Cochlear mechanics without the traveling wave:

the cochlea as a surface acoustic wave resonator

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Abstract:

Current models of the cochlea are almost invariably based on a traveling wave set up on the partition by a pressure difference across it, a von Békésy-style picture in which the pressure common to both sides – the common-mode pressure – is ignored. But here the speculation is made that the sensing elements – the outer hair cells – respond to common-mode pressure in a way that creates reverberating wave activity between the cells and produces an active amplifying system analogous to a surface acoustic wave (SAW) resonator. In particular, the three rows of outer hair cells appear to act like the interdigital electrodes of a SAW resonator so that, through their combined motile responses to intracochlear fluid pressure, they impart slow ripples of very short wavelength – tens of micrometres – to the undersurface of the gelatinous tectorial membrane immediately above. A repeated cycle of sensing ripples and executing motile responses to them creates reverberation between the rows, establishing a virtual resonant cavity with inherent positive feedback, amplification, and high Q – characteristics that underlie the cochlear amplifier. Also emerging naturally from such a local interaction on the partition are spontaneous, evoked, and distortion-product emissions, the profile of the cochlear tuning curve, and, perhaps, even musical properties. Differential pressure is seen to have an effect, but again it is localised. Oscillating differential pressure, at moderate intensities, moves the tectorial membrane up and down, a motion that creates a second ripple source at the point where the jelly-like membrane contacts the hard edge of the vestibular lip. The slow ripples emanating from this interaction produce cycles of delay at the inner hair cell which emulate delays attributed to the conventional traveling wave; moreover, interaction between the two sources provides a straightforward account of peak-splitting and interference notches. Thus, using some novel but not physically unreasonable assumptions, a comprehensive, consistent, and place-specific account of cochlear mechanics – in many ways akin to von Helmholtz's resonance theory of hearing – can be given without recourse to the usual traveling wave.

I. INTRODUCTION

Notwithstanding the immense diversity of cochlear models that have been put forward, almost all current approaches are based on models of a traveling wave as developed by von Békésy (von Békésy, 1964; for reviews focusing on the physics involved see de Boer, 1980, 1984, 1991; Allen, 1980; Patuzzi, 1996).

Traveling wave models have been more or less successful in capturing the major features of cochlear behaviour, but they do experience difficulties in accounting for active behaviour at low sound pressure levels (Kolston, 2000), a region in which the 'cochlear amplifier' (Davis, 1983) is called upon to improve gain and tuning. The basis of the cochlear amplifier is clearly connected with the active properties of outer hair cells (OHCs), but its mode of operation is still the subject of debate. This paper offers a speculative alternative to standard traveling wave theory. Whereas it does not seek to give a systematic critique of traveling wave theory, one striking property of the cochlea is noted: that zero-crossings of its impulse response stay firmly fixed, in the time domain, over almost the entire dynamic range of hearing. On this basis, Shera (2001) concluded that there were contradictions in many, if not most, cochlear models. Likewise, de Boer (2003) noted the difficulty of formulating a satisfactory time-domain model and suggested that "non-causal" factors were at work.

The focus here is to construct a physical interpretation of the cochlear amplifier based on cooperative activity of neighbouring OHCs in response to common-mode pressure, an approach that puts aside the traveling wave and instead draws on resonance for its operation. In brief, this paper

conjectures that the cochlear amplifier functions in a manner analogous to the surface acoustic wave (SAW) resonator familiar in solid-state electronics (Campbell, 1998). The rows of OHCs are the analogue of the interdigital electrodes, and their complementary fast motile responses to intracochlear fluid pressure – alternating rows of in-phase and anti-phase responses – generate slow, short-wavelength surface waves on the tectorial membrane (TM) which are then communicated to nearby inner hair cells (IHCs). The motile response to pressure results from a supposed primary pressure-sensing function of the body of the OHC; their stereocilia are seen as secondary feedback elements: when a ripple is generated by one OHC in response to pressure, a neighbouring OHC can sense it via deflection of its stereocilia, and again a ripple-generating motile response ensues. The process repeats, producing reverberation of ripples between the 'electrodes', a scheme which provides feedback and amplification.

Most of the conjectural model is specified physically, except that the exact form of the slow wave that conveys feedback between the three OHC rows (via the TM) is uncertain, although a surface-borne shear wave of some kind would be most likely. The mechanical properties of the TM are not sufficiently documented to allow exact calculation and mathematical modelling, and this remains a major limitation of the model at this point. Nevertheless, the ability of the model to provide an alternative, consistent, and reasonably complete account of cochlear mechanics – without use of the usual traveling wave – is such as to make an account here worthwhile.

The paper uses as its starting point a marked similarity between the physical construction of the cochlea and that of SAW resonators. If the parallel is accepted, then the behaviour of the cochlea can be predicted from known physical properties of the electronic device. On this basis, the

expected behaviour of the model accords well with the known characteristics of the cochlea, and it reproduces, at least at a descriptive level, major features of cochlear functioning such as properties of spontaneous and evoked otoacoustic emissions and the shape of the cochlear tuning curve.

An elaboration of the model is developed which describes cochlear behaviour at higher intensities (60–80 dB SPL and above), levels where the cochlear amplifier becomes saturated. Here, a second speculation is made: that differential forces become sufficiently large that the amplitude of up-and-down movement of the whole partition exceeds the amplitude of local OHC-generated ripples. However, as will be explained, cochlear mechanics can still be well described without calling on the conventional traveling wave; instead a second, passive, source of ripples can be identified.

In both cases, the ripples are localised and predominantly radial – that is, orthogonal to the direction of the usual von Békésy traveling wave, which is from base to apex.

II. GENERAL DESCRIPTION OF THE MODEL

The model takes as its basis the generally accepted view that OHCs are the underlying active elements of the cochlear amplifier (e.g., Patuzzi, 1996). Since the discovery of OHC motility by Brownell et al. (1985), the puzzle has been to understand how the cells perform amplification with appropriate gain and feedback to produce a sharply tuned system at each point of the cochlear partition. The approach taken here is to invert the usually accepted causal chain: instead of motion of the partition stimulating OHCs, the suggestion is that OHCs are exquisitely sensitive pressure

sensors, so that – through their active pressure-to-movement response to sound-induced intracochlear fluid pressure – they *cause* localised motion of the partition. That is, at sound pressure levels near threshold, OHCs require no partition motion – no traveling wave – in order to be stimulated. Literature-derived evidence for the pressure-sensing ability of OHCs is presented later.

The model now builds on a remarkable fact: in all higher animals, including humans, OHCs lie in three (or more) closely defined rows. An example from a rabbit cochlea is shown in Fig. 1. No explanation has been offered for this regular arrangement. This paper provides a rationale, with the SAW model relying on the precise geometrical arrangement of OHCs into rows, each row effectively forming the interdigital electrode of a SAW resonator. SAW devices are electronic signal-processing modules in which finger-like electrodes are interleaved on the surface of a piezoelectric substrate to create slow electromechanical ripples of wavelength equal to the periodicity of the interdigital electrodes (Fig. 2), and, as will be pointed out, SAW resonators bear a number of other structural similarities with the organ of Corti.

The model is most easily conveyed by reference to Fig. 3, which shows a cross-section of the cochlear partition. The key components are the three rows of OHCs overlain by the gelatinous TM in which the stereociliar tips are embedded. OHCs are motile, and the TM, as a weak gel (Hardesty, 1908; Steel, 1983), may be expected to show low internal rigidity. Indeed, recent measurements by Abnet and Freeman (2000) confirm that the TM is a viscoelastic body with high compliance: point stiffness figures of about 0.2 N/m were measured, values in close agreement with a number of previous investigators (e.g., Zwislocki and Cefaratti, 1989). They conclude that the TM should undergo shear when subject to forces from stereocilia aggregates – although this will depend on

adequate stiffness of the stereocilia and OHC body, and here consensus is lacking. Some researchers believe that the TM is effectively rigid and its function is to provide shear to stereocilia; others believe that the TM is sufficiently soft compared to other cochlear structures that it sustains changes in shape from dynamical interactions with them (He and Dallos, 1999). The SAW model takes the position that elongation and contraction of the OHCs in response to sound has sufficient strength to deform the TM and produce a mechanical wave motion upon its surface. If the response polarity of OHC1 and OHC3 is opposite to that of OHC2, waves with a wavelength equal to the distance between OHC1 and OHC3 (about 30 μm) will be produced.

This implies that, for feedback between the rows to operate at acoustic frequencies, the propagation speed of these waves must be extremely low: for example, a wave will need to travel 30 μm in 1 ms (30 mm/s) to give a 360º phase delay and reverberation at 1 kHz. This speed is not unlike that of capillary waves – ripples of surface tension – on the surface of water (about 80 mm/s), or of shear waves in soft gels (3 m/s and perhaps lower). A discussion of possible wave modes is given in Section VI, but the existence of slow, short-wavelength waves of some sort, herein called ripples, is assumed.

Such ripples provide a ready basis for positive mechanical feedback and amplification in the OHC–TM system. A wavefront expanding circularly from, say, OHC3, can later be sensed by the stereocilia of OHC1, again causing a fast motile response – a length change of the cell body – and creating another circularly expanding wavefront, part of which will now propagate (with increased amplitude) towards the IHCs and another part (similarly amplified) will return to OHC3.

The sensing and amplifying process will repeat, resulting in reverberation between the outermost rows of OHCs. A standing wave will appear between these cells, while a progressive, but attenuating, wave will move towards the IHCs and beyond. It is worth noting that the reverberation process is taken to be just that underlying spontaneous otoacoustic emissions (SOAEs; see Robinette and Glattke, 1997, for reviews) and represents (if the damping is insufficient) the continuous ringing of what could be described as the cochlea's resonant elements.

