 80 dB (bottom). The peak at 17.8 kHz is here assumed to be the resonance associated with the L_{-1} cavity, and that at 17.1 kHz to be the L_1 cavity. Then L_3 (11.6 kHz), L_{-5} (8.7 kHz), L_{-7} (6.7 kHz), and L_7 (6.4 kHz) fall at the positions marked.

(Adapted from Fig. 5 of Nuttall et al. 1997 and used with permission of the authors and Elsevier Science Ltd.)

It was noted earlier that the oblique direction often appears favoured by the stereociliar alignment (e.g., Fig. 5), especially near the apex. If this led to the oblique representing the characteristic frequency at low frequencies, then this would explain why BM and acoustic nerve tunings in this region have less-steep high-frequency slopes (see tuning curves in **Fig. 8** reproduced from Liberman and Mulroy, 1982). In such a case, resonators would be present at frequencies both higher than the CF (resonators shorter than the oblique CF one) and at lower frequencies (the resonators longer than the CF one). Contrast this situation with the higher frequency tuning curves (as modeled) where the shortest resonator is at CF, giving an asymmetrical tuning curve and a very steep high-frequency cutoff. Moreover, at the highest frequencies, stereociliar arms are almost collinear (180˚), so that oblique resonators fail to contribute, explaining the shape of the 7 kHz acoustic nerve recording in Fig. 8. More extensive modeling of the tuning curve, taking account of the extent to which angling of the stereociliar bundles favours certain directions, is required to confirm the details, but as a first step this explanation is the first to give any account of the varied shapes of partition tuning curves.

One other consequence of the characteristic frequency deriving from an oblique alignment is that less variation in surface tension is required from base to apex, since the lowest frequencies would be represented by cavities 2 or 3 times longer than the distance between OHC1 and 3. This means that the instead of a required 600-fold variation in surface tension from base to apex, the actual figure to give a full range of tuning may be just 200:1 or even less.

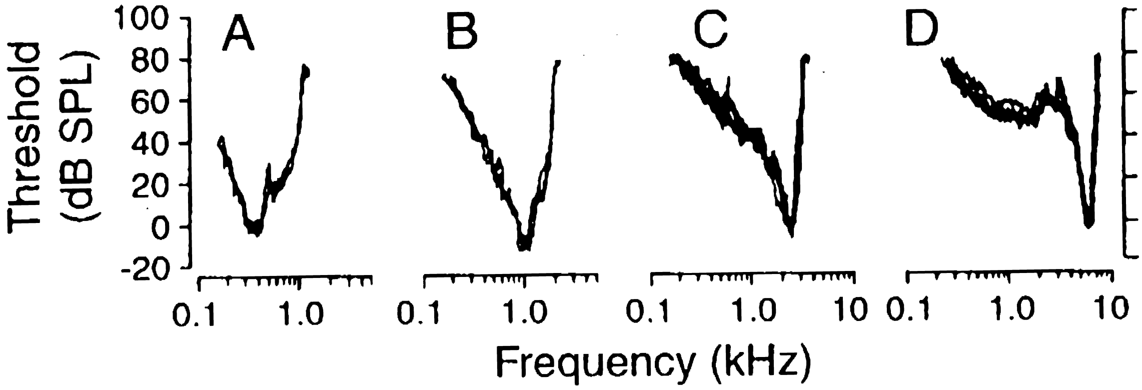

FIG. 8. Acoustic nerve recordings at characteristic frequencies of 0.4, 1, 3, and 7 kHz (from Liberman and Mulroy, 1982, and used with the permission of Lippincott, Williams & Wilkins). Observe the correspondence of the theoretical summation (Fig. 6) with the high-frequency recordings. Note also that if the strongest resonator was an oblique one (e.g., if L_3 was favoured because the angle of the stereocilia 'V' was such that the arm was at right angles to the cavity), then the summation would have a peak at the corresponding frequency and there would be shorter resonators (higher frequencies) adjoining it – meaning that the high frequency slope would be more gentle and show notches, as the 0.4 and 1 kHz curves demonstrate. In fact, near the apex the stereocilia do form more acute angles (Fig. 5c), whereas near the base the V is obtuse, almost 180° (Fig. 5a).

B. Deviations from regularity and SOAEs

There are 4000–5000 sets of OHC 'triplets' ranged along the length of the organ of Corti, each possessing a characteristic frequency and carrying a dozen or more associated frequencies with it. If these banks of oscillators were perfectly placed along the partition, their summed response would be nearly complete cancelation. However, if some irregularity in the frequency–place mapping were to occur, cancelation would be imperfect and certain frequencies would come to dominate (Sutton and Wilson, 1983; Wit *et al.*, 1994). It is therefore no coincidence that humans have both the highest prevalence of spontaneous emissions compared to other animals (Probst *et al.*, 1991) and the most irregular arrangement of outer hair cells (Bredberg, 1968; Lonsbury-Martin *et al.*, 1988), often possessing extra or missing cells. A link between these two facts has already been suggested (Manley, 1983).

In terms of this hypothesis, it means that a centre of energetic activity, which gives rise to a discrete set of SOAEs, can arise as much from a gap as from a supernumary cell.

C. Origin of cochlear distortion

The micromechanical model so far described calls for an array of active resonant cavities stretching from one end of the cochlea to the other, with the tuning governed by the graded propagation speed of a transverse wave in the tectorial membrane. The resonance of the strongest-resonating cavity (typically L_0 or L_1 at mid and high frequencies), can be associated with the 'characteristic frequency' or tuning tip of the cochlear partition at a certain point. There are some 400 OHCs (140 radial resonators) per millimeter, and between 1 and 2 kHz, where the ear is most sensitive and SOAEs are most prevalent, the number of radial resonators corresponds to a step size of about 2 Hz per cavity. The observed bandwidth of an SOAE at that frequency is typically 1–5 Hz (Kemp, 1981), suggesting that an SOAE could be the result of just one OHC cavity.

But as well as this primary resonance, each cavity carries with it a set of oblique resonators, some pointing towards the base and some towards the apex, which bear relationships to the primary of (typically) 1.06, 1.22, 1.44, 1.71, 2.00…. When the L_0 cavity is energised, it cannot help but excite associated oblique resonators (and vice versa) because they have hair cells in common. As a rough analogy, whereas a piano normally has three equally tuned strings per struck note, each 'note' of the cochlear piano appears to possess a handful of strings tuned over at least an octave. Such a configuration has obvious implications for detection of ratios in tonal complexes and for music in general, but at this juncture the possibilities are only pointed to.

An arrangement of adjoining resonators with hair cells in common renders the cochlea naturally liable to high levels of intermodulation distortion. The 'essential non-linearity' of the cochlea, in which distortion can be detected even at the lowest stimulus levels (Goldstein, 1967), may be seen as distortion remaining at the intrinsic idling levels of the active resonators. The proximity in frequency from the CF resonator to its neighbours also defines the width of the cochlear tuning curve at that point, and hence would also closely relate to the frequency-resolving capability of the ear – its critical band (Scharf, 1970).

The intrinsic linking of resonators also suggests that when an SOAE arises in one cavity, it is likely to generate other (weaker) SOAEs in neighbouring cavities. This process would explain the occurrence of linked bistable emissions (Burns *et al.*, 1984), many of which appear at a ratio of about 1.06 (see **Table 3**).

This picture allows stimulus-frequency emissions (SFOAEs) to be viewed as a case of entrainment to an external tone by a number of cochlear resonators matching the tone in frequency. The signal in the ear canal will be the sum of all the contributing resonators, which will include not only the L_0 resonator at its characteristic place but also oblique resonators at other (more basal) locations that match the frequency of the incoming tone. The phases between all these contributions will vary, and so the summed response detectable in the ear canal will be complex (although stable and repeatable) as observed. In a similar fashion, distortion-product OAEs can be considered as the interaction of two stimulus-frequency emissions. Harris *et al.* (1989) found that distortion reaches a maximum for f2/f1 ratios of 1.22–1.25, and that sharp notches occurred at particular ratios; these ratios depend on the subject, but it is noteworthy that certain values close to those listed in column 2 of Table 2 – 1.03, 1.06, 1.14, and 1.19 – recur in their results. (For example, in their Fig. 5, we see that at 4 kHz, the right ear of the subject has successive dips in distortion at ratios of 1.03, 1.07, 1.15, 1.22, 1.32, and 1.41). One interpretation is that distortion is at a minimum when two tones can excite two readily coupled sympathetic resonators – one the strong L_0 or L_1 resonator and the other one of its allied resonators. On this picture, distortion occurs at one particular place on the partition; there is no 'traveling of the distortion product to the site of its primary' as present accounts of distortion generation suggest.

It is significant that interactions between emissions take place via resonators that are always longer (lower in frequency) than the characteristic frequency. Audiological texts describe how combination tones (involving non-linear interaction of two primary tones in the cochlea) are audible as difference frequencies (such as 2f1–f2) but sum tones (f1+f2, for example) are never heard; the paradox is that a non-linearity should generate both types (de Boer, 1984). An explanation lies in seeing that interaction between the two primaries at one point on the partition can only occur via longer (lower frequency) cavities, which allows the difference tones to physically excite a resonator, but there are no equivalent shorter resonators (higher in frequency) to carry the sum tones.

D. The gel as a delay line: evoked emissions

The resonant cavity construction also accounts for that other enigmatic phenomenon arising from an active cochlea, evoked otoacoustic emissions.

