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Sensors, motors, and tuning in the cochlea: interacting cells could form a surface acoustic wave resonator

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Abstract

The outer hair cells of the cochlea occur in three distinct and geometrically precise rows and, unusually, display both sensing and motor properties. As well as sensing sound, outer hair cells (OHCs) undergo cycle-by-cycle length changes in response to stimulation. OHCs are central to the way in which the cochlea processes and amplifies sounds, but how they do so is presently unknown. In explanation, this paper proposes that outer hair cells act like a single-port surface acoustic wave (SAW) resonator in which the interdigital electrodes—the three distinctive rows—exhibit the required electromechanical and mechanoelectrical properties. Thus, frequency analysis in the cochlea might occur through sympathetic resonance of a bank of interacting cells whose microscopic separation largely determines the resonance frequency. In this way, the cochlea could be tuned from 20 Hz at the apex, where the spacing is largest, to 20 kHz at the base, where it is smallest. A suitable candidate for a wave that could mediate such a short-wavelength interaction—a 'squirting wave' known in ultrasonics—has recently been described. Such a SAW resonator could thereby underlie the 'cochlear amplifier'—the device whose action is evident to auditory science but whose identity has not yet been established.

1. Introduction

We now know the cochlea is an active transducer. Kemp's discovery of sound emerging from the ear (Kemp 1978) has revolutionized our approach to cochlear mechanics. Thus, an essential element of the auditory organ is a 'cochlear amplifier' whose action improves gain and tuning. If the gain is excessive at some frequency, the cochlea will spontaneously oscillate, and hence 'spontaneous otoacoustic emissions'—soft, pure tones—can be detected with a microphone placed in the ear canal. Most human ears continuously emit such tones at frequencies of 1–4 kHz and with bandwidths ranging down to 1 Hz or less. These developments are reviewed in Robinette and Glattke (2002).

What sort of biological structure could produce such pure signals? It is clear that the outer hair cells (OHCs) are intimately involved, for these sensing cells are known to be active, having a property known as 'electromotility'. When an audiofrequency voltage is applied to an isolated cell, it synchronously changes length (Brownell *et al* 1985). However, how the cochlear amplifier harnesses electromotility is unknown.

Stimulation of hair cells is presumed to occur by a hydrodynamic travelling wave moving along the partition. The difficulty is how to sharpen the response of such a broadly tuned system to give the fine frequency resolution required (Patuzzi 1996). This paper proposes that the unique structure of the sensing surface of the cochlea is designed for narrow-band frequency analysis. It conjectures that the cochlear amplifier is based on the cooperative activity of neighbouring OHCs, and functions like the surface acoustic wave (SAW) resonator familiar in solid-state electronics (Campbell 1998). If so, it would then aptly reflect Gold's suggestion that the cochlea—sharply tuned but subject to the viscosity of enveloping fluid—must operate with active anti-damping circuitry (Gold 1987).

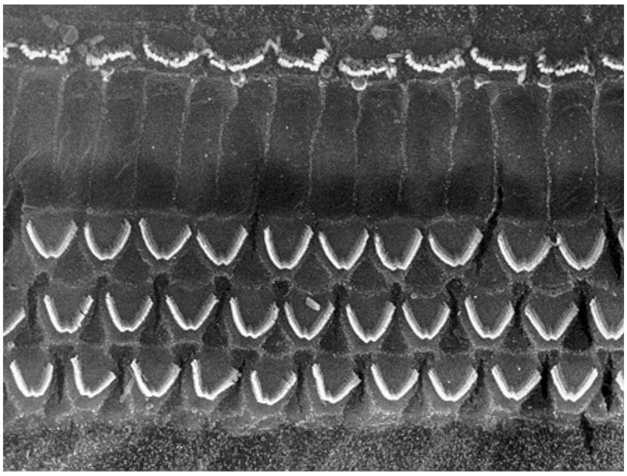

Figure 1. Three rows of outer hair cells (bottom) and one row of inner hair cells (top) in the cochlea of a rabbit. Spacing between OHC rows is about 15 μm. (Reprinted from S A Counter, E Borg and L Lofqvist 1991 Acoustic trauma in extracranial magnetic brain stimulation *Electroencephalogr. Clin. Neurophysiol.* **78** (3) 173–184 with kind permission from Elsevier Science and S A Counter.)