The physical mechanism outlined above is conceptual, and the precise electrophysiological and force-generating mechanisms are left open at this point. To form a useful hypothesis, however, the key assumptions on which the SAW model is based need to be made explicit. These are:

1. *That the TM has properties conducive to the propagation of slow transverse waves,* either shear waves (Rayleigh waves or bending waves) or capillary (surface tension) waves. Transverse here means at right angles to the direction of propagation – which is predominantly radial – and the waves are called 'ripples' as a simple working description of general vertical and horizontal displacements at the surface of the TM. If the TM is a compliant gel, then ripples of some kind should propagate at low speed. Discussion of possible wave modes and their velocities is presented in Section VI, but recent measurements of the shear modulus of the TM (Abnet and Freeman, 2000) indicate a shear modulus of some 10–20 kPa, from which a bulk shear wave velocity of 3 m/sec or so is expected. This is within 1 or 2 orders of magnitude of that required for the SAW model and, for reasons given in Section VI, the calculated wave speed is considered an overestimate. Nevertheless, the exact wave mode involved is presently unspecified.

2. *That the speed of the waves varies from base to apex in a systematic way, thereby supplying the required tonotopic tuning.* As just indicated, midway along the partition, at a characteristic frequency (CF) of 1 kHz, the wave will need to have a speed of 30 mm/s. But near the base of the cochlea, with a CF of say 10 kHz and a spacing of 20 μm, the necessary speed would be 200 mm/s; in contrast, near the apex of the cochlea where the CF is say 0.1 kHz and the spacing is 50 μm, the corresponding speed would fall to 5 mm/s. Because these values are within an order of magnitude or so of the velocity of surface tension waves on the surface of water, surface tension could be the controlling variable if it could act in a graded way from base to apex. Appreciable surface tension of the TM has already been observed (Hardesty, 1908; Olson, 1998). On the other hand, anatomical studies show that the thickness of the TM increases systematically from base to apex (e.g., Hardesty, 1908). This suggests that bending waves may occur at the base where the thickness is less than one wavelength (OHC1–OHC3) and that shear waves may be important at the apex where the thickness is greater than a wavelength. A continuous variation in wave velocity may be possible if the relevant moduli are suitably graded.
3. *That OHCs are dual sensors, responding instantaneously to both intracochlear fluid pressure (via compression of their cell bodies) and TM ripple amplitude (via deflection of their stereocilia).* Both stimuli cause a change in membrane potential, and this voltage then drives the fast motor in the OHC wall (a process known as electromotility (Evans and Dallos, 1993) which is based on a motor protein called prestin (Zheng et al., 2000)). The pressure sensitivity allows the OHCs to respond virtually instantaneously to common-mode pressure – the fast compressional wave passing into the cochlea at the speed of sound in water (some 1500 m/s) – and avoids reliance on the complicated mechanics of a slow-

moving traveling wave. The stereocilia can be taken to be feedback elements which help in sensing a ripple, and, by providing 'kick back' (Flock, 1988), assist in returning and amplifying a ripple.

4. In proposing that OHCs are pressure sensors (see Bell, 2003), it is recognised that the body of the OHC is constructed in some ways like a pressure vessel in that its walls are relatively rigid and its contents under pressure (Brownell, 1990). An important additional feature is a weak spot – a highly compliant region – in the region of the cuticular pore (Engström et al., 1962) where, developmentally, the kinocilium originally was (strangely, the kinocilium disappears before or soon after birth). This arrangement would, if there were compressible material within, afford detection of pressure at a site where the sensing channels associated with the kinocilium may still reside. It is proposed that the body-sensed pressure signal is actively converted into up-and-down movement of the cells, a motion that creates ripples on the overlying TM. Indeed, it is suggested that the TM's purpose is just this, and its location and properties are perfectly suited to support such a process.
5. To complete the analogy with a SAW resonator, *the response of OHC2 is taken to be in antiphase to OHC1 and OHC3.* This means that when OHC2 elongates (moves up) in response to a rising pressure pulse, the hair cells in flanking rows shorten (move down), and vice versa. This bi-phasic movement makes the generation of short-wavelength ripples on the TM particularly efficient. In keeping with this idea, it is noted that the reticular lamina appears more compliant than the basilar membrane in that the former moves 5–10 times more than the latter when OHCs are electrically stimulated (Mammano and Ashmore, 1993).
6. *IHCs respond directly to ripple energy delivered across the surface of the TM by the combined OHC activity. Below about 60–80 dB SPL, this is where most of the stimulus*

> *energy originates. Above that level, IHCs begin to be stimulated by a passive mechanism, discussed later, which involves whole-scale movement of the partition induced by differential acoustic pressures.* This lack of generalised vertical displacement of the partition below 60–80 dB SPL translates into a statement that the ease with which a traveling wave can be set up, and its role in transferring energy and displacement from base to apex, is less than previously supposed. It also implies that perhaps the basilar membrane has less longitudinal coupling or is more acoustically transparent and that the short-circuiting action of the helicotrema is stronger than has been assumed (Dallos, 1970).

In summary, OHCs are seen as piezoelectrically driven motors, effectively converting the common-mode intracochlear pressure (not differential pressure across the partition as required by traveling wave theory) into surface acoustic waves on the undersurface of the TM. Once generated, the waves are sensed by the OHC stereocilia, which act as feedback elements, again causing the OHC to lengthen and shorten, amplifying the ripple and leading to reverberation. Together the elements form a SAW resonator, and they resonate in sympathy with imposed intracochlear pressure, with which they are in continuous hydraulic connection via the spaces of Nuel. To introduce an analogy of Hudspeth (1997), the separated OHCs form a distributed amplifier in which, like a pendulum clock, the oscillator frequency is determined by physical properties (the length of the SAW cavity or the length of the pendulum), while the timed release of energy (from the fast OHC motor — the escapement) overcomes damping and sustains activity.

The resemblance of the SAW model to a regenerative receiver is noteworthy, for it was this topology which was invoked by Gold (1948) to describe the action of the cochlea. In particular,

amplification (by the OHCs) takes place before detection (by the IHCs), a scheme that optimises signal-to-noise ratio. Later, in discussing the cochlea's need to overcome fluid damping and generate high *Q*, Gold drew an analogy to the functioning of an 'underwater piano': only by introducing a sensor onto each string and supplying positive feedback could such a device be made to operate (Gold, 1987).

In the following section the similarities with SAW resonators are more fully examined. The SAW model is tested by making general predictions of what properties a SAW topology would confer on the cochlea, and these are compared to observations. The topology is able to give a good general account of cochlear mechanics, providing descriptions of a wide range of phenomena that are currently more or less opaque: the shape of the cochlear tuning curve, the most common ratio between SOAEs, bistable linked SOAEs, peak splitting and interference notches, the time-invariant responses of the cochlea to clicks of varying intensity, the half-octave shift, the 'V' shape of the stereociliar arms, and, speculatively but intriguingly, a way by which the cochlea may directly perceive musical ratios.

III BASICS OF SAW RESONATORS

SAW resonators are solid-state devices that generate slow electromechanical waves – commonly ripple-like Rayleigh waves – between two sets of interdigital electrodes on the surface of a piezoelectric substrate (Bell and Li, 1976; Smith, 1981). They are used in analog signal-processing applications where a number of cycles of signal need to be stored and operated on, such as in

spread-spectrum mobile phones. The easiest way to see how the device operates is to see it as a variation of the SAW delay line in which one set of electrodes launches the ripples, and a neighbouring set senses them (Fig. 2). Feeding the output back to the input creates a high-*Q* resonance typically in the megahertz range. The resonator is simply a degenerate case of the delay line in which the two sets of fingers are merged into one combined set of sensors and effectors. Ripples now reverberate back and forth between the fingers.

A key feature of all SAW devices is that the interdigital electrodes alternate in polarity. The minimum number of fingers required is three.

IV A SAW RESONATOR IN THE COCHLEA

In the mammalian cochlea we find at least three rows of OHCs, and it is proposed that each row acts as the interdigital electrode of a SAW device, alternating in the polarity of their cycle-by-cycle length changes in response to intracochlear pressure. Effectively, the cells are piezoelectric transducers, turning pressure signals into electrically mediated length changes. In this connection, Dong et al. (2002) found that the cell wall material responsible for OHC motility has a piezoelectric coefficient of 20 μC/N, 40 000 times larger than Rochelle salt. The transduction process, it is supposed, causes cells in OHC2 to quickly lengthen, and those in OHC1 and 3 shorten, in response to an increase in pressure; half a cycle later, the situation is reversed as the pressure cycle reaches a minimum. Figure 3 illustrates the process, with a standing wave produced between OHC1 and OHC3.

In other words, a cavity is formed between the outermost rows, and wave energy escapes the cavity in the same way as a laser beam emerges from the cavity between its reflective ends. Wave energy escaping the 'acoustic laser' is communicated to the nearby IHCs.

There are a number of major structural analogies between a SAW resonator and the anatomy of the cochlea.

1. The three rows of OHCs are the interdigital electrodes. It is significant that the required minimum number of fingers is three, and in all vertebrate animals there are three or more rows of OHCs (Bredberg, 1968). Additional rows are usually found at the low-frequency apex where additional gain may be needed to counteract middle ear transmission losses.
2. The TM is the uniform substrate upon which ripples are generated. Whereas the gelatinous body of the TM is embedded with multidirectional collagen fibres, high magnification views of the lower surface of the TM show a thin, almost homogeneous, layer (Kimura, 1966) in which the fibres run largely parallel. This base layer, only about 1 μm thick, has been called Hardesty's membrane and its uniformity is assumed crucial in channeling and propagating surface waves.
3. Wave energy propagating on the surface of a SAW resonator is absorbed and/or reflected by impedance discontinuities, and this is normally done by etching grooves or placing strips of material on the surface of the device. The TM possesses a peculiar dense stripe known as Hensens stripe, which is placed strategically next to the stereocilia of the IHCs (Hardesty,

1908). Hensens stripe is ideally placed to intercept the wave energy emerging from the OHC cavity and direct it to the IHC stereocilia.