When a sound burst is conveyed to the ear, a delayed form of it, a 'Kemp echo', can be recorded some time later (Kemp, 1978). A key property of this echo is that the delay is surprisingly large, typically 7 ms or 10–15 cycles (Wilson, 1980a). It is difficult to accommodate this delay as that incurred by the delay of a traveling wave in the forward and reverse directions (O'Mahoney and Kemp, 1995). Significantly, the echo sometimes recirculates, with a fixed cycle time of some 6 ms (7.4 periods in one clear instance; Wit and Ritsma, 1980). Although the envelope delay changes with stimulus intensity, the wave delay remains constant (Wilson, 1980a).

Looking at **Fig. 9**, the incoming compressional wave in the cochlear fluids can be pictured as immediately stimulating the resonant cavity at the edge of the tectorial membrane. However, energy emerging from the cavity would first pass the inner hair cells and then continue on towards the inner edge of the tectorial membrane. There it would encounter a sharp edge where the TM overlies the space of the inner spiral sulcus, and a wave encountering this discontinuity would be reflected back to its source. In this way, re-excitation of the cavity could occur, leading to repeated echoes. Note that the distance from OHC 1 to the limbal edge is about 5 cavity lengths, giving the right round-trip delay (about

10 cycles). Again the slow wave speed in the TM has been called upon, this time to produce a delay line.

IV. A SECOND MECHANISM AT HIGHER SOUND PRESSURE LEVELS – SKETCH FOR THE ORIGIN OF THE TRAVELING WAVE

What is the purpose of having a sharp lip from which waves can be reflected? It is suggested in the companion paper (Bell, 2001) that reflections from the vestibular lip, and the associated 10-cyle delay in the acoustic signal, would create a convolved signal above the IHC, similar to the way in which SAW resonators are configured as convolvers. This may have a role in detecting correlations in sound processing, particularly in speech analysis where autocorrelations are sought. But since the cochlear amplifier saturates gracefully at 60–80 dB SPL, what happens above that level? It is unlikely that the correlation process would act differently at high and low SPLs. Putting the question another way, what is the function of the vestibular lip at moderately high sound pressure levels? Why is there a sharp lip and not a diffuse bulge, like the marginal band, to absorb excess energy?

A possible answer is that the sharp lip is ideal for *generating* ripples. When sound enters the cochlea, differential forces act across the partition, and these will tend to move the partition bodily up and down. However, at low SPLs, this movement will be small, much less than the amplitude of ripples generated on the underside of the TM by the SAW resonator's response to common-mode pressure. However, at about 60 dB SPL, a level where the cochlear amplifier reaches its limit, the two amplitudes will be commensurate, and at yet higher intensities the differential-force-driven movement will dominate. Such a movement will cause ripples to be generated at the vestibular lip, which will then travel towards the IHC, reaching them with about a 3–5 cycle delay (depending on the physical dimensions of the TM at the frequency concerned).

So in addition to the frequency-analysing cochlear amplifier at low SPLs which sends ripples towards the IHC, there is also a high-level mechanism sending ripples towards the IHC from the opposite direction. The first mechanism, involving the SAW resonator, is sensitive and highly tuned, and creates localized undulations; the second, involving whole-scale up and down movement over a wide area, will be less sensitive and broadly tuned, peaking at the frequency where the mass and compliance of the TM match. Single-point experimental observations of the partition will, of course, be unable to distinguish the two, and a compressive input–output curve will be recorded.

Consider a high-level acoustic impulse entering the cochlea: it will generate acoustic forces across the TM and simultaneously launch ripples from the length of the vestibular lip. The ripples will undergo a several cycle delay before they reach the IHC, the high-frequency IHCs at the base will be stimulated first, followed by successively lower frequencies until the apical IHCs are stimulated. Viewed from outside the cochlea, it appears that a wavefront travels from the base to the apex. This fits the description of a traveling wave.

The origins of this traveling wave are somewhat different than normally considered. In this case, the TW energy is not carried by the hydrodynamics of the cochlear fluid but by energy in the surface tension of the ripples. At each cross-section of the TM we will see a ripple front progressing, although looked at from above there will appear to be oblique wave-fronts moving from base to apex. However, this wave in itself will carry no energy, and is thus appropriately labeled epiphenomenal.

The cochlear amplifier and its SAW mechanism can be classed as pure resonance in that energy is accumulated cycle by cycle – like an organ pipe with sound waves propagating in the pipe from one end to the other in a cyclic manner. However, the second higher-level mechanism is based on unidirectional progressing ripples, and these wave fronts are obviously traveling waves. From this perspective, we have a resonance phenomenon at low levels acting in concert with a traveling wave mechanism at higher levels. The two long-standing theories of the cochlea are not mutually exclusive: both theories play a part in performing frequency analysis, but at different intensities.

A. Reinterpreting the traveling wave

The picture set out above reinterprets the traveling wave in terms of TM ripples, not scala eddies and similar hydrodynamic phenomena (Tonndorf, 1973). That difference in itself is not fundamental for the traveling wave theory as currently understood, in that ideas of scala fluid behaviour are largely theoretical – only the experiments of Olson (1998, 1999) give actual data on how the traveling wave energy is stored. In the main, descriptions of fluid coupling are of a general nature. For example, Allen and Sondhi (1979) call for coupling of fluid motion to the BM, and Nobili *et al.* (1998) describe subtle, instantaneous, long-range hydrodynamic coupling between different BM elements. Olson's experiments are therefore of great interest in that they show that the fluid component of the traveling wave is minimal, confining itself to a layer 15 μm deep adjacent to the BM. More will be said about this result in Section V, but for now it is sufficient to recognize that it is entirely compatible with ripples generated on the partition by OHC activity (at low SPLs) or by vestibular lip ripples (at higher levels).

Most of the experimental studies on the traveling wave propagation have been done at levels above 60 dB SPL, so that the time delays seen in those experiments relate to the higher-level mechanism – the slow propagation time of ripples from the vestibular lip to the IHCs.

B. Consequences of two ripple sources

If the SAW cavity is sending waves towards the IHC in one direction and the vestibular lip is sending waves from the other, then interference of those waves is expected. This interference is offered as the explanation for peak splitting and response notches found in recordings from the auditory nerve, where at 60 dB SPL or so we see virtual cancellation (Lin and Guinan, 2000; Rhode and Recio, 2000).

Peak shifting (or splitting) is a short-hand description of how the phase of a recording from an inner hair cell, or cochlear nerve, favours one particular phase of the stimulus at low intensities but shifts to a different phase, or responds at two separate phases, at higher intensities. A detailed description of peak shifting and splitting can be seen in Fig. 4 of Lin and Guinan (2000), where clear interference of two sources is seen. Response notches are a special case where the two sources are equal and opposite, so that destructive interference occurs.

Again, Lin and Guinan give detailed data, and they note that the responses they observed often "waxed and waned… as if the response were due to the mixing of two excitatory drives of slightly different frequencies" (p. 2623). The authors suppose that " 'tip drive' produces the low-level, long-latency click responses, and the 'tail-drive' produces the high-level, short latency … click responses" (p. 2626), and that the excitation drives represent mechanical drives that are carried over separate physical paths and add at some point. The tectorial membrane is one candidate (among others) that they put forward. No specific physical explanation is available, and they say that "An important implication of our working hypothesis [multiple resonant modes] is that standard cochlear models have serious shortcomings" (p. 2628).

Rhode and Recio (2000) provide further insight into this cancellation process. Their Fig. 11C is a time record of the BM displacement at an interference notch and it shows the interfering waveforms. The time delays between the two interfering sources show up clearly. Thus, at the beginning of the record, in response to a gated pulse, the 11500-Hz signal from the tip drive is seen, after which the signal starts waning as the tail drive signal comes in. The decrease comes after about 6 cycles, which is roughly the difference in path length (measured in wavelengths) between the OHC cavity – IHC path and the vestibular lip – IHC path. Similarly, when the 11500 Hz pulse ends, the tip drive peters out, allowing the tail drive to build in amplitude for another 5 or 6 cycles before it too ceases.

One important consequence arises from having two ripple sources, and this may be best appreciated from the literature on SAW devices, in which the implementation of convolvers is considered. As Kino (1976, p. 728) puts it: "When two surface waves pass each other in opposite directions, it is possible to obtain an output signal at their sum frequency which is an integral of the product of the two signals within the device. This is equivalent to taking the convolution of the two input signals in real time." Translated to the cochlea, that means that the IHC would be capable of detecting the convolution, or autocorrelation, of one signal from the OHC cavity and another delayed signal from the vestibular lip.

V. COROLLARIES OF A RESONANCE THEORY – DISCUSSION

A. Energy flow in the cochlea

When the stapes moves to and fro within the oval window in response to sound, the main effect is to create oscillating pressure within the cochlear fluids. Ever since the first mathematical model of the cochlea was formulated by Peterson and Bogert (1950), this effect has been separated into a common-mode, or 'excess' pressure (P_+), equal on both sides of the partition, and a differential pressure (P_-), which is created by the acoustic impedance of the basilar membrane and helicotrema. The common-mode pressure causes propagation of a compressional acoustic wave – a 'fast' wave – and the differential pressure leads to formation of the traveling wave – a 'slow' wave. Since the traveling wave has been the point of interest, the fast wave has been overlooked. Lighthill (1991) says that the fast wave is "uninteresting… in producing no motion of the cochlear partition. Accordingly, the fast wave becomes quite unimportant and I shall omit any further mention of it."

More recently, studies by Cooper and Rhode (1996) demonstrate that the fast wave has important consequences for cochlear mechanics (particularly if a hole has been drilled in the otic capsule). Experiments by Olson (1998) lead her to state that "the significance of the fast mode … to cochlear mechanics should not be underestimated" (p. 3460). She reports that "the traveling wave pressure is not the only pressure across the [organ of Corti] complex, and, moreover, that it is not always the dominant pressure" (p. 3460).