2. Basic description of the model

The SAW model builds on a remarkable fact: in all higher animals, including humans, OHCs lie in three (or more) well-defined rows (figure 1). This paper provides a rationale, with the rows effectively forming the interdigital electrodes of a single-port SAW resonator.

SAW devices are signal-processing modules in which finger-like electrodes are interleaved on the surface of a piezoelectric substrate to create slow electromechanical ripples whose wavelength corresponds to the periodicity of the interdigital electrodes. The SAW resonator (figure 2(*A*)) has a topology in which the electromechanical waves on the surface are arranged in a feedback loop between two sets of electrodes—a 'two-port' system, normally operated as a delay line, in which one set of electrodes launches the ripples and a similar set some distance away detects them (Campbell 1998).

SAW modules are used whenever a number of cycles of signal need to be stored and operated on. Feeding the output of the second set of electrodes back to the input set creates a high-Q resonance typically in the megahertz range. Resonance can also occur when the two sets of electrodes are merged into a 'single-port' resonator (Bell and Li 1976); in this degenerate case, ripples now reverberate back and forth between the fingers instead of between the two electrode sets. The hypothesis is that audiofrequency resonances arise in the cochlea as in the latter case.

The model is most easily conveyed by reference to figure 2(*B*), which shows a cross-section of the cochlear partition. The key components are the three rows of OHCs over which lies the soft tectorial membrane (TM); the tips of the hair-like stereocilia are embedded in the TM's gelatinous matrix. Experiments suggest that other partition structures are also relatively soft, so that forced oscillation of an OHC might

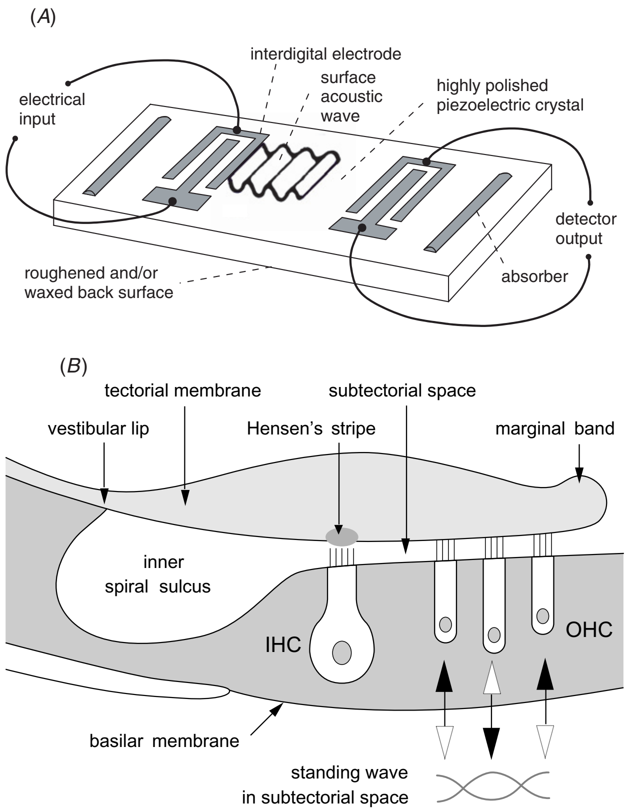

Figure 2. The cochlea resembles a surface acoustic wave (SAW) device. (*A*) In the SAW device (top) electromechanical ripples are generated and detected by two sets of interdigital electrodes on a piezoelectric substrate. Driving and sensing functions can be combined into a single set of electrodes with resonance between the fingers. (*B*) When applied to the cochlea (bottom), a standing wave (shown schematically) could form between the rows of OHCs, since they are both sensors and effectors. Arrows indicate phase of motility.

send out waves that are relatively slow and of correspondingly short wavelength.

A prime candidate for such a wave has recently been identified (Bell and Fletcher 2004): a slow, highly dispersive wave known in ultrasonics as a 'squirting wave' (Hassan and Nagy 1997). These waves can arise when a thin fluid layer is sandwiched between two deformable plates, as occurs in the cochlea (figure 2(*B*)). Because squirting waves rely on the interaction between the mass of the fluid and the elastic restoring force of the plates, they are characteristically slow—measured in the cochlear case in millimetres per second.