4. Energy escaping the OHC cavity towards the outer edge of the TM is not useful and – to avoid unwanted propagation modes – needs to be either absorbed or reflected so as to re-enter the cavity with appropriate phase delay. At the outer edge of the TM another aggregation of material is found, a rounded thickening known as the marginal band (Hardesty, 1908), and this may perform one or other of these functions.
5. To absorb and disperse unwanted bulk propagation modes, the back of a SAW resonator is either roughened or waxed. In the cochlea the top of the TM is covered with a covering net (Hardesty, 1908) which appears suited to this purpose.
6. The speed of electromechanical ripples in a solid-state SAW resonator is about 5 orders of magnitude lower than the speed of the electrical signal applied to it, a reduction which makes it possible to compactly store many cycles for correlation and other signal analysis (Maines and Paige, 1976). In the same way, the speed of the hypothetical ripple on the TM is 4–5 orders of magnitude lower than the speed of the input signal (sound) in the surrounding cochlear fluids, some 1500 m/s. As shown below (section VII), the pea-sized cochlea should in this way be able to store and analyse up to 10 cycles of acoustic signal.

V KEY EVIDENCE SUPPORTING THE MODEL

There are four main strands of evidence supporting the SAW model, and these are set out below.

A. OHCs respond directly to oscillating acoustic pressure

Experiments by a number of workers extending over several years have found that OHCs react not just to stimulation of their stereocilia but to water-jet stimulation of their cell body as well (Canlon et al., 1988; Canlon and Brundin, 1991; Brundin and Russell, 1993, 1994). A synthesis of this evidence was assembled by Bell (2003) who conjectured that the common underlying effective stimulus in these experiments was *pressure*. The conjecture is supported by Tolomeo and Steele (1998), who successfully modelled some of the findings of these experiments by using a piezoelectric model of the OHC wall and assuming that the effective stimulus was external pressure.

Canlon et al. (1988) placed isolated OHCs on a microscope slide and directed oscillating water jets (from a nearby fluid-filled pipette connected to a 200-Hz vibrating source) at the body of the cells, and 80% of them responded with a lengthening or a shortening. Similar results were reported in Brundin et al. (1989) over a wide frequency of stimulation and they found that the responses were tuned, with the shorter cells responding best to higher frequencies.

Canlon and Brundin (1991) performed experiments along the same lines, and found that the response of the cells was the same whether the cells were held by the pipette at the base or whether the pipette enclosed (and protected) the stereocilia. Indeed, direct stimulation of the stereocilia did not induce a response.

Brundin and Russell (1993) took the fluid-jet experiments a stage further by finding that the length changes were not just tonic (d.c. shifts) but, to the limit of their experimental technique (15 nm resolution), were phasic (a.c.) as well, and surmise that the d.c. changes were in fact due to non-linear rectification and amplification of the a.c. responses. They put forward the idea that a similar behaviour may occur in vivo, and calculate that, allowing for middle-ear pressure gain of 30 dB, the observed threshold of response corresponds to 19–34 dB above hearing threshold. But here the SAW model introduces a significant factor. The single-cell experiments are studying *open-loop gain* – that is, the activity of a single OHC before the feedback action of the cochlear amplifier comes into play. When the rows of OHCs build up the signal through the conjectured reverberation process, the sensitivity is multiplied by the *closed-loop gain*. Since the gain of the cochlear amplifier – the closed-loop gain – can exceed 40–60 dB, the sensitivity figure quoted above is sufficient to see detectable responses at 0 dB SPL.

Brundin and Russell (1994) studied the phasic response in more detail, and observed that a single OHC was able to respond in phase or 180º out of phase, depending on stimulation level. A responsiveness that can either be in phase or out of phase, depending on row number (possibly controlled by turgor pressure and/or polarization voltage), is central to the SAW hypothesis and is discussed in the following section.

It is noted that biphasic responses have only been observed for water-jet stimulation of electrically isolated OHCs. It has not been seen when the cells are voltage-clamped and electrically stimulated (e.g., Frank et al., 1999, and references therein).

B. Two populations of OHCs with opposite response polarities

It appears that no measurements have been done to distinguish the properties of cells in OHC2 from those in other rows. Nevertheless, there are clear results, largely in the same water-jet experiments described above, that show that OHCs do not all behave alike – an isolated cell (of unknown row number) will sometimes respond in antiphase to others under test.

The dual responses can be seen in Fig. 2 of Canlon et al. (1988), where cells from the mid-frequency region of the cochlea were equally likely to expand or contract by a small amount (meaning that underlying a.c. responses were either in phase or out of phase with the pressure stimulus).

Fig. 3 of Brundin et al. (1989) shows tuning curves for 6 OHCs that lengthened after water-jet stimulation, and for one that shortened, results generally confirmed in Canlon and Brundin (1991).

In Brundin and Russell (1993), the phases of the a.c. responses of OHCs were always independent of the amplitude of the water-jet, but in Brundin and Russell (1994) the authors report – as mentioned above – that the phase of the responses could alter with level of stimulation, changing by 180º at a certain (uncalibrated) threshold. Whereas the piezoelectric model of Tolomeo and Steele (1998) explains certain features of the OHC response, in particular a response to external pressure, it does not predict this sudden change of phase.

Zenner et al. (1988) placed isolated OHCs within an alternating electric field (1–502 Hz) and observed that the cuticular plate of 62% of motile OHCs tilted when the plate was closest to the ground electrode and 38% tilted when the plate was closest to the active electrode. Although not demonstrating different response polarities, it does point to the existence of two distinct classes of OHCs, at least for low-frequency stimulation.

Electrical stimulation of an isolated gerbil cochlea showed that the nuclei of OHC1 and 3 moved out of phase to OHC2 (Karavitaki and Mountain, 2000).

Recent experiments with cochlear explants have observed rapid phase reversals between OHC2 and OHC3 (Scherer et al., 2003), and these may be relevant here.

A vital clue to what may be underlying this anomalous behaviour can be found in Kakehata and Santos-Sacchi (1995), where the authors demonstrate that the peak non-linear capacitance of an OHC – the electrical signature of electromotility – shifts with polarization level (and turgor pressure). Moreover, the polarity of a current through the cell wall will be *positive or negative* depending on whether the voltage is less than or more than the peak. This crucial property is illustrated in Fig. 4. A unifying hypothesis, therefore, is that cells in OHC2 are relatively depolarised (resting potential of say –50 mV) and/or have lower turgor pressure compared to cells in OHC1/3 (where the resting potential is more like –80 mV). In this way, the required antiphasic response to pressure can be readily produced. In the experiments above, the polarization of the cells under investigation could be either high or low. Control of polarization by efferent activity would

be a simple way of adjusting the sensitivity of the cochlear amplifier – for if all the rows of OHCs should be driven to the same level of polarization, the gain of the amplifier would fall to zero.

C. Radial wave motion on the partition

The SAW model calls for transverse wave motion in the cochlea's 'radial' direction (inside to outside of its spiral coil as illustrated in Fig. 3), and so it predicts that there will be rapid phase changes in this direction amounting to 5 or 6 complete cycles between the vestibular lip and the marginal band. Nilsen and Russell (1999) have observed rapid phase changes on the basilar membrane of a guinea pig using a 5 μm detecting spot from a laser diode, and results for one animal are shown in Fig. 5. The phase excursions, which measure up to 180º, are nearly those expected from a wave emerging from the OHC cavity towards the IHC, as shown in Fig. 3: OHC1 and 3 in phase with IHC, with an out of phase response surrounding these points. There is also an indication of a dip below OHC2. The SAW model predicts a dip down to 0º here (dotted line in Fig. 5), but it is difficult to experimentally resolve such rapid phase changes because the laser spot is directed onto the basilar membrane and this surface will tend to spatially integrate the response of the three OHCs some distance above.

Other workers have seen hints of phase variations across the partition (e.g., Nuttall et al., 1997; Cooper and Rhode, 1996; Recio et al., 1998), but never as large or as rapid as Nilsen and Russell (1999), while others have reported virtually none (e.g., Cooper, 2000; Ren et al., 2003). The phase measurements are difficult, and results appear to depend on experimental technique – such as

whether or not reflecting beads were used, spot size of the laser beam, and so on. This question is far from settled, but note that absolute phase measurements showing several cycles of change – not just relative measures within ±180º as reported by Nilsen and Russell (1999) – would offer powerful evidence in favour of the SAW model.

D. Second harmonic generation and detection

Finally, one piece of evidence derives from echolocating bats. Certain species use the second harmonic of their call for echolocation, and this characteristic leads to a special configuration of the SAW resonator in their cochleas.

First, consider the configuration of a SAW device intended to generate harmonics. Such harmonically operated devices can generate higher frequencies and can overcome certain limitations of devices that operate at the fundamental. For example, a device excited at 200 MHz can be made to resonate successfully at 2.2 GHz (the 11th harmonic) using a substrate and electrode dimensions appropriate for the 200-MHz fundamental (Campbell, 1998, Ch 6.8, pp. 184–191).