The fast wave conveys useful information about the environment, and it would make sense for nature to use that signal and not disregard it. Measurements by Dancer and Franke (1980) indicate that in guinea pig cochleas the common-mode pressure can exceed the differential pressure, leading them to state, based on corresponding impedance calculations, that "No decrease of the impedance due to the action of the helicotrema (as predicted by Dallos) is observed" (p. 192). In the context of appreciable common-mode pressure, it is therefore significant that the OHCs are intimately connected to the entire cochlear fluids by the spaces of Nuel, an arrangement that allows OHCs unrestricted access to cochlear input pressure. The OHC are unique in the body for the large fluid spaces surrounding them: all other cellular tissues are arranged with cell bodies touching and minimal contact with extracellular fluid.

This paper proposes that outer hair cells are pressure detectors. The details of the transduction process are given in the accompanying paper. Briefly, OHCs are depicted as piezoelectric transducers which produce voltages when their capacitive membrane wall is squeezed. The transducer currents are amplified, it is suggested, by specially tailored sodium currents, and the amplified voltage causes corresponding length changes. Because OHC2 is out of phase with OHC1/3, a SAW resonator is created which provides tuning and further amplification. The amplified energy is then delivered to the IHCs via ripples on the tectorial membrane.

Transduction therefore involves pressure variations in the cochlea being converted into oscillatory energy of the OHC's cytoskeletal spring (Holley and Ashmore, 1988). For a single OHC, such an oscillation would lack adequate *Q*: nature's answer has been to link OHCs together, via ripples on the tectorial membrane, to produce a cochlear amplifier in the form of a SAW resonator. In this way the system can be highly tuned, displaying high *Q* even in a fluid-filled environment — Gold's "underwater piano". The OHC resonant cavity behaves as a regenerative receiver of oscillating sound pressure, acting like a radio receiver in the cochlea picking up signals broadcast from the transmitter at the oval window.

OHCs sense the oscillating pressure in their environment through their cell bodies. At the lowest SPLs, there is no need for bodily movement of the partition – only localized radial undulations. OHCs are immersed in virtually incompressible fluid, and the otic capsule is composed of the hardest bone in the body, so the rapidly traveling pressure wave creates a uniform, quasi-static pressure field throughout the cochlea. In the same way as pressure causes deformation of the OHCs, the reverse process occurs. Thus, when feedback between the rows of cells causes SOAEs, this activity generates a pressure wave which is transmitted throughout the cochlea, with some passing through the cochlear windows and into the ear canal, where they can be detected with a microphone. This process is identical to the 'hair cell swelling model' of Wilson (1980b), formulated to explain the very small delays between observed mechanical (sound input to the cochlea) and electrical (cochlear microphonic) events. Wilson postulated that the activity of an OHC creates a small change in volume, enough to create small oscillating pressures in the cochlea; this paper recognizes the bi-directional transduction properties of OHCs and supports the hypothesis of hair cell swelling. The degree of swelling is small: Wilson estimates that a swelling of less than 0.01% over a 1-mm segment of the partition is sufficient to give a pressure of 20 dB SPL in the ear canal.

In addition to data presented in Wilson (1980b), there is a range of data showing fast responses in the cochlea to sound stimuli, responses that are too fast to be mediated by a slow TW. Thus, Brown and Kemp (1985) measured delays in the generation of acoustic distortion products in gerbils, and found that many group delays were below 1 ms, some as short as 0.1–0.2 ms (their Figs 2 and 3). They calculate that a one-way traveling wave envelope should take 0.8–1.5 ms for the highest frequency primary (4 kHz) to reach its characteristic place. To explain the fast responses, the authors suggest that "[a] possible alternative to reverse travelling waves, is that the acoustic DP generated could be conducted to the base as fluid borne sound waves impinging on the oval window and resulting in restimulation of the cochlea from the base." Confirmation of this fast response is given by Avan *et al.* (1998) in which they measured the forward and backward travel times of cubic difference tones and found them both to be shorter than 0.2 ms. In comparison, the overall round-trip delay was about five times longer, suggesting that "local filtering processes" – the build-up time of the presumed SAW resonators – produce most of the observed delay. This result is a simple demonstration that the inward stimulus as well is carried by a fast pressure wave.

Another characteristic supporting pressure response of the cochlea are those observations which find that opening the cochlea to examine its behaviour invariably causes a loss of at least 5–10 dB (e.g., Olson, 1998; Nilsen and Russell, 1999). This result has normally been attributed to extreme sensitivity of the cochlea to surgical trauma, but could also be interpreted as loss of pressure due to the drilling of a hole in this pressure vessel.

B. Radial phase variations across the partition

The SAW resonator model predicts that at low SPLs the partition will undergo extensive radial phase changes. **Fig. 9** illustrates that there will be 5 or 6 complete cycles of wave activity on the tectorial membrane from the vestibular lip to the marginal band (reckoning the distance from OHC1 to OHC3 as 1 wavelength). Such considerable phase variations are not predicted by standard traveling wave models.

Evidence from the literature points towards these phase changes. The most clear and remarkable are the measurements made by Nilsen and Russell (1999) on the BM of guinea pigs using a 5 µm spot from a laser diode. **Fig. 10** shows the wide phase variations they measured from two animals, a result that the authors suggested may be due to rotation of the

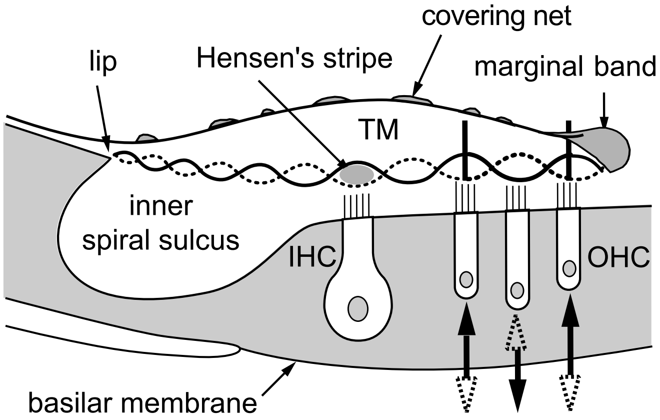

FIG. 9. Radial cross-section of the tectorial membrane showing excitation of the resonant cavity between the rows of outer hair cells. Most of the energy — propagating as a slow capillary wave — is absorbed at Hensen's stripe, stimulating the inner hair cells. Some continues on towards the lip of the inner sulcus where it is reflected and re-enters the cavity, creating evoked emissions ('Kemp echoes') with about a 10-wave delay. The cycle can repeat, causing reverberation.

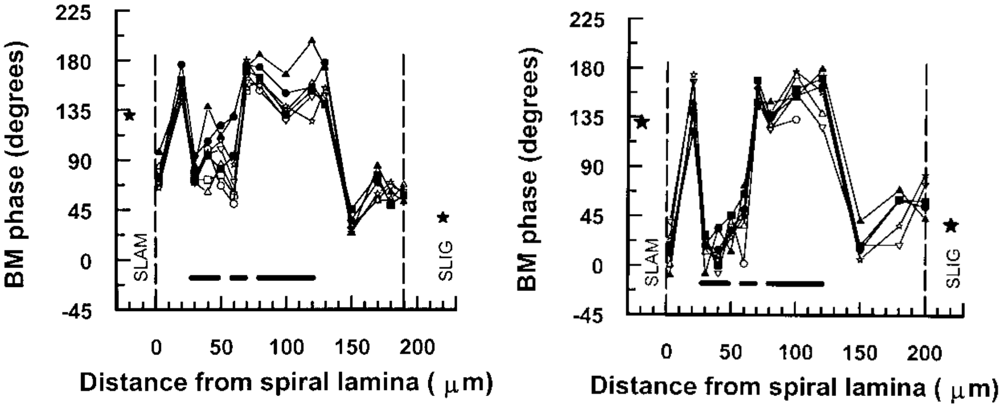

FIG. 10. Rapid phase variations across the basilar membrane of two guinea pigs made by Nilsen and Russell (1999) using a 5 um spot from a laser diode. The phase excursions, which measure up to 180° in the animal at right, are those expected from a SAW resonator model: IHCs in phase with OHC1 and 3, and an out-of-phase response surrounding these points (IHCs at 20-um distance; OHCs above right-most bar). There is even an indication of a dip below OHC2, which the SAW model predicts, but which is difficult to resolve experimentally because the laser spot is directed onto the basilar membrane, and this surface will tend to integrate the response of the three OHCs some distance above. (From Nilsen and Russell, 1999, and used with permission of the authors and *Nature Neuroscience*.)

reticular lamina about the tunnel of Corti. However, the phase excursions, which measure up to 180º, are exactly what we would expect from the SAW resonator: IHC in phase with OHC1 and 3, with an out-of-phase response surrounding these points. There is even an indication of a dip below OHC2, which the SAW model predicts, but which is difficult to resolve experimentally because the laser spot is directed onto the basilar membrane and this surface will tend to integrate the response of the three OHCs some distance above.

Other experimenters have measured radial variations across the BM, but none have seen the detailed phase behaviour recorded by Nilsen and Russell. This is because others used coarser measuring techniques that tended to smear out detail. Thus, whereas OHCs are 7–10 µm in diameter and spaced about 10 µm apart, it is noted that:

- Nuttall et al. (1997) dropped gold-coated glass beads 20 µm in diameter onto the BM to make doppler velocimeter measurements;
- Cooper and Rhode (1996) used 25-µm gold-coated polystyrene beads (some were dropped onto the covering net of the TM, in other experiments onto the BM);
- Reccio et al. (1998) used glass beads 10–30 µm in diameter onto the BM.