To operate at a harmonic, special disposition of the interdigital electrodes is required. A normal SAW device has the fingers equally spaced, so that an electrode of one polarity sits in the middle of oppositely polarized electrodes flanking it. The result is that even harmonics are impossible, as Fourier analysis will show. (In this context, it is noteworthy that in humans, where OHC rows are equally spaced, frequencies of multiple SOAEs are never found at precisely octave intervals.) To be

able to produce strong even harmonics, a SAW device must be configured with the electrodes off-centre, and the ideal spacing is a ratio of 2:1 (Campbell, 1998, Fig. 6.16). Figure 6 (reproduced from Kössl and Vater, 2000) shows the reticular lamina of a second-harmonic detecting bat, *Pteronotus parnellii*, and inspection shows that the spacing OHC1–OHC2 to OHC2–OHC3 is close to 2:1, as required. This 2:1 spacing has also been observed in other second-harmonic detecting bats (e.g., *Rhinolophus ferrumequinum*, Bruns and Goldbach, 1980). Since in all other species examined OHC2 is closely aligned in the middle of OHC1 and OHC3, this micrograph and others like it suggest that the three rows are working together as a SAW resonator.

VI WHAT IS THE WAVE PROPAGATION MODE?

SAW devices can operate using a wide range of wave propagation modes: Rayleigh waves are the most common, but Lamb, Love, Bleustein–Gulyaev–Shimizu, Stonely, Sezawa, and other wave modes are employed (Ballantine et al., 1997, Ch 3; Campbell, 1998, Ch 2). Which mode may operate in the cochlea is difficult to decide, particularly when the TM is a fibre-reinforced viscoelastic gel covered with a thin surface layer (Hardesty's membrane) and immersed in an electrolyte (endolymph) and an electrical field.

Simple capillary (surface tension) waves, with their characteristically slow speed, are a first consideration. The speed, c, of a surface tension wave of wavelength λ is (Lighthill, 1978):

$$c = (2\pi T/\lambda\rho)^{\frac{1}{2}} \qquad (1)$$

where T is the surface tension and ρ is the density. Surface tension may have a role, but it is difficult to see how this parameter can be made to vary systematically from base to apex by a factor of 10^4 or more in order to tune the partition over a frequency range of at least 2 decades. Note that capillary waves are dispersive.

A shear wave of some type is a strong possibility because the shear moduli of gels are small, very much smaller than their compressional moduli. In its most basic form, the speed, ν, of a bulk shear wave is given by

$$\nu = (\mu/\rho)^{1/2} \qquad (2)$$

where μ is the shear modulus and ρ is the density. These waves are non-dispersive (speed independent of frequency); a Rayleigh wave, a shear wave on the surface, travels at about 90% of this speed. Acoustic measurements of one soft gel, a so-called "ringing gel" (showing the peculiar property of ringing like a bell when struck), gave a shear modulus of 14 kPa and a shear-wave velocity of 4.1 m/s (Sinn, 2000).

Recent measurements of the mammalian TM show that its shear moduli are comparably low. Using 20-μm–diameter magnetic beads placed on the surface of a 50-μm–thick mouse TM, Abnet and Freeman (2000) measured the tangential point stiffness of the TM to be about 0.2 N/m in the radial direction, a figure that equates to a shear modulus of 20 kPa. Using Eq. (2), this figure produces a

bulk shear wave velocity of about 4.5 m/s. At this speed, resonance between OHC rows 30μm apart would occur at a frequency of 150 kHz. The hearing range of mice extends up to 100 kHz, so this value is broadly in keeping with the theory.

Unfortunately, the Abnet and Freeman measurements were made on sections of the TM whose distance from the apex (and hence operating frequency) was unknown, although it seems samples were taken from the whole length of the TM. They measured radial stiffnesses ranging from 0.07–1 N/m, values which correspond to shear moduli of 7–100 kPa and wave velocities of 2.6–10 m/s. The lowest velocity still gives a frequency of 87 kHz, which is still too high, as half-way along the mouse's partition, which was presumably sampled, the animal has its most sensitive hearing at a frequency of 15 kHz, and resonance between the OHC rows at this point would require a wave velocity of about 0.5 m/s, an order of magnitude lower than measurements indicate.

However, as Abnet and Freeman suggest, their measurement technique is likely to give larger stiffnesses than in situ. First, of course, there is the geometrical consideration that the point stiffness derived from samples no bigger than their beads will be lower than for the larger samples they used, where the bead has to deform a larger area of TM. The intrinsic shear modulus may be about half that measured on a larger sample. Second, the reverse side of the TM was firmly cemented to a glass dish, preventing bending modes (Lamb waves) that would possess much lower stiffness and slower propagation speeds. Third, the retarding effect of the surrounding fluid mass on propagation speeds needs to be taken into account in calculating wave speeds. Finally, the TM is multilayered, with its underside covered with a very thin layer called Hardesty's membrane, and it is possible that

this relatively homogeneous layer, about 1 μm thick, is even more compliant than the fibrous bulk on which it sits (since the bulk would dominate measurements when using 20-μm beads).

Hardesty's membrane resembles the soft overlayer used in some SAW devices to slow the shear wave and trap acoustic energy near its interface with surrounding liquid (Ballantine et al., 1997, p. 89 ff.). This configuration, therefore, may be a desirable one for the cochlea to have. If Hardesty's layer is softer than the body of the TM, then the SAW theory would predict that its stiffness would be no more than that of the OHCs (for in this way power transfer from one to the other would be maximised). Figures for the axial stiffness of individual OHCs range from 0.5–10 mN/m (Brownell et al., 2001), some 2 or 3 orders of magnitude less than the point stiffness of the TM measured by Abnet and Freeman (2000). Logic alone says that if OHC axial stiffness is really orders of magnitude less than that of both the TM and the basilar membrane, as current measurements indicate (He and Dallos, 2000, discuss this disparity), then OHC motility would be ineffective and pointless. Either the OHC is stiffer in vivo, or the TM or basilar membrane is softer. If the TM's shear modulus matched the stiffness of the in vitro OHC (say 1 mN/m), Eq. (2) indicates that shear wave velocities well below 1 m/s would be possible.

Clearly, at this point more measurements are needed. Other possible wave modes include bending waves (Lamb waves or, if immersed in a liquid, Scholte waves) which travel very much slower than shear waves, although in a dispersive manner. But whatever the actual wave mode may be, one particular constraint is worth noting. The unequal row spacing evident in Fig. 6 was used as evidence in favour of the SAW model. However, it also indicates that the waves involved are non-dispersive – that is, their speed is independent of frequency. For if the second harmonic traveled at a

speed different to the fundamental (i.e., the waves were dispersive), there would be no need to displace OHC2 away from the centre in order for the second harmonic to be able to excite the cavity and be detected. This suggests that, whatever wave mode is at work here, it is non-dispersive. This conclusion is attractive in the sense that it simplifies the analysis of OHC geometrical patterns: it means that calculated resonant frequencies are simply inversely proportional to the indicated length.

As already indicated, the wave speed will need to vary over a range of at least 100:1 from base to apex in order to tune the system. This means that, for a non-dispersive wave, the elastic modulus will need to change by 4 orders of magnitude; alternatively, for a bending wave, the thickness will need to change by 10-fold or more (since for a bending wave the stiffness will vary as the cube of the thickness). The TM is sometimes seen to vary in thickness by about 10 times (Hardesty, 1908), although apparently not in the mouse (Abnet and Freeman, 2000). With numbers for many relevant dimensions and physical properties lacking, detailed comparison of the cochlea with particular SAW analogs is not possible at this stage.

When considering possible modes for low frequency resonance, a prime candidate is the Lamb wave detector, a SAW device that uses a thin piezoelectric membrane. Its flexural modes permit voltages to be efficiently converted into mechanical deformations and vice versa (Ballantine et al., 1997, p. 111 ff.), and its wave speed is the slowest of all types.

VII REINTERPRETING EVOKED OTOACOUSTIC EMISSIONS

Evoked otoacoustic emissions (EOAEs) have become a mainstay of diagnostic testing for intact cochlear function, yet the mechanism underlying these cochlear echoes is far from clear. If a pulse of sound is projected into the cochlea, a faint echo of that sound can be detected in the ear canal some time later (Kemp, 1978). The long latency of the sound – several milliseconds or about 10 cycles (Wilson, 1980a) – is an indication that the sound has a cochlear origin. Conventionally, the long delay has been attributed to forward and reverse travel times of a traveling wave, but various studies suggest that such an interpretation is inconsistent with measurements (e.g., O'Mahoney and Kemp, 1995).

The SAW model offers a fresh interpretation of EOAEs, one which provides the necessary long delays but which avoids calling on the von Békésy traveling wave. The mechanism does in fact involve a progressive wave, but one which is much more localised, and it is best illustrated by reference to Fig. 3. A brief sound pulse activates the OHC cavity, which causes a wave train to travel towards the IHCs. Here, a proportion of the energy is captured by Hensens stripe and passed to the IHCs below, but some energy will continue on towards the vestibular lip, a remarkably sharp edge which forms the upper part of the inner spiral sulcus. Here the wave will encounter a sudden impedance discontinuity and undergo reflection. It will then return towards the OHCs, where it will re-enter the cavity, exciting it once more. The time delay will be about 10 cycles, a number derived by simple observation of a cochlear cross-section. The distance from OHC1 to OHC3 is regarded as 1 wavelength, so that the distance from OHC1 to the vestibular lip will be about 5 wavelengths and therefore the round trip will provide a time delay of about 10 cycles, as required.

The excitation process can repeat, and an example of this can be seen in Fig. 4 of Wit and Ritsma (1980) in which the process repeats indefinitely every 7.4 cycles of the evoked emission frequency.

The model relies on the OHC-swelling model of Wilson (1980b) which was developed to explain observations that in some cases the echo was almost simultaneous with cochlear microphonic signals. Wilson supposed that when the sound interacted with an OHC it caused a small volume change (as well as a microphonic signal), and therefore a compressional wave could almost instantly travel back to the ear canal, outpacing any reverse traveling wave, where it could be detected. Wilson calculated the volume change required need only be small: an oscillating volume change of less than 0.01% over a 1-mm segment of the partition is sufficient to give a sound pressure level of 20 dB in the ear canal.

VIII SETS OF COCHLEAR RESONATORS

Unlike the impression conveyed by the cross-section of Fig. 3, the cochlear resonators do not only lie in the radial direction. Instead, the majority of micrographs of the organ of Corti (such as Fig. 1), show that OHCs generally line up in various oblique directions as well. Typically, the cells lie in a regular, quasi-crystalline array as shown in Fig. 7A. The arrangement of cells can be considered as a two-dimensional rectangular lattice in which OHC2 sits in the centre of the unit cell. The dimensions of the unit cell are *a* and *b*, where the longitudinal distance between the cells (along the rows) is *a* and the distance between the first and third rows, the defining cavity length, is *b*.

The radial direction is an alignment of only two cells, and hence the efficient SAW resonator mechanism is not available in this direction. Conceivably, two cells acting together may be able to generate some reverberating activity, but this aspect can only be resolved with further modeling.

Note, however, that the diagonal of the unit cell is an alignment of three cells that could act like a single SAW resonator element; this resonator appears at an angle θ to the radial, where θ = arctan a/b.

Given the unit cell as described above, it follows that there will be further alignments of two and three cells at other oblique orientations as shown in Fig. 7B. This scheme is an explanation of why OHC stereocilia appear in a 'V' configuration, for it allows each arm to act independently of the other in forming simultaneously active cavities angled towards the base and the apex. Note that the arms in one row often sit parallel to arms in neighbouring rows which are displaced longitudinally by two or three cells, in this way strongly defining an oblique cavity. For example, in Fig. 1 one favoured alignment (L_{-3}) lies at an angle of about 50º from the radial direction.

For a unit rectangular cell of angle θ, it follows that alignments will appear at a series of angles given by arctan (n tan θ), where n = 0, 1, 2, 3, 4, 5, …. For the 19º unit cell, simple trigonometry shows that these alignments occur at 0º, 19º, 35º, 46º, 54º, 60º…, with lengths of 1.00, 1.06, 1.22, 1.44, 1.71, 2.00… If simple ray theory is used to predict acoustic behaviour, then this associates frequencies of 1.00, 0.94, 0.82, 0.69, 0.59, 0.50… times the fundamental with these propagation directions.

IX COCHLEAR PROPERTIES DERIVING FROM RESONATOR SETS

The idea set out in the previous section of *a linked set* of oblique cochlear resonators makes sense of observations that a point on the partition may carry frequencies other than the CF. The frequency of the strongest-resonating cavity, normally the shortest, can be associated with the CF or tuning tip at that point, but there are other contributing resonators too, longer and lower in frequency.

A. Ratios between SOAEs

It is a well known result that the most common ratio between adjacent SOAE frequencies is close to 1.06 (Braun, 1997). This result fits well with the observed arrangement of OHCs, where, referring to Fig. 7, if the radial cavity has a given length, then the neighbouring oblique cavity will be longer by a factor $1/\cos\theta$.

Measurement of a large number of published micrographs (set out in Table 1 of the paper at footnote 1) reveals that the most common value for θ, the angle of the first oblique, is $19 \pm 2^{\circ}$, although the angle varies systematically along the partition. The angle is smallest at the apex, where values as narrow as 16° ($a/b = 0.3$) are seen; at the base angles as wide as 30° ($a/b = 0.6$) are evident.

The most common value of 19° is found midway along the partition corresponding to CFs of 1–3 kHz, the region devoted to detection of speech and from which SOAEs are most common. Focusing on this region gives the following results. An angle of 19° means that, if $b \equiv 1$, $a = \tan\theta =$

0.35, and the length of this resonator will be 1/cos 19º times the length of the radial alignment. The frequency of this oblique cavity will therefore be 1.06 times lower than the radial cavity, suggesting that SOAEs frequently arise from simultaneous activity in these neighbouring cavities.

B. The shape of the cochlear tuning curve

If the responses of all the resonators at a point on the partition are summed, the result resembles the typical cochlear response curve. That is, take, for illustrative purposes, a single high-Q resonator at L_0 with high- and low-frequency slopes of 100 dB/octave – reflecting the presumed resonance of a single SAW cavity due to reverberation of ripples within it – and add to it the responses of all the other similar cavities at that point on the partition. Assume that the intensity of a ripple wavefront attenuates as a simple exponential and is further weakened because of circular expansion by a $1/r$ factor. Longer resonators will therefore make successively weaker contributions at frequencies the inverse of their length. In this elementary model, alignments of both two and three OHCs have, for the sake of simplicity, been treated (unrealistically) as making equal contributions to the response. Similarly, the orientation of the stereociliar arms has been ignored (so that the cells are treated as point sources and detectors of ripples), but the intent is to convey the underlying principle. The summation, shown in Fig. 8, exhibits a sharply tuned tip flanked by a very steep high-frequency slope and a more gently sloping low-frequency tail – like the cochlear tuning curve. Note that notches between the points may well appear.

An instance of a tuning curve in which the contributions of the individual resonators can be seen is an investigation of the vibration 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 response of the bead to broad-band noise is shown in Fig. 9, 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 relative frequency of these peaks is consistent with alignments of hair cells based on a/b of 0.383 and, in this case, a slight tilt of the lattice by 4º (the tilt improves the match and is a feature seen in some micrographs).

If the orientation of stereociliar arms is such as to favour an oblique cavity (a feature often seen in micrographs taken near the apex), this cavity may become the strongest resonator (and hence represent CF). The result is that shorter resonators contribute to responses above CF, reducing the steepness of the high-frequency flank of the tuning curve, another feature often seen at apical locations. On the other hand, near the base OHCs are seen to enclose obtuse angles (the arms are almost collinear), and so there are no contributions from oblique resonators, eliminating the low-frequency tail. In this way, the general variation of cochlear tuning curves between base and apex can be explained.

C. Distortion in the cochlea

An arrangement of resonator sets sharing a common hair cell renders the cochlea naturally liable to high levels of intermodulation distortion. The 'essential non-linearity' of the cochlea, in which distortion between the two tones can be detected even at the lowest stimulus levels (Goldstein,

1967), may be seen as distortion remaining at the intrinsic idling levels of the virtual resonators (if the OHCs lack activity, there can be no virtual resonator).

Distortion product emissions can therefore arise from interactions of resonators at a single point on the partition – not by overlapping of traveling wave envelopes as standard accounts suggest.

It is significant that interactions between two stimulating sounds take place via resonators that are always longer (lower in frequency) than the CF. 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). The explanation lies in seeing that interaction between two primary tones 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 than CF) to carry the sum tones.

D. Ratio detection and musical possibilities

Given the most common values of OHC unit cells, the ratios of the lengths (frequencies) of the resulting resonators can give a remarkable set of musically significant intervals (Bell, 2001, 2002*a*). The ratios appear for certain values of spacings between neighbouring OHCs. These selected values are not atypical, but are idealisations of measurements made on published micrographs from specimens that have probably suffered shrinkage and distortion during preparation. Possible

frequency dispersion of the wave carrying the ripple is another complication, and so the derived ratios are only suggestive of how musical perception may arise; given the uncertainty, this aspect is not discussed here, although the potential link is worth noting.

X DOVETAILING WITH EXISTING TRAVELING WAVE THEORY

The SAW model specifies a way by which cochlear behaviour can be explained without recourse to a conventional traveling wave. And yet, traveling wave–like behaviour has been observed: at each point on the partition one sees, as frequency increases, displacements with steadily accumulating phase until, in the region of CF, a plateau of typically 4 or 5 cycles is reached (e.g., Olson, 2001, where the displacements were registered with a nearby pressure sensor). How can these observations be reconciled? The suggested answer involves differential forces across the partition and the role of the vestibular lip.

As traveling wave theory assumes, forces on either side of the partition will cause it to move up and down; the SAW hypothesis agrees that vertical movement will occur, but it need not induce a traveling wave and it will only begin to have a stimulatory effect on the IHCs at sound pressure levels of about 60 dB when a second ripple source comes into play. Below that level, the cochlear amplifier, deriving from OHC activity, is the primary source of drive to the IHCs. The differentially driven motion will be broadly tuned in accordance with the passive mechanical properties of the partition, and it is assumed that, at a given point on the partition, the passive tuning is about half an octave lower than the tuning of the SAW cavity. However, the differential movement need not

cause a traveling wave to begin propagating longitudinally along the partition towards the apex (as the conventional picture has it); rather, what it might do is create a very localised ripple at the passively tuned location as follows.

As the partition moves up and down, let us focus on what might happen at the vestibular lip. It was noted above, in connection with evoked emissions, that this sharp edge is important in reflecting ripples propagating beyond the IHCs. But what is the purpose of these reflections? Perhaps it would be useful from an information-processing view if they provided the cochlea with a way of generating a 10-cycle delay in the acoustic signal, which will then meet with a similar non-delayed signal emerging from the OHC cavity. The two wavefronts will be traveling in opposite directions above a detector (the IHCs), an arrangement that constitutes a signal correlator. SAW devices are configured as correlators (or convolvers) in just this way (Campbell, 1998, Ch 17), and such a signal processing arrangement in the cochlea could, for example, be useful for detecting, or compensating for, ambient echoes.

But any such signal correlation scheme would not be of much use if it were confined to low sound intensities (since the cochlear amplifier saturates at about 60–80 dB SPL). How could the correlation scheme work with a saturated cochlear amplifier? Again, the sharp edge of the vestibular lip could still play a central role at higher intensities (above about 60 dB SPL) *if the lip were to become a source of ripples in its own right*. This could happen, it is conjectured, if the partition were moving up and down under the influence of differential pressure. With the TM vibrating against the stationary lip, ripples would be generated at this point and they would propagate towards the IHCs.