The mass of the monitoring beads would also interfere with partition movement in response to OHC movement. Despite these limitations, a number of biphasic responses have been seen. Nuttall *et al.* (1999) noted that, with electric stimulation of the cochlea, the arcuate zone of the BM moved in the opposite direction to that of the pectinate zone.

Electrical stimulation of the cochlea, by the insight it gives into reverse transduction, also sheds light on what is happening with forward transduction. Imposed electrical currents presumably affect the piezoelectric transducer and lead to OHC length changes, which are either detected in the ear canal by a reverse TW process (the conventional interpretation) or by a hair-cell swelling effect (the understanding presented here). Of relevance to the ripple-generation hypothesis, such studies indicate that the reticular lamina moves substantially more than the basilar membrane (Mammano and Ashmore, 1993; Khanna *et al.*, 1989) when the OHCs alternately expand and contract, exerting equal and opposite forces on the reticular lamina and the BM. This work suggests that ripples on the TM are therefore likely to be larger in amplitude than those that potentially might arise from a corresponding process on the BM (if its surface tension and bulk properties permitted – a less likely possibility). Nevertheless, it remains true that the tuning of the partition can be observed from the BM, reflecting the activity of the OHCs above it. In this way, cochlear amplification is clearly expressed at the BM, and in fact BM tuning is very similar to neural tuning (Narayan *et al.*, 1998), although the ripple hypothesis suggests that greater displacement amplitudes are co-occurring on the undersurface of the TM.

A different approach to detecting phase variations across the partition was used by Mountain and Cody (1999) who measured distortion of IHC receptor potentials of IHCs as an indicator of mechanical inputs. They found that the waveform of the IHC receptor potential was complex, suggesting it is the result of two or more inputs to the cell. Noting that all of these inputs are mechanical in nature (based on previous experimental results), the authors raise the possibility, suggested by an explanatory model, that "the OHCs may be driving the IHCs directly over a wide frequency range", and that "the influence of OHC motility on the [reticular laminar] side of the organ of Corti, and therefore on the IHCs, is significantly greater than on the BM side", conclusions supporting the SAW resonator mechanism. In a more general context, the authors cite the earlier (1994) conceptual model of Liberman and Kiang which again called for two out of phase components to explain IHC receptor potentials: "the first component (component I) being more sensitive and more sharply tuned than the second component (component II). [Liberman and Kiang] suggested that component I involves functional coupling between the OHCs and IHCs since this component was absent in cochleas with damaged OHCs." The model used by Mountain and Cody, to which the data were fitted, summed multiple independent pathways of excitation to the IHC hair bundle, and assumed that the pathways represented independent vibrational modes. The first mode, a passive, linear component, is assumed to derive from BM displacement; of particular interest, this mode – which represents the classical TW excitation – is found to have a gain of only 0.008. This minute figure can be interpreted another way: that partition movement is far less significant than OHC motility, or as discussed later, that the resonance theory of hearing is preferred to the TW theory, at least at low SPLs. Mountain and Cody suggest that the low gain may derive from the mechanical isolation of the IHCs from the rest of the organ: from a functional perspective, such an arrangement implies that IHCs are not designed to detect BM displacement at all.

The most direct evidence that radial vibrations are more important than transverse ones are observations of hair cell damage caused by excessive stimulation of the cochlea. A consistent finding is that not all three rows of OHCs are damaged equally (e.g., Stopp, 1982). This finding is hard to reconcile with traveling wave mechanics, but is easier to appreciate if the rows have different set points, such as for turgor pressure, and vibrate with different amplitudes and phases.

C. Diplacusis echotica: Justification for a very slow propagation speed

This theory calls for very slow propagation speeds in the cochlea. One curious phenomenon – diplacusis echotica, or double hearing – provides a degree of justification for such low speeds. Double hearing is a phenomenon in which subjects complain of hearing both a sound and its echo. It occurs in less than 1 in 500 audiology patients (Götze, 1963) and has been generally overlooked in modern audiology, although it is well recorded in older text books (Urbantschitsch, 1910). Remarkably, the echo occurs as long as ½ to 1 second after the sound (Götze, 1963; Shambaugh, 1940), a delay that appears impossible acoustically unless it is assumed that some longitudinal transmission of energy along the TM can occur. Since the length of the TM in humans is about 30 mm, then with a wave speed of 40 mm/sec or less, delays of the order of 1 second are indeed possible.

Although the phenomenon is not common, it should not be overlooked either, even though current explanations may tend towards peculiar psychophysical activity in the brain. The explanation here is one that could place the phenomenon on a solid audiological footing, and close examination of individuals with double hearing would provide good evidence for the theory presented here.

D. 'V'-shape of OHC stereocilia: ratio detection and musical possibilities

In the context of pianos, one other intriguing aspect of this hypothesis demands attention, and that is the presence of musical ratios. As well as containing the semitone, the cochlear geometry in Fig. 3 contains the octave as the length of L_5:L_0. (Note also in Fig. 7 that L_{-5}:L_1 is close to 2:1 and L_3:L_1 is about 3:2.)

A preliminary examination of the maps of stereociliar position in a monkey (Lonsbury-Martin *et al.*, 1988) shows that the lengths of obliques commonly involve ratios of 2:1 or 3:2 (see Appendix 9 referred to in footnote 1). Note also in Fig. 1 alignments of 0°, 23°, 40°, 52°, and 59° to the radial, giving corresponding lengths of 1.00, 1.09, 1.31, 1.62, and 1.97. Significantly, 1.62/1.09 is close to 3:2, and 1.97/1.00 is nearly 2:1. Similarly, the length ratios seen in the Fig. 5 geometry include, as well as the octave, some other small-integer ratios (e.g., L_4:L_0 = 1.68, close to 5:3; L_2:L_0 = 1.21, close to 5:4; L_6:L_0 = 2.26, close to 9:8).

By adjusting the *a*/*b* ratio, and by tilting the unit lattice a few degrees, it is possible to create many small-integer ratios of musical significance (Appendix 9 and 10 referenced by footnote 1). The question, of course, is whether the ear in fact uses such a scheme — detecting simultaneous excitation in the two arms of an outer hair cell — to detect harmonic ratios. Only extended measurements on hair cell geometries can decide the issue, but if confirmed, it would open a startling new window on music. No doubt Helmholtz would have been delighted to find musical ratios lying hidden within the cochlear geometry.

VI. COMPARISON OF THE RESONANCE THEORY WITH CONVENTIONAL TRAVELING WAVE THEORY

Békésy (1969) drew a simple but apt analogy to differentiate resonance behaviour from traveling waves. He imagined a series of pendulums – bobs hanging from strings of graded length – all attached from a common rod. If the rod is suddenly jerked, the pendulums will all start moving simultaneously, but the bobs at the end will move in such a way that a traveling wave will appear to move from the short pendulum to the longest. That is, delays in a set of graded resonators can be seen as a traveling wave. However, because no energy is transmitted (the resonators are independent), the wave is an epiphenomenon.

Contrast this situation with another, where strings (and small masses) connect the original pendulums. When the rod is jerked, the coupling will ensure that this time energy will be transferred from one pendulum to the next, and a damped traveling wave will ensue. The wave is efficacious (it could bend hairs, for example) because it transfers energy, and this is the model – a ‘true’ traveling wave – that Békésy thought applied most aptly to the cochlea. He set out a criterion for distinguishing resonance from a true traveling wave: “[w]hether or not along the cochlea we have true resonance or a travelling wave is .. determined by how much coupling exists between the adjacent sections along the basilar membrane.”

On this basis, the SAW model that has been developed here is a resonance model, in that the resonating elements are more or less independent (except for their oblique partners), and can accumulate energy from an external source (oscillating acoustic pressure transmitted from the stapes, in fact). A traveling wave of sorts is produced, but this is the epiphenomenal kind. Békésy illustrated another way by which resonance can be distinguished from a traveling wave, and that is to plot the amplitude of vibration against frequency: a resonant system will have a very narrow bandwidth around the resonance frequency, whereas a traveling wave system will display a broad peak. The very narrow bandwidths derived for the cochlea’s low-level responses speak of resonance.

Békésy called attention to Helmholtz’s work, and noted that the cochlea’s sensitivity to amplitude and frequency, but not phase, supports a resonating system, “but unfortunately no mechanical resonating system which was satisfying was found in the cochlea.” In concluding, Békésy notes that “[t]he main reason against such a possibility [true mechanical resonance] is the same as it was 100 years ago, mainly that the sharper a filter action is, the longer the onset and decay time becomes. This is correct for a resonance system or any other type of filter system of pure physical nature.” However, the advantage of the SAW model is that it can build up cycle by cycle, but it can also stop within a cycle by applying what all pianos have: dampers. That is, by rapidly shifting the electrical set point of the OHCs through efferent control, the oscillating cavity can be very quickly halted.

At high intensities of course, the SAW cavity saturates, and the preferred model is that of the traveling wave. The only change to existing TW models suggested by this paper is that the wave propagates by ripples. These ripples propagate in one direction – from the vestibular lip to the IHC – and so they can best be characterized as traveling waves, although of limited spatial extent, carrying energy from one point to the next; they are clearly not resonating. At the same time, it is important to note that vibration energy at a particular point on the partition is not transmitted progressively to the next point. Although the wave appears to propagate along the partition as graded time delays (3 or 4 cycles) come into play, this movement carries no energy from base to apex. All the energy that will excite an IHC is always local, existing at that distance along the partition as surface tension between the vestibular lip and the IHC. Again the term to use for a TW of this kind is epiphenomenal.