There are now two ripple sources traveling in opposite directions towards the IHCs: one arriving with a delay of about 1 cycle from an active source, and the other with a delay of some 4 or 5 cycles from a passive source (taking the distance OHC1–OHC3 as 1 wavelength and comparing it with the distance seen in micrographs from the vestibular lip to the IHCs). Herein is the source of the apparent traveling wave delay: at CF, IHCs will sense a 4–5 cycle delay as the ripples propagate radially towards them.

The ripple sources are comparable in intensity at about 60–80 dB SPL, the level where the cochlear amplifier saturates. The lip therefore becomes relatively less important in reflecting ripples as sound levels increase, and instead becomes a significant source of its own. Provided the SAW cavity continues to put out ripples, correlation information will still be available at the IHC (although with a maximum of 4 or 5 cycles of delay). In summary, the ripple from the vestibular lip becomes the dominant source of stimulation for the IHCs at high sound pressure levels whereas at low levels the reverse is true.

These two identified sources of ripples – the OHC cavity and the vestibular lip – can provide an understanding of a striking interference phenomenon in the cochlea called peak splitting. Since the SAW cavity is sending waves towards the IHCs in one direction and the vestibular lip is sending waves from the other, then interference of those waves is expected. Destructive interference explains ‘peak splitting’ and interference 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).

Lin and Guinan note that the responses near this level waxed and waned, as if the response were due to the mixing of two excitatory drives of slightly different frequencies, and the authors suppose that 'tip drive' produces the low-level, long-latency click responses, while 'tail-drive' produces the high-level, short latency click responses, a picture which well describes the situation modeled here. The authors go on to deduce that the excitation drives represent mechanical drives that are carried over separate physical paths and add at some point.

In a strict sense, of course, the ripple propagating from the vestibular lip to the IHCs is a traveling wave, although it is not the same entity – a von Békésy-style wave traveling in the longitudinal direction – that is usually meant by the word. To avoid confusion it may be better to use the term *propagating ripple* with the implication that this ripple is propagating in the cochlea's radial direction. The major difference between the two is that the propagating ripple is local to a specific broadly tuned region of the partition (and does not travel more than the width of the TM), whereas the classical traveling wave begins at the base and moves towards the apex.

The half-octave difference between the sensitive and highly tuned active resonance of the OHCs and the less-sensitive, broadly tuned passive resonance of the partition explains the 'half-octave shift' which takes place in partition tuning as intensity rises (McFadden, 1986).

The vestibular lip mechanism gives an alternative explanation of apparent traveling wave delays, and in particular, why measurements of the delay (either from direct sensing of partition displacement or from nerve-fibre recordings) reach a plateau at a fixed number of cycles. The

reason is a simple physical one: there are no more cycles of delay available than what the width of the TM can provide. To date, no other explanation of the functional significance of the vestibular lip and its remarkably sharp edge has been proposed.

Of course, even at low sound pressures traveling wave–like behaviour is seen, but in this case the delays can be seen as a 1-cycle delay between the OHC cavity and the IHC (again, based on distances seen in partition cross-sections), in addition to which is the unavoidable delay (roughly Q cycles) involved in increasing the amplitude of a high-Q resonance by 10 dB. However, in this case it is predicted that no distinctive phase plateaus would be evident.

The new model also gives a reason for why recent measurements of the spatial extent of the traveling wave displacement show it to be so narrow. Basalward of a resonance region, there does not appear to be appreciable displacement. Thus, Russell and Nilsen (1997) estimate that a region of the partition only 0.15 mm long (53 OHCs) is responding to a tone at 15 dB SPL, and similarly Ren et al. (2003) noted that the traveling wave at 40 dB SPL appeared to be confined to a region near the CF that extended no more than 600 μm longitudinally.

Recently, pressure-probe recordings (Olson 1999, 2001) give an additional insight into the nature of the traveling wave, and provide further results that can be interpreted from a SAW perspective.

Olson (2001) used miniature pressure transducers to record pressure on both sides of the partition, and found appreciable common-mode pressures. She points to indications, from phase data, that a resonance appears to be occurring in some test animals, although strangely there is no evidence of

this in the magnitude of the displacement signal, which peaks about half an octave lower than where the phase plateau begins. Her suggestion that the signature of peak amplification may be occurring radially – and hence invisible to her sensors – agrees with the SAW picture. It predicts a sharply tuned radial resonance driven by common-mode pressure (and unaccompanied by bodily vertical motion of the partition, although there will be some interchange between these two motion types), and a broadly tuned up and down motion of the partition driven by differential pressure.

Similar results were reported in Olson (1999), but a key finding was that the fluid layer associated with the presumed traveling wave was minute, having a penetration depth of only 15 μm, and was, surprisingly, independent of frequency. Detailed discussion is not possible here, but the suggestion is made that the OHC activity is causing small fluid displacements (detected as near-field pressure – Bergeijk, 1964), not that the minute fluid layer is causing the entire basilar membrane to execute a traveling wave.

XI DISCUSSION

By formulating a model of the cochlea as a pressure-driven SAW resonator, this paper reintroduces a resonance theory of hearing not unlike that advocated by von Helmholtz more than 100 years ago (von Helmholtz, 1885). The major difference is that the resonance frequency here derives not from combined mass and compliance of individual elements (as Helmholtz supposed) but from a distributed arrangement of minute delay lines. The present hypothesis speculates that the cochlea is more sensitive to common-mode pressure than it is to differential pressure, which is normally

considered the source of the classical traveling wave. However, by considering the action of differential pressure in moving the partition up and down – and producing ripples from the vestibular lip that mimic the phase delays ascribed to the conventionally understood traveling wave – no such entity taking energy from base to apex is required.

Resonance theories have periodically resurfaced after being supplanted by the traveling wave theory early last century. Of most interest, Gold (1948) observed the 'phase memory' of the ear and concluded that only a resonance theory could accommodate his findings, and for the first time postulated an active cochlea. This latter concept was ahead of its time when introduced, but has since been vindicated. However, his 'regenerative receiver' notion, and his advocacy of von Helmholtz-like resonance, has still not been accepted. The SAW topology proposed here satisfies both of Gold's requirements. It was some years before Naftalin (1965) attempted to revive the resonance theory by calling for resonant biochemical/electrical activity in the TM. Soon after, Huxley (1969) raised the possibility that the spiral geometry of the cochlea may allow some form of resonance to occur. More recently, Dancer and colleagues (Dancer and Franke, 1989; Dancer et al., 1997) have suggested resonance, although no mechanism has been proposed.

Relying on resonance – a recurring theme in theories of hearing (Wever, 1949) – has the advantage of providing a ready understanding of how the sensitivity of the cochlea can be brought close to its theoretical limits (Wit and Ritsma, 1983). Another potentially fruitful avenue is the natural introduction of signal-processing functions, such as correlation, of which SAW devices are capable. The model also raises the possibility of the ear having built-in ratio-detection abilities, an aspect that should be of considerable interest to music theory (Bell, 2002a).

Because this model seeks to reinterpret how the cochlea transduces sound at a fundamental level, it impinges on a vast literature, which is beyond consideration here. More detailed treatments of the SAW model, and consideration of some potential counter-arguments, can be found on the Web[2]. Traveling waves may be apt for describing the behaviour of a passive cochlea at extremely high sound pressure levels, as investigated by von Békésy, but this paper proposes that the active cochlea can be described without reference to them. The von Békésy-style traveling wave has never been observed in a living cochlea – in the sense of basal activity *causing* apical activity with increasingly long phase delays (of course, both accounts will give correlations between base and apex). Experimentally, at a particular observing location, the general finding is of sharply circumscribed activity and accumulating phase delays as a function of frequency (e.g., Russell and Nilsen, 1997; Ren et al., 2003).

The SAW hypothesis proposes that all the effects attributed to a traveling wave are only the result of local effects generated at a single point on the partition. Dispensing with the traditional traveling wave has the advantage of circumventing a number of lingering problems in cochlear mechanics; the disadvantage is that the traveling wave meshes easily with the notion that OHCs are displacement sensors stimulated solely through their stereocilia. The new model calls on OHCs to be dual sensors that respond most sensitively to pressure via their cell body, a conjecture that requires reinterpretation of previous work and additional experiments.

The SAW model introduces the notion that at each point along the partition there exist a set of widely tuned resonators extending over more than an octave. The best frequency is normally

associated with a short resonator, but sometimes (particularly at the apex) the OHC stereociliar arms are angled to make longer, oblique resonators the strongest ones. This supposition explains, at least conceptually, the different shape of low-frequency and high-frequency tuning curves and ties together a wide body of literature in which additional frequency mappings have been observed (e.g., Allen and Fahey, 1993). In this respect, the model again resembles a piano in that each note, when struck, excites a number of strings, the difference being that here the multiple strings vary widely in tuning.

XII CONCLUSION

This paper has sought to provide an alternative to standard traveling wave theory. The TM has been presented as a central structure for supporting slow, short-wavelength ripples. Its physical properties – a highly compliant gel – and placement within the cochlea – in contact with motile OHCs – make it perfectly suited to perform this task, allowing frequency analysis and information processing to be done in very much the same way as solid-state SAW devices are able to do.

The revised cochlear mechanics appears to be comprehensive and consistent, albeit speculative. Two ripple-generating mechanisms have been postulated. One, an active source identified with the cochlear amplifier, is generated between the rows of OHCs – an arrangement likened to a SAW resonator – and acts only at low sound pressure levels. But once this model is accepted, another source of ripples on the TM can be readily envisioned. This second source originates from the

vestibular lip and results from vibration of the TM against it. Together, these two localised ripple sources provide the energy that eventually stimulates the IHCs.