Since most studies of TW behaviour have been conducted at higher intensities, there is no argument with the characteristics measured, such as propagation speed. Similarly, it is agreed that differential pressure is the primary cause of this traveling wave. However, it would be inappropriate to apply these characteristics to measurements below about 60 dB SPL, at which a different cochlear mechanism is at work. In fact, one way of confirming the theory presented here would be to measure the speed of the traveling wave both above and below 60 dB: it is predicted that the speed would vary depending on intensity.

In particular, at low intensities, the propagation speed would appear to be unusually fast because the acoustic energy is traveling from the stapes to the SAW cavity at the speed of sound in water (1500 m/s). Some time will elapse as the intensity builds up in the cavity, but the initial response should be almost instantaneous. In fact, such anomalously 'fast' responses have already been seen and referred to in section V-A above.

A. Problems with Existing TW Theory

1. Mass–stiffness ratio

One persistent problem with TW theory is that it requires the combined mass–stiffness of the partition to vary by a factor of 10^6 in order to tune the vibrating elements over a range of 10^3 (that is, 20–20kHz). Even if a restricted frequency range of 300:1 applies (Zhang *et al.*, 1996), that still gives a huge range in stiffness (9×10^4), noting that a factor of 10^4 corresponds to the difference in stiffness between low-density polythene and tungsten (Hubbard and Mountain, 1996).

Békésy (1960) found that the stiffness of a human cochlea varied by only a factor of 100 from base to apex, a result confirmed by Naidu and Mountain (1998) in the gerbil, and prompting them to conclude that "conventional theories that explain cochlear frequency analysis based on an enormous stiffness gradient and simplistic motion of the [organ of Corti] require substantial modification" (p. 130).

In this context, the idea raised earlier of cochlea tuning being controlled by the propagation speed of ripples between rows of OHCs carries the advantage that ripples are dispersive, so that wave speed increases with frequency. This means that the ratio of surface tension between base and apex need only be about 400 : 1 or less.

2. BM on bone

One of the long-standing arguments against the traveling wave theory, related by Hardesty in 1908 and never satisfactorily answered, is that the basilar membrane can be sometimes found in certain specimens to be resting on inflexible bone, even though the hearing faculty is apparently unimpaired, as judged by an anatomically intact organ of Corti. This observation is compatible with ripples emanating from the tectorial membrane, but it weighs against the idea of the basilar membrane as being the frequency-resolving component.

3. Holes in BM

A related argument is that anatomy sometimes reveals that the basilar membrane is perforated, allowing additional connection of the galleries and theoretically preventing propagation of the traveling wave via the basilar membrane. Tonndorf (1959) describes an earlier case where a post mortem found a hole in the BM in the first turn, although before death the subject's hearing was normal at low frequencies. Of course, such findings can still be compatible with the ripple hypothesis by invoking a different hydrodynamics in which tectorial membrane movement generates ripples against the vestibular lip.

B. Other resonance theories

Although the TW has been the dominant theory over recent times, a number of attempts at establishing a resonance theory have been made. The papers of Naftalin (e.g., Naftalin, 1963; 1965, 1970; 1981) and Huxley (1969) are the most prominent, although more recently Dancer and colleagues (Dancer and Franke, 1989; Dancer *et al.*, 1997; Avan *et al.*, 1998; Magnan *et al.*, 1999) have made efforts in this direction.

Naftalin's papers are noteworthy in that they promote a resonance theory at a time when the TW theory enjoyed virtually total support and appeared indomitable; however, the basic argument – that there was insufficient energy at threshold to move the entire organ of Corti and its surrounding fluid – is a compelling one, and is a strong stimulus for devising alternative resonance theories. His theory called for a direct interaction of sound with the tectorial membrane, relying on piezoelectric properties of the membrane itself. Interestingly, he measured low sound propagation speeds in gels (5 m/sec for a compressional wave in gelatine) and noted how this property would compress wavelengths (5 mm in gelatine) and that "[t]his wavelength might be even smaller in the tectorial membrane".

Huxley's paper drew on the spiral nature of the cochlea to identify wave propagation modes that might lead to resonance.

Dancer and Franke (1989), Dancer *et al.* (1997), Avan *et al.* (1998), and Magnan *et al.* (1999) raise the possibility of cochlear resonance on the basis that their measurements of phase delays in guinea pigs gave values of only about half a cycle – comparable to what is expected from a passive resonator. They speculate that the larger delays are due to an "active" process, so that the underlying "passive" mechanics may be resonance, not a traveling wave. However, measurements by others (including Recio *et al.*, 1998) show that passive (dead) cochleas can still produce large phase delays, presumably originating from the activity of the high-level ripples from the vestibular lip. Partial support for Dancer's proposal is given in Olson (1998).

VII. POSSIBLE OBJECTIONS

This paper has introduced the hypothesis that OHCs respond directly to intracochlear pressure as a way of understanding cochlear mechanics at low sound pressure levels, particularly the action of the cochlear amplifier. A number of individual studies have been cited as generally supporting this notion, but there appear to be some that contradict it, and it is necessary to address these.

Perhaps the most important of these is the study of Voss *et al.* (1996) who, by applying controlled acoustic signals to the oval and round windows of cats, investigated whether the pressure difference or the common-mode pressure was the effective stimulus for generating cochlear microphonic potentials. That is, they applied in-phase and out-of-phase signals to the two windows and gauged the effectiveness of each in stimulating the cochlea. A response to a common-mode signal would be an indication that pressure is stimulating cochlear receptors. The results, expressed in terms of common-mode rejection ratio (CMRR), were that the common-mode signal was at least 35 dB less than the difference signal.

This is a large value, although the results suggest that the ratio is not infinite: it is likely that the CMRR is between 25 and 60 dB. However, there are several caveats on this result. The major one is that the experiments involved high SPLs (data in their Fig. 5 cover 90–120 dB, although allowing for the missing middle ear and its 30 dB gain, the comparable levels are 60–90 dB SPL). The only data shown below 80 dB is that for one animal in their Fig. 4, and the graphs show that at these lower intensities strange things are starting to happen, with strong deviations from the expected linear responses. It is a reasonable suspicion that a larger common-mode response may be present at low sound pressure levels. The other reservation concerning this work is that tetrodotoxin (TTX) was used to eliminate interference from compound action potentials. While this pharmacological agent undoubtedly does so, it works by blocking voltage-gated sodium channels, and therefore would also block the fast sodium channel; as the companion paper describes, this channel may facilitate the operation of the cochlear amplifier. It is perhaps significant that the results obtained before TTX are about 5 dB more sensitive than after (their Fig. 9), and that the largest deviations from linearity of round-window potential with sound level were found in measurement sets with no TTX (their Fig. 4). Notably, similar experiments – without TTX – by Wever and Lawrence (1950) returned a CMRR of less than 5 dB at 100 Hz; moreover, even though both the 1950 and 1995 experiments set the cochlear microphonic to a standard 10 µV level, the earlier work found the ears of the same experimental animals (cats) 7–30 dB more sensitive.

A. Compressibility?

The paper of Voss *et al.* also raises the issue of compressibility. Unless the cochlea displays some degree of compressibility, it argues against the idea of OHCs being pressure transducers because every such transducer must possess some compressibility. However, it should be understood that the compression need only be small: quartz is piezoelectric even though its bulk modulus is very large; similarly, the calculations of Wilson (1980b) show that a hair cell compressibility of 0.01% over a small length of the partition is adequate to explain SOAEs.

If the cochlear contents are incompressible, the volume velocities of the two windows must be equal and opposite. On the other hand, if we assume that the cochlear receptors confer some compressibility to the cochlea, then the volume velocity of the input (the oval window) will be larger than the output (the round window). Shera and Zweig (1992) endeavoured to set an upper bound on cochlea compressibility based on volume velocity considerations, and came to the conclusion that the cochlea does indeed possess a small degree of compressibility: a value of about 1% (differential impedance divided by common-mode impedance) gave the best fit to the data, or expressed in other terms, that the volume velocity of the oval window is 0.2 dB greater than that of the round window. The authors make the point that the values could not be zero otherwise people lacking middle ears could not hear at all. But such people do, albeit with elevated thresholds. This result confirms Békésy's original investigations (Békésy, 1960) of the hearing abilities of subjects lacking middle ears. Similarly, blocking the round window does not appear to impair hearing abilities to a large degree (Kostelijk, 1950; p. 69, p. 154), a result that is hard to square with no common-mode response.

An interesting finding of Békésy's was that the person lacking middle ears hears a sound with a phase difference of 180° to normal (Békésy, 1960; p. 107). If it is assumed that the subject is hearing using the cochlear amplifier mechanism (via ripples from the OHC cavity), whereas a normal subject will use the traveling wave mechanism (ripples from the vestibular lip), then the observation is compatible with the half-wavelength phase difference of these sources at the IHC which allows them to destructively interfere – the origin of the interference notches at about 60 dB SPL. A prediction of this paper is that the 180° phase difference would disappear if the normal person were tested at low SPLs.

Kringlebotn (1995) also provides evidence for compressibility, even though the intent is to demonstrate the opposite. The author measured the volume velocity between the oval and round windows in isolated ears of eight pigs and one human temporal bone. Data for the human specimen gave a volume velocity of the round window some 3 dB less than that of the oval window (larger than the 0.2 dB of Sera and Zweig, 1992, and corresponding to a round window volume displacement only 60–70% of the oval window's). An earlier study again gave, for the best 20 out of 68 human specimens studied, a ratio near 3 dB. The results for the pig ears gave values for which the error bars mostly encompassed zero; the two exceptions (for 0.1 and 1 kHz) returned values (about 1 dB) in favour of the oval window. Taken together, most studies show a predominance towards the oval window, which is what is expected from compressibility in the cochlea.