In this picture, the basilar membrane is not a major element in cochlear mechanics; it is there mostly to support the sensing structures and help in tuning the partition at high levels. In particular, the basilar membrane does not need to support a traveling wave. The SAW theory supposes that the OHCs create movement on the basilar membrane that looks like a traveling wave, but the point of difference is that the traveling wave appears as a by-product of the initial motion – an epiphenomenon – and not its cause.

Clearly, the gel-like properties of the TM are crucial to the operation of the model, and more investigation of these is needed. In addition, although the conjectured model has good explanatory power, additional exploration using detailed mathematical modelling is called for.

Several suggestions for experimental confirmation of the SAW model are implicit in the picture as put forward above[3]. However, it is worth explicitly listing the following.

- Isolated OHCs, as pressure sensors, should show a response to a pure pressure stimulus and should therefore possess some degree of compressibility (Bell, 2003).

- Physical measurements of shear moduli and wave velocities in TMs should reveal suitably low values.

- Close study of linked bistable emissions should confirm the proposed unit cell geometry underlying their occurrence.

- Long latency studies of cochlear echoes using pure tone stimuli (in the manner of Wilson, 1980a) should show that the delays involved provide appropriate dimensions for the TM from the vestibular lip to the OHCs.

It is hoped that the ideas raised here will promote further investigation and understanding.

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1. Table 1 of Bell, A., "The Underwater Piano: Revival of the Resonance Theory of Hearing," at http://cogprints.soton.ac.uk/abs/bio/200005001.

2. Wider discussion of the SAW model can be found in preprints by Bell deposited at http://cogprints.soton.ac.uk/view-bio-theory.html.

3. For personal ethical reasons this work was conducted without animal experimentation. This paper cites work in which animals were sacrificed, the author acknowledging that experiments once done cannot be ignored. The author's preference is that testing of this theory be conducted without sacrifice of animals.

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FIGURE CAPTIONS

FIG. 1. Precise arrangement of the hair cells of a rabbit, showing three rows (below) of outer hair cells, with their characteristic sawtooth arrangement of stereocilia, and one row (top) of inner hair cells. It is conjectured that the three rows of outer hair cells function like the interdigital electrodes of a surface acoustic wave resonator. [Micrograph courtesy of Allen Counter and the Karolinska Institute and used with the permission of Elsevier Science Ireland 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. Basic elements of a surface acoustic wave device. Surface acoustic waves are launched when an electrical signal is applied to an interdigital electrode on the polished surface of a piezoelectric crystal; detection is done with a similar electrode set. A resonator is formed by feeding the output back to the input; alternatively, driving and sensing functions can be combined into a single set of electrodes in which the period of the interdigital transducer matches the wavelength of the surface acoustic wave. [After Smith, 1981].

FIG. 3. Visual representations of the SAW model, with a three-dimensional rendition (above) and labelled cross-section (below). Both show how ripples are formed on the undersurface of the gelatinous tectorial membrane (TM) when piezoelectric outer hair cells move in response to common-mode fluid pressure in the cochlea. Feedback between the rows of cells produces a standing wave; energy emerges from the cavity, like light from a laser cavity, and propagates to the IHC, where it is detected. The arrows indicate how, in response to pressure, the middle row of cells moves in opposite directions to that of its flanking rows; the vertical marks indicate the boundaries of a "cavity" in which the standing wave forms. [Top illustration after Lim (1980) *J. Acoust. Soc. Am*. 67, p. 1686; used with permission of the author and the Acoustical Society of America.]

FIG. 4. Non-linear capacitance of an isolated outer hair cell varies with membrane potential (from Kakehata and Santos-Sacchi, 1995). The inset waveforms are gating currents derived by applying fixed voltage steps to the cell at various holding potentials; note the reversal of the gating current on either side of the peak; such opposite responses, controlled by polarization and turgor pressure, are conjectured to be key differences between OHC row 1/3 and row 2.

FIG. 5. Rapid phase variations across the basilar membrane of a guinea pig observed by Nilsen and Russell (1999). The phase excursions, which measure up to 180º in this animal, are close to those expected from the SAW resonator model except that a sharp dip above OHC2 (additional dotted lines) is predicted. [From Nilsen and Russell, 1999, and used with permission of *Nature Neuroscience*.]

FIG. 6. Reticular laminar of the mustached bat, *Pteronotus parnellii*, an animal which detects the second harmonic from its call for echolocation. Note that, unlike almost every other vertebrate cochlea, OHC2 is not equidistant from OHC1 and OHC3. Instead, the inter-row spacing is 2:1, a ratio required by a SAW device when operating in a harmonic mode. [Adapted from Kössl and Vater, 2000, and used with the permission of *J. Assoc. Res. Otolaryngol*.]

FIG. 7. Geometrical arrangement of outer hair cells. (**A)** Typically, OHCs are found to occupy a regular rectangular arrangement in which a is the longitudinal distance between cells (along the length of the cochlea), and b is the distance between the first and third rows. The diagonal of the unit cell then appears at an angle θ given by arctan a/b. Elaboration of this scheme over a number of unit cells, (**B**), shows that multiple alignments of hair cells occur at increasingly oblique angles. For typical parameters $a = 0.35$ and $b = 1$, a set of alignments occurs as shown. Simple trigonometry shows that the cavity lengths are 1.00, 1.06, 1.22, 1.44, 1.71, 2.00, …

FIG. 8. Summing the response of each of the cochlear resonators produces, using simple assumptions, a curve that resembles the mechanical response of the cochlear partition. Here, each resonator L_0, L_1, L_2, L_3, …L_{11} of a set similar to that in Fig. 7 (a = 0.3, b = 1, tilt of 2.9°) is arbitrarily assigned a Q of 20 derived from multiple reflections between hair cells. Each member of the set (•) produces a peaked response (like that shown dotted for one representative member). The X-axis is simply the inverse of the normalised cavity length (shortest cavity = 1). The Y-axis response is given as $(k/L)\exp(-L)$, where k is 2.73 and L is the normalised cavity length. The exponential term is a simple expression of wave attenuation with distance, and the other term accounts for intensity decreasing inversely with distance as a circular wavefront expands.

FIG. 9. 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 4º, a value consistent with measurements of micrographs. The response of glass beads to wide-band noise was measured with a laser doppler velocimeter (Nutall et al., 1997). A number of peaks, marked with vertical lines, recur between levels of 90 dB SPL (top) and 80 dB (bottom) and can be matched with certain alignments of the specified outer hair cell array. [Adapted from Fig. 5 of Nuttall et al., 1997, and used with permission of the author and Elsevier Science.]

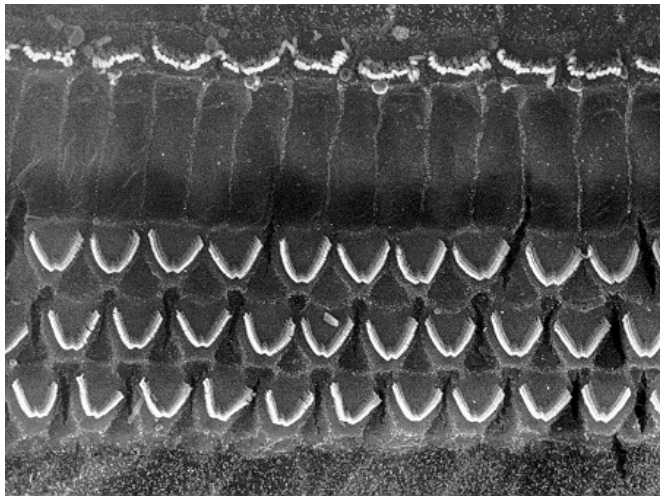

FIG. 1

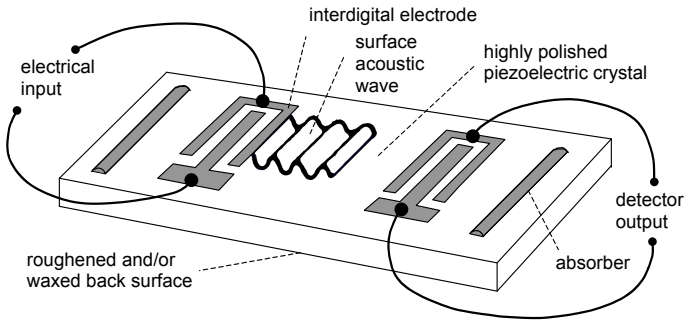
interdigital electrode
surface
acoustic
wave
highly polished
piezoelectric crystal
electrical
input
detector
output
roughened and/or
waxed back surface
absorber

FIG. 2

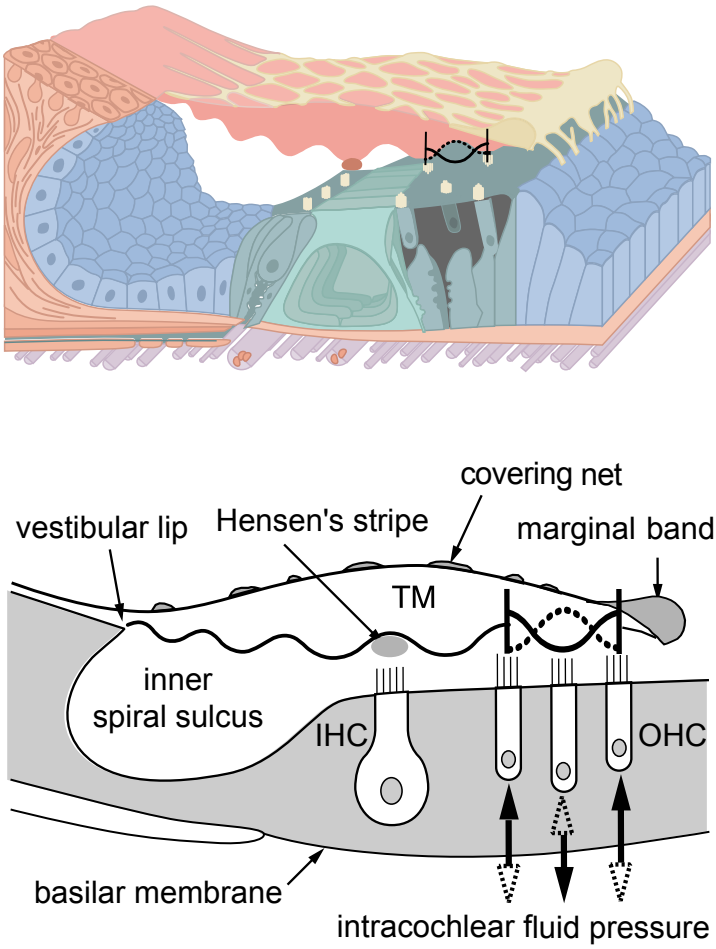
covering net
vestibular lip
Hensen's stripe
marginal band
TM
inner
spiral sulcus
IHC
OHC
basilar membrane
intracochlear fluid pressure