Microscopic studies on individual OHCs also show that some compressibility is possible. Zenner *et al.* (1992) saw volume changes of 1.8–2.0% in an OHC when a pressure of 98 Pa was applied, but it is not clear whether the changes were due to osmotic effects over time or measurement errors (Gitter *et al.*, 1993). Even allowing for osmotic effects, the model of Ratnanather *et al.* (1993) led them to the conclusion that if μ/K (the shear modulus divided by the area modulus) is 0.1–0.2 then the OHC wall is not incompressible, and resported values for this ratio fall in this range (Ratnanather et al., 1993, give a value of 0.1; Adachi et al., 2000, provide a value of about 0.15). The layered structure of the subsurface cisterns in the cell wall would be one place that non-aqueous compressible material, such as a lipid, could reside; another candidate could be the associated Hensen body which has a pressure-sensor-like construction of layers surrounding a wide cistern.

VIII. ADDITIONAL REFINEMENTS

There are a number of ideas which, although not necessary for the functioning of a SAW resonator in the cochlea, would help it to operate more efficiently.

1. Helicotrema impedance

The impedance of the helicotrema is a factor in determining the relative sizes of the P+ and P– components of cochlear pressure. The P+ is the component that leads to the propagation of the fast pressure wave throughout the cochlea, and it is this pressure to which the OHCs respond. The conventional traveling wave theory supposes that the narrow bore of the helicotrema makes its acoustic impedance high, so that it acts like an acoustic plug, preventing acoustic pressure from equilibrating throughout the cochlea except at low frequencies. It is presumed to act as an inductor that only lets frequencies below about 100 Hz to pass.

From the point of view of pressure detection, however, it would help if the acoustic impedance of the helicotrema were lower than normally supposed in the TW theory, so that a uniform pressure field could be readily established at acoustic frequencies.

In this regard, no direct measurements of the acoustic impedance of the helicotrema have been made. There are some inferences from interspecies comparisons (Dallos, 1970) where low-frequency responses appeared to decrease as the size of the helicotrema narrowed. However, Dancer and Franke (1980) cast doubt on this interpretation in that their data show that the cochlear impedance does not appear to show any drop at frequencies as low as 30 Hz.

From measurements of the relative size of the helicotrema, however, it is a reasonable supposition that its acoustic impedance is relatively low, that is, it acts like an acoustic short circuit rather than an inductor. According to Békésy (1960, p. 435), the helicotrema has a cross-sectional area of about 0.4 mm^2, joining two galleries that each have a cross-sectional area of about 1.2 mm^2. The cut-off frequency for this arrangement is unknown, but it would seem that a short pipe having a cross-section one-quarter of the sections it joins (each having close to zero impedance), must be very close to zero as well. The volume velocity in the cochlea due to movement of the stapes is extremely small near threshold: the displacements are sub-nanometre and the pressures (after gain of the middle-ear transformer) are less than 1 mPa. For such tiny pressures and flows, even at mid-frequencies, even a small leak is likely to dissipate the pressure, and so treating the helicotrema as a short circuit may be appropriate.

2. Impedance of TM vs BM

The acoustic forces are generated across the TM, rather than the BM, for the following reason. (Of course, depending on the impedance of the BM and the helicotrema, some force will also be generated across the BM, as the conventional TW theory requires, but these forces are likely to be less than across the TM.) The TM is a gel with peculiar physical properties; its special moduli of elasticity mean that the speed of sound in the gel is appreciably different to the speed in water. The TM therefore has appreciable acoustic impedance: sound 'sees' the gel and is reflected off it, generating acoustic forces. That is, the TM behaves very much like the BM is supposed to. Moreover, the cross-section of the TM increases appreciably from base to apex, so that its resonance frequency will similarly range from high to low. If the frequency map generated in this way is half an octave lower than the map created by the SAW resonators, many cochlear properties, including the 'half-octave shift' (McFadden, 1986) fall together coherently. A number of papers have called for the TM to be tuned half an octave below the characteristic frequency (e.g., Brown et al., 1992).

If the conjecture about high level ripples is correct, then the focus of cochlear mechanics shifts from the BM to the TM. The BM is essentially fluid-filled cells, and therefore its acoustic impedance must approximate that of water. Like a thin veil floating in a swimming pool, sound waves pass straight through without generating acoustic forces. The standard formulation of the TW theory relies on the acoustic impedance of the helicotrema being high, forcing the BM, as a boundary, to respond with a displacement.

In this situation, differential pressure across the partition only becomes significant when sound pressure levels rise, or when a hole is drilled in the cochlea wall to create a pressure release point or impedance ground. Békésy's experiments were done with the cochlea wide open, and his models were built with a rubber membrane having water on one side and air on the other, allowing the impedance of the membrane to show up. But with the membrane floating in the middle of a fluid-filled capsule, its acoustic impedance will be imperceptible and the membrane will become acoustically invisible.

3. Mode of ripple generation

The assumption has been made that differential forces across the partition cause it to move and down, a movement that launches ripples from the vestibular lip. In the light of recent acoustical findings, an alternative mechanism can be considered. Stinson and Daigle (1997) observed that surface waves can form at an impedance discontinuity, in their case sound over snow, but it is a process that would be expected to take place at the surface of the tectorial membrane as the compressional wave traversed the cochlea. The compressional wave travels at 1500 m/s, so during the half-period of a 1 kHz displacement of the stapes, the wave will traverse the 30 mm long spiral of the cochlea 25 times. Like wind blowing over the flat surface of a lake, this excitation would produce waves on the tectorial membrane. The attraction of this mechanism is that the spiral shape of the cochlea will mean that the wave will interact with the TM at grazing incidence, accentuating the effect.

4. Impedance of RW

Of course, this discussion assumes that the round window membrane is not an acoustic ground, as often presented, but requires some force to stretch. This assumption will be considered later, but for now it is sufficient to say that the impedance of this membrane is enough to allow compression of the OHC, which must accompany every transducer, to take place. Experimentally, the impedance of the cochlea is resistive, not compliance-dominated as the conventional view of the TW mechanics would imply.

5. Phase plateaus

One distinctive property of the traveling wave, which is difficult to explain, is that the phase delay steadily increases with frequency until at some point just beyond the characteristic frequency it suddenly reaches a plateau of about 3 or 4 cycles (Robles *et al.*, 1986; Olson, 1998). Beyond that frequency, the phase delay remains constant. It does appear significant that the plateau often occurs at a delay of 3½–4 cycles and that this is the approximate distance in wavelengths between the vestibular lip and the IHC. However, the phase behaviour is often more complex, and cannot be always explained that simply.

Nevertheless, with a general lack of theoretical treatment of the plateau, this new perspective could be illuminating.

IX. GENERAL DISCUSSION

This paper began by deriving a physical mechanism that would explain SOAEs. Its starting point was that those faint tones were the continuous ringing of the ear's (somewhat overactive) resonant elements. Once the elements are identified as the reverberation between adjacent rows of hair cells, many previously puzzling phenomena have a natural explanation: the shape of the physical tuning curve of the cochlea (with its steep high-frequency slope and gently sloping tail); cochlear 'echoes' (when a sound is introduced to the cochlea, a tiny echo comes back a short time later); and even the occurrence of musical ratios in the spacing of hair cells.

An incidental outcome of this new theory of how the ear works is that it reinstates the resonance model of hearing proposed by Helmholtz last century. The resonating elements, however, are not physical fibres, as Helmholtz thought, but reverberation between rows of outer hair cells, which both detect, and generate, ripples on the surface of the gelatinous tectorial membrane in response to incoming sound. Our eye can perceive sound by noting the pattern of ripples produced on the surface of a tray of water sitting on top of a loudspeaker; in a similar way, the ear can detect sound by sensing the ripples induced on the surface of a gelatinous 'pond' in the inner ear called the tectorial membrane.

Sitting on a cliff-top, Helmholtz too was intrigued by the motion of waves beneath him (Helmholtz, 1873), describing it as "an instructive spectacle, which I have never been able to view without a certain degree of physico-scientific delight, because it displays to the bodily eye, on the surface of water, what otherwise could only be recognized by the mind's eye of the mathematical thinker in a mass of air traversed in all directions by waves of sound" (p. 78). The pattern of waves he refers to includes "a system of circular waves" generated perhaps by "a bird of prey darting after a fish" (p. 78). Later (p. 79) he notes that although the similar spectacle of waves in air "is veiled from the material eye, we have another bodily organ, the ear, specially adapted to reveal it to us. This analyses the interdigitation of the waves."

Helmholtz then goes on to describe the power of sympathetic resonance, so that "In the same way that a mere boy [can] swing a heavy bell, the tremours of light and mobile air suffice to set in motion the heavy and solid mass of steel contained in a tuning-fork" (p. 81). Finally, he comes to anatomy, and conjectures that "[t]he process which actually goes on in our ear is probably very like [the resonance process] just described" (p. 83). He then goes on to discuss anatomically what may be resonating, settling (on this occasion) on the arches of Corti "lying orderly beside each other, like the keys of a piano" (p. 84).

The SAW resonator model developed here fulfils Helmholtz's quest for resonant elements in the ear. That these elements resemble a self-sustaining tuning fork, an electromagnetically driven version of which he built and described (Fig. 33 of Helmholtz, 1875), would no doubt have appealed to him. The hypothesis also satisfies Gold's demand for some type of regenerative receiver in the cochlea. Gold knew in 1947 that one would not wish to put a 'detector' — that is, a nerve fibre — right at the front end of a receiver (Gold, 1989), and this hypothesis clearly separates the regenerative stage (the outer hair cells) from the detector stage (the inner hair cells).

This hypothesis has identified two separate processes leading to stimulation of the IHCs. One is a description of the cochlear amplifier (process one), which operates at low sound pressure levels, and the other is a description of the higher-level traveling wave mechanism (process two). The companion paper (Bell, 2001) gives a detailed account of process one; details of process two are only sketched here, and are left to further investigation.

This paper, and its companion, are based on existing evidence available in the literature, and they aim to synthesize the evidence in a coherent way. There are no obvious contradictions with known findings, although the SAW model does call for special properties of the tectorial membrane. In its favour, the model gives a detailed account of the physical mechanism involved in the generation of SOAEs and at the same time provides a comprehensive description of basic cochlear mechanics. Two of the theory's strengths are its ability to explain cochlear tuning curves, as well as the rapid phase variations across the basilar membrane seen by Nilsen and Russell (1999).

Extrapolating from insights gained from the resonance theory, another ripple-based mechanism was identified at SPLs beyond 60–80 dB. This process depends on movement of the TM generated by differential pressure, and in fact shares many of the properties ascribed to the conventional TW. Since the experiments of Békésy, auditory science has assumed that the TW is the mechanism by which the hair cells receive their stimulation. This paper re-formulates the mechanism in terms of ripples rather than hydromechanical eddies, but the essential features and properties of the TW as formulated by Békésy remain, except that the core frequency-resolving component of the partition is the tectorial membrane, not the basilar membrane. Indeed, the new theory sees the movement of the basilar membrane on which the hair cells sit as a mechanism for *damping* excessive response of the detectors so that their sensing elements (the hair-like stereocilia) are not broken, a proposal made by Braun (1994).

An illuminating perspective on the mode of energy transfer in the traveling wave is given in Wever *et al.* (1954), a paper co-authored by Békésy and the two major proponents, Wever and Lawrence, of the "fluid hypothesis" – that the energy in the traveling wave is carried by energy passing from the stapes directly through the fluid to the membrane. Wever and Lawrence were long-term opponents of the "membrane hypothesis", in which the stapes is said to inject energy through the fluid in its immediate vicinity to the basal end of the basilar membrane, after which the 'flicked rope' effect begins, and the energy travels along the membrane until it reaches its characteristic place. Most modern descriptions of the traveling wave seem to integrate the two (e.g., Patuzzi, 1996; Allen and Sondhi, 1979; Allen, 1980; Nobili *et al.*, 1998), calling for the stiffness of the partition to couple with the inertia of the fluid.

Békésy's position regarding the fluid and membrane hypotheses, as outlined in the 1954 contribution, was agnostic. "Békésy did not consider that his visual observations [of a traveling wave] gave any decisive evidence on the paths of energy flow in the cochlea, and therefore he has not taken any position of this issue." The authors agreed that the term 'traveling wave' simply indicates "a temporal pattern of motion" and that "nothing is implied about the underlying causes."

As mentioned earlier, the hydromechanics of the TW have largely escaped experimental investigation. A notable exception is the study of Olson (1999), who found that the depth of fluid associated with the traveling wave on the BM was very small. Using miniature pressure probes inserted next to the BM, she found that the ‘penetration depth’ (the distance from the partition where the fluid velocity falls by a factor of *e*) was just 15 µm. This minute distance is, as Olson notes, “a distance less than one-tenth the width of the partition and smaller than the length of a hair cell” (p. 528), and more in line with the membrane hypothesis than the fluid hypothesis. It seems hard to understand how this tiny mass can couple to the stiffness of the partition throughout its length and carry all the acoustic energy from end to end.

Thus, the closer we look at the TW, the more tenuous it becomes. Together with Olson’s studies confining it to a 15-µm layer, the work of Russell and Nilsen (1997) localizes it to a narrow segment involving only a handful of active hair cells. The latter authors used a laser diode interferometer with a 10 µm spot to measure the basilar membrane responses of guinea pigs to a 15 kHz tone and found that amplification of the tone was confined to a remarkably narrow segment: some 1.25 mm “vibrat[ing] in unison” (p. 2662) for levels between 35 and 55 dB SPL. For 15 dB SPL, the region shrank to just 0.15 mm or just 18 OHC resonators. At 0 dB SPL, one can assume excitation of perhaps only a single resonator. Such a narrow response, with no sign of preceding basal activity, is what one expects to see from resonance. For TW theory, this finding is unsettling, for unless the TW passes through an active region on its way to CF, viscous damping will dissipate it.

Both of the above observations sit more comfortably within a resonance picture. Olson (1999) found that the penetration depth did not vary with frequency, and says that “[t]he insensitivity of the penetration depth to frequency is remarkable, particularly when interpreted with respect to cochlear models [in which] the penetration depth is expected to depend on wavelength” (p. 528). However, the Olson results are readily interpreted as measurements of the near-field displacements of active pressure sources (the OHCs expanding and contracting in response to intracochlear pressure). A distinguishing feature of near-field displacements is that they are independent of frequency (van Bergeijk, 1964). For an oscillating sphere, the near-field displacement falls off as $1/r^2$, and $1/r$ for a line source. An exponent between these cases would be appropriate for a traveling localized peak of activity, and in fact Olson finds that the particle velocity falls off as $1/r^{1.3}$. Thus, it is suggested that the "compressive pressure" that Olson (1998) measured is the effective stimulus for the OHCs, and the associated "traveling wave pressure" is the near-field effect of the OHCs' amplified response.

The ripple hypothesis, in both its low-level and high-level aspects, should be classified as a fluid hypothesis. The high-level mechanism describes a process where energy from the stapes at a particular frequency is transferred directly via the fluid to that section of the tectorial membrane where mass and compliance match, and at that instant a ripple is generated at the vestibular lip; a few wave periods later, the ripple reaches the IHC. From an outside perspective, a traveling wave appears to be moving along the partition from base to apex, but that is only a "temporal pattern".

The presence of a second hair cell stimulus at low SPLs is the novel idea propounded here. The logic of its presence is that it enables a SAW mechanism to operate in response to common mode pressure, and allows a feedback mechanism to operate. Békésy conducted his initial experiments at 120–140 dB SPL, and one of the persistent criticisms of his work was that extrapolating such unphysiological levels to lower levels may be misleading. Indeed, the occurrence of a compressive nonlinearity in the cochlea was one of the first clues that the passive TW may not be the complete picture. Thus, Békésy's linear extrapolation to 0 dB, giving a threshold displacement of about 0.1 pm, cannot be sustained. Modern estimates of threshold displacement are about 1000 times greater, about 0.1 nm, due to the action of the cochlear amplifier.

Nevertheless, the energies near threshold are minute: Wit and Ritsma (1983) calculate that the minimum stimulus energy required to disturb an acoustic emission is of the order of 1 eV, a value so small that it could involve the activity of a single molecule. Naftalin's original supposition that there was insufficient energy available to move the whole partition and its surrounding fluids, has considerable force. Such an extreme sensitivity exceeds the thermal limit for a passive resonator (Bialek and Wit, 1984; Bialek and Schweitzer, 1985); only by adopting an active feedback mechanism can this limit be surpassed – indeed they calculate it approaches the quantum limit (about 10^{-18} W). In this context, an advantage of pressure sensitivity (compressibility) is that acoustic energy can be funnelled directly to the hair cells – pressure 'seeks out' the compressible hair cells – without the requirement to move the entire partition. Moreover, the distributed design of the resonator (spread out over three OHCs), and strong attachment of the hair bundle to the tectorial membrane above, minimise the opportunity for thermal noise to produce large amplitude movements, which a free-standing stereocilia would necessarily be subject to.

From studies of the spontaneous emissions (SPOAE) of geckos, Manley *et al.* (1996) suggested that "in lizards, where there is no basilar-membrane traveling wave, … SPOAE are probably derived from a side-to-side movement of the tectorial structure [sallets] driven by directly or indirectly generated movements of the hair-cell bundles" (p. 1598). They speculated that the whole chain of individual sallets is continuously in slight motion, a condition they did not think could apply to the continuous membranes of other species.

Kössl and Vater (1996) proposed "reverberant oscillations" between the TM and BM to account for their observations on bats, although the proposed cavity was thought to be longitudinal, operating between reflection points 20% and 45% from the base. A later paper by Russell and Kössl (1999) elaborated on the concept, and speculated whether the standing wave resonance could be the product of "an acoustic laser" (which is how a SAW resonator operating at acoustic frequencies could be characterised).

A difficulty for the SAW resonator theory is that the gel of the tectorial membrane must have special properties: the compliance, surface tension, or other properties must be such as to support a very low propagation speed of the ripples (or other wave propagation mode), for in this way the microscopic distance involved, some 30 μm, can be tuned to acoustic frequencies. Relevant properties of the tectorial membrane are presently unknown, although one useful indication from Abnert and Freeman (2000) is that the amplitude of vibration imposed at a point on an isolated tectorial membrane decays with a space constant of 20–30 μm, a value not unlike that used in deriving a representation of a cochlear tuning curve (Fig. 4). Nevertheless, further work on surface tension can be done.

It is hoped that this alternative perspective on cochlear mechanics will generate fruitful discussion and experiment.

X. CONCLUSION

This paper speculates that the cochlea may be stimulated by two separate mechanisms. It sees a meeting of the resonance theory of Helmholtz and the traveling wave theory of Békésy, united by the phenomenon of capillary waves (ripples) on the undersurface of the tectorial membrane. The first is the cochlear amplifier which operates at low sound pressure levels to give the ear its exquisite sensitivity and fine tuning. The second arises at higher levels, and involves generation of radial-directed traveling waves as ripples from the vestibular lip, and behaves as a rugged, compressive process that helps give the ear its huge dynamic range.