FIG. 3

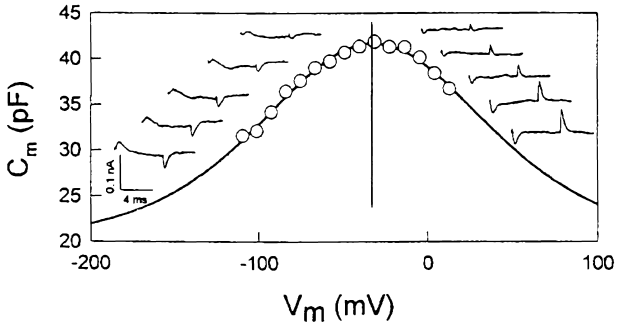

FIG. 4

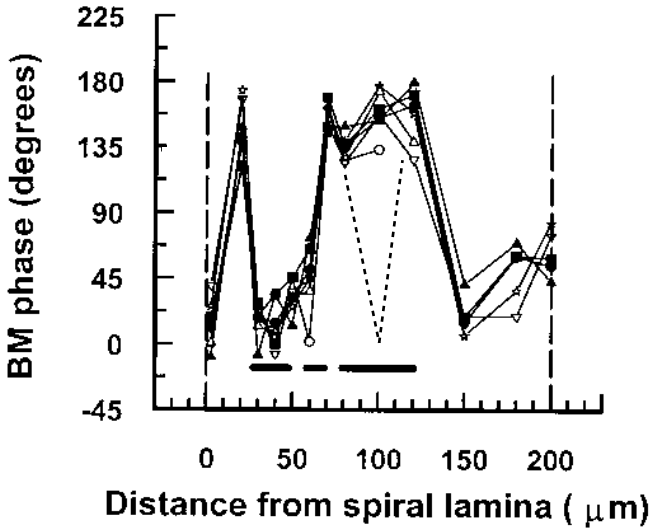
225
180
135
90
45
0
-45
BM phase (degrees)
0
50
100
150
200
Distance from spiral lamina (μm)

FIG. 5

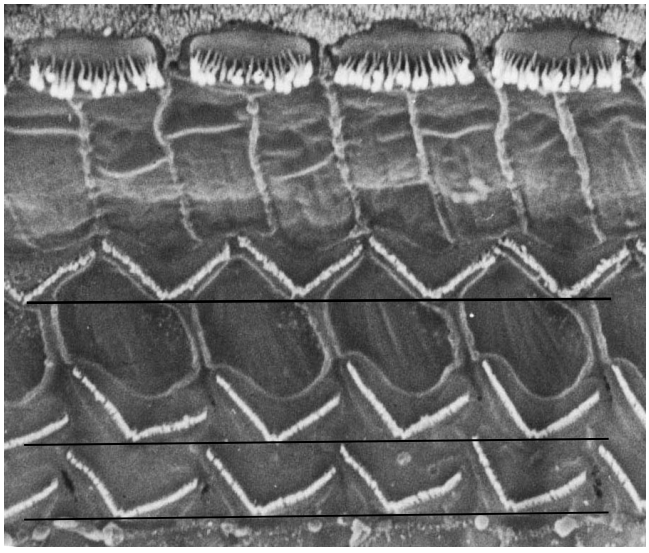

FIG. 6

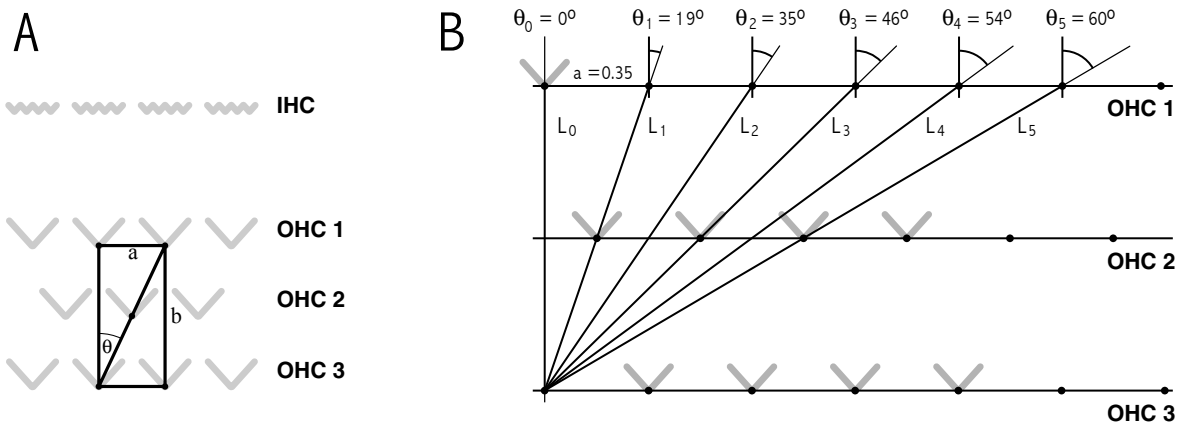
A
IHC
OHC 1
OHC 2
OHC 3
a
b
θ
B
θ0 = 0°
θ1 = 19°
θ2 = 35°
θ3 = 46°
θ4 = 54°
θ5 = 60°
a =0.35
L0
L1
L2
L3
L4
L5
OHC 1
OHC 2
OHC 3

FIG. 7

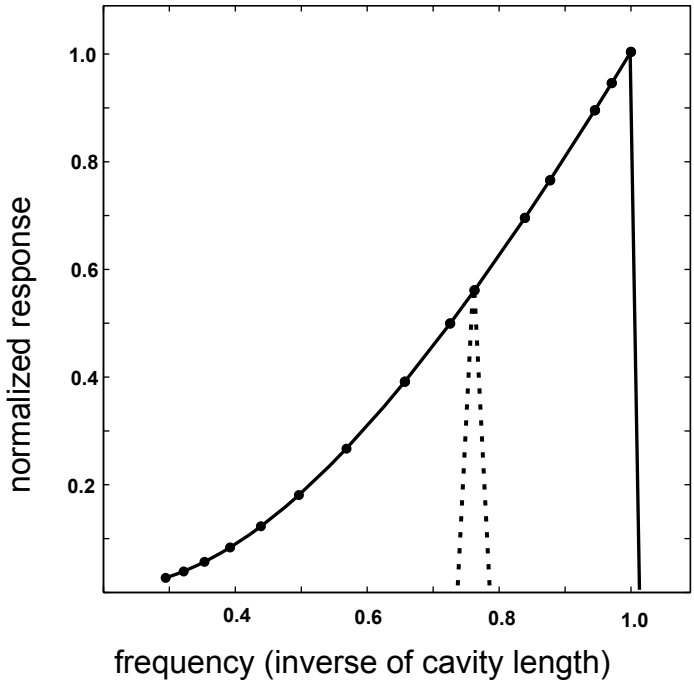
normalized response
1.0
0.8
0.6
0.4
0.2
0.4
0.6
0.8
1.0
frequency (inverse of cavity length)

FIG. 8

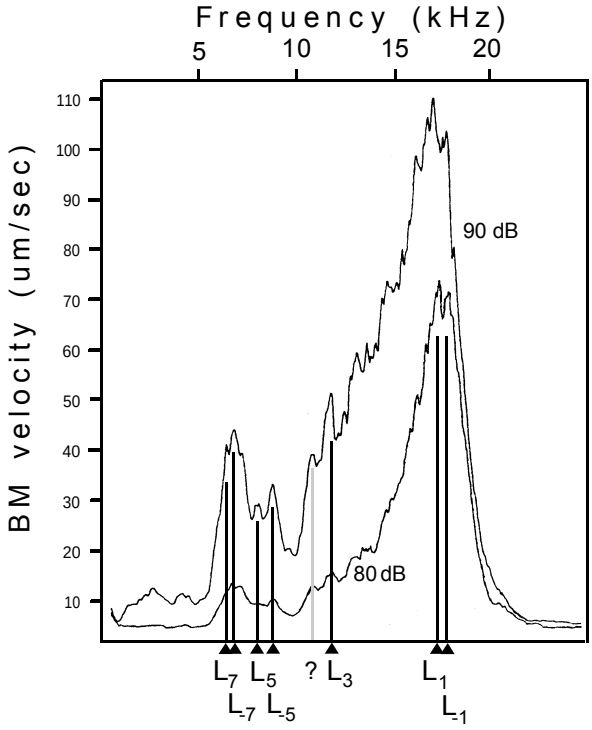
Frequency (kHz)
5
10
15
20
BM velocity (um/sec)
110
100
90
80
70
60
50
40
30
20
10
90 dB
80 dB
L7
L5
? L3
L1
L-7
L-5
L-1

FIG. 9