Békésy's distinction (Békésy, 1969) between resonance and traveling wave in the cochlea was based on the degree of coupling between elements. With no coupling, it is resonance, but with appreciable coupling we get a traveling wave. On this basis, it is clear that mechanism I (the cochlear amplifier) is a resonance phenomenon, with the ripples behaving just like waves propagating to and fro in an organ pipe. Mechanism II is less clear cut: in effect there are a multitude of traveling waves propagating as ripples away from the vestibular lip. The result at the IHCs can only be classed as an apparent traveling wave because there is virtually no energy carried in the longitudinal direction.

This paper therefore seeks only to reinterpret, rather than discard, the traveling wave theory in the light of micromechanical processes in the cochlea. However, the causal power of the traveling wave is downgraded to that of an epiphenomenon, and this hypothesis does seek to discard the hydrodynamical processes – eddies and the like – presently invoked to explain the traveling wave.

Davis (1983) gave a picture of the cochlear amplifier in which the cochlear amplifier's 'horn' rode on top of a traveling wave envelope, a description which is non-committal as to what carries the movement. In this paper, both the horn and the envelope are considered epiphenomenal. At low SPLs, the horn and the TW are one and the same, representing activity in the OHC cavities; at high levels, there are two independent mechanisms: a horn traveling ahead of the TW peak, and the TW itself, which is the merged wavefront generated by a set of ripples launched simultaneously from the vestibular lip. At a single point on the partition, the processes can be appreciated as two ripples, the first emerging from the OHC cavity and a companion one at a corresponding point on the vestibular lip.

The proposal outlined here for reverberant cavities in the cochlea points to how a number of puzzles in auditory theory might be solved, and produces many testable predictions. It offers an alternative view of cochlear mechanics that may prompt a re-evaluation of the near-universal reliance of cochlear theorists on the traveling wave.

ACKNOWLEDGEMENTS

I thank my wife and children for long-standing support. Staff of CSIRO Australia, particularly Ken Hews-Taylor, have provided generous cooperation. This research has benefited from an association over two decades with the Research School of Biological Sciences at the Australian National University. I am grateful to Neville Fletcher, Paul Kolston, and Martin Braun for fruitful dialogue, and acknowledge useful feedback from members of the Auditory and Cochlea e-mail lists. For ethical reasons, this work was conducted without additional animal experimentation.

FOOTNOTE AND REFERENCES

1. Data available on the Web. See Bell (2000), "The Underwater Piano: Revival of the Resonance Theory of Hearing," at http://cogprints.soton.ac.uk/abs/bio/200005001.

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TABLE I. Measurements of outer hair cell unit cells in published micrographs and in tracings of cell positions in the adult human organ of Corti. The first oblique angle was derived by measuring the average longitudinal spacing, a, and radial spacing, b, of hair cells in OHC rows 1 and 3 and taking the arctan of that ratio. Distance a was taken as the average over the number of equi-spaced (no missing or supernumerary cells) cells visible; b was derived by drawing lines by eye through the rows of hair cells and measuring their separation. Reference point on all hair cells was the junction of the two stereocilia arms. Values of arctan a/b cluster near 20°, which also represents the median. Narrow angles originate from the apex and broad ones from the base.

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(*Table I, cont’d*)

author[a]	figure number	location	*a* (µm)	*b* (µm)	*a*/*b*	arctan *a*/*b* (degrees)
Tracings and maps of hair cell positions (cochleograms)						
Retzius (1884)	Fig. 8				0.36 ±0.02	19.7 ±0.7
Bredberg *et al.* (1965)	Fig. 19	base–middle			0.36, 0.37, 0.36, 0.37, 0.37	19.8, 20.1, 19.8, 20.1, 20.1
Bredberg (1968)	Fig. 40	base			0.37 ±0.02	20.1 ±0.7
Micrographs						
Kimura *et al.* (1964)	Figs 3A, 3B	base	7.7	19	0.41, 0.32	22.5, 18.0
Johnsson & Hawkins (1967)	Fig. 10a	base	15	31	0.49	26.3
	Fig. 10b	middle	12	49	0.25	14.2
	Fig. 10c	apex	11	44	0.25	14.2
Bredberg (1968)	Figs 39, 41A, 42			20 (base) –50 (apex)	0.32, 0.45, 0.39	17.9, 24.6, 21.2
Wright (1984)	Figs 1, 2	middle	9.2	35	0.27, 0.37	14.9, 20.1

a) G. Retzius (1884) in G. Bredberg, *Acta Otolaryngol.* Suppl. 236, (1968), p. 41; G. Bredberg, H. Engstrom, H. W. Ades, *Arch. Otolaryng.* 82, 462 (1965); G. Bredberg, *ibid.;* R. S. Kimura, H. F. Schuknecht, I. Sando, *Acta Otolaryngol.* 58, 390 (1964); L.-G. Johnsson and J. E. Hawkins, *Arch. Otolaryng.* 85, 43 (1967); A. Wright, *Hearing Res.* 13, 89 (1984).

TABLE II. Ideal resonant cavity lengths and a simple model of resonator strength. Calculations here are of cavity lengths, corresponding frequencies, and strength of cavity resonance generated by a hair cell lattice in which *a* = 0.3, *b* = 1, and tilt is 2.9°. The cavities are ranked from shortest to longest and are labelled L_n as per the figure. Columns 3 and 4 give the lengths relative to cavity L_0 and L_{-1}, and the reciprocal of these lengths (related to frequency) is shown in square brackets. Figures in **bold** indicate matches to peaks in relative frequency shown in Fig. 4. The final column shows the response of a simple model (plotted in Fig. 6) in which the strength of a cavity resonance depends only on the energy remaining in a wavefront after it has traveled from one end of a cavity to the other (after which it is sensed by the hair cell stereocilia and returned from whence it came by a fixed amplification factor). The wavefront is assumed to undergo two-fold attenuation: once due to viscosity effects (exp –L) in the gel of the tectorial membrane, and again as expansion of the circular wavefront (L^{-2}). The result is a product of these two terms, together with a normalisation factor *k* (2.73).

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(*Table II, cont'd*)

cavity	length (L)	length re $L_0 = 1.001$ [reciprocal length = f]	length re $L_{-1} = 1.0595$	response = $k \exp(-L) * (1/L^2)$
L_0	1.001	1.000		1.00000
L_{+1}	1.031	1.030 [0.97]		0.88818
L_{-1}	1.059	1.058 [**0.95**]	1.000	0.79694
L_{+2}	1.141	1.140 [0.88]	1.077 [0.93]	0.58701
L_{-2}	1.193	1.192 [0.84]	1.126 [0.89]	0.48753
L_{+3}	1.312	1.311 [0.76]	1.239 [0.81]	0.32541
L_{-3}	1.379	1.378 [0.73]	1.302 [**0.77**]	0.26209
L_{+4}	1.524	1.522 [0.66]	1.439 [0.69]	0.16796
L_{-4}	1.601	1.599 [0.63]	1.512 [0.66]	0.13414
L_{+5}	1.761	1.759 [0.57]	1.663 [0.60]	0.08589
L_{-5}	1.845	1.843 [0.54]	1.742 [0.57]	0.06867
L_{+6}	2.016	2.014 [0.50]	1.904 [0.53]	0.04436
L_{-6}	2.103	2.101 [0.48]	1.986 [0.50]	0.03582
L_{+7}	2.281	2.279 [0.44]	2.154 [0.46]	0.02349
L_{-7}	2.371	2.369 [0.42]	2.239 [0.45]	0.01912
L_{+8}	2.554	2.551 [0.39]	2.412 [0.41]	0.01274
L_{-8}	2.646	2.643 [0.38]	2.499 [0.40]	0.01045
L_{+9}	2.832	2.830 [0.35]	2.672 [0.37]	0.00707
L_{-9}	2.926	2.923 [0.34]	2.763 [0.36]	0.00584
L_{+10}	3.115	3.112 [0.32]	2.939 [0.34]	0.00400
L_{-10}	3.210	3.207 [**0.31**]	3.031 [0.33]	0.00332
L_{+11}	3.400	3.397 [0.29]	3.208 [**0.31**]	0.00231

TABLE III. A tabulation of pairs of linked bistable emissions from human subjects shows frequency ratios close to 1.06 (a semitone). This result suggests alternation of neighbouring SOAEs that derive from the shortest OHC cavity and the first oblique cavity.

author[a]	f_1 (Hz)	f_2 (Hz)	f_2/f_1	semits
Keefe et al. (1990)	1595.6	1701.8	1.0666	1.12
	1408.1	1524.1	1.0824	1.37
	1330.6	1410	1.0597	1.00
Wit (1990)	1612	1700	1.0546	0.92
Wilson et al. (1988)	3002 ± 5	3233 ± 5	1.077	1.28
Bell (unpublished)	2165.5 ±0.1	2295.6 ±0.1	1.0601	1.01

a) Keefe, D. H., Burns, E. M., Ling, R. & Laden, B. in *Mechanics and Biophysics of Hearing* (eds Dallos, P., Geisler, C. D., Matthews, J. W., Ruggero, M. A. & Steele, C. R.) 194–201 (Springer-Verlag, Berlin, 1990); Wit, H. P., op. cit. 259–268; Bell, unpublished; Wilson, J. P., Baker, R. J. & Whitehead, M. L. in *Basic Issues in Hearing* (eds Duifhuis, H., Horst, J. W. & Wit, H. P.) 80–87 (Academic Press, London).