Squirting waves provide a ready basis for positive mechanical feedback and amplification in the partition. The proximity of motors (OHC bodies) to sensors (OHC stereocilia) invites feedback, and if the phase delay of the wave reaches 360°, oscillation between the rows of OHCs will occur. Using a simplified model and analytical wave equations, Bell (2007a) has shown that, with polarity of the input signal alternating, SAW-like, from one row to the next, a standing wave will appear as a whole wavelength between the outermost rows (OHC1 and OHC3). At the same time, a progressive, but attenuating, wave will move towards the inner hair cells (IHCs), the ear's detectors. We now have a SAW resonator amplifying an input signal and passing it to a detector.

This scheme meets Gold's prescription (Gold 1948) for a 'regenerative receiver' in the cochlea. Here, to avoid compromising signal-to-noise ratio, positive feedback is used to amplify a signal before its detection. Later, Gold (1987) 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 viscously loaded instrument be made to operate, and this is what the SAW model achieves.

The SAW resonator can be identified with the cochlear amplifier and would explain spontaneous emissions and other active aspects of cochlear mechanics. Passive behaviour of the partition might still rely on the standard travelling wave, although separating the two aspects may not be a simple matter. The tendency of the SAW model is to produce high Q responses, whereas the travelling wave is inherently low Q. The modelling of Bell (2007a) suggests a possible interplay between the two aspects, leading perhaps to the moderately tuned responses actually observed. Provided the gain and Q of the SAW model can be independently controlled, realistic amplitude and phase responses might be achieved. An attractive feature of the model is that it can mimic the 2π phase jumps observable in cochlear data.

With uncertainty still surrounding the SAW speculation, it is probably helpful, given the promising aspects, to explicitly set out the underlying assumptions.

(1) That the OHCs and their surroundings have properties conducive to the propagation of a slow wave—probably a squirting wave—communicating the motion of one row to the next.

(2) That the speed of the waves varies from base to apex in a systematic way, in this way supplying the cochlea's tonotopic tuning. Bell and Fletcher (2004) show that the dispersive properties of a squirting wave allow the human cochlea to be tuned over its full frequency range (20–20 000 Hz) based largely on the spacing of OHC rows.

(3) To complete the analogy with a SAW resonator, the response of the middle row (OHC2) is taken to be in antiphase to OHC1 and OHC3. Such a bi-phasic movement, like that of a xylophone, makes the generation of short-wavelength squirting waves particularly efficient. However, at this stage other excitation modes cannot be ruled out.

(4) IHCs respond directly to wave energy delivered to them from combined OHC activity.

(5) The path by which the sound input initially stimulates the OHCs is left unspecified. It could reside in the standard travelling wave, but direct stimulation of the OHC body by the fast cochlear pressure wave (Bell 2003) would be in keeping with the SAW analogy and have the advantage of providing a cochlea-wide, near-instantaneous input. Recent experiments provide evidence that the travelling wave is not the only stimulus to the cochlea (Guinan *et al* 2005), opening the way for fast pressure wave excitation.

3. Parallels between SAW devices and the cochlea

There are strong correspondences between a SAW resonator and the anatomy of the cochlea, which are listed below. Comparison is aided by reference to figure 2 and Slepecky (1996).

(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 OHC rows. Additional rows, sometimes present, would supply extra gain.

(2) Wave energy propagating on the surface of a SAW resonator can be absorbed or reflected by impedance discontinuities, and, when required, this is normally achieved by etching grooves or placing strips of material on the surface of the device. The TM possesses Hensen's stripe, a rounded feature located above the IHC stereocilia which is well placed to redirect wave energy emerging from the OHC cavity towards this transducer.

(3) Energy escaping the OHC cavity towards the outer edge of the TM is not useful and 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, which may act in just this way.

(4) To absorb and disperse unwanted bulk propagation modes, the back of a SAW resonator is roughened or waxed. In the cochlea the top of the TM is criss-crossed with a covering net.

(5) Towards the inner edge of the TM we find a sharp discontinuity—the vestibular lip—and here reflections could occur, returning wave energy back into the amplifying cavity and allowing real-time convolution and autocorrelation of the signal to take place (Campbell 1998, chapter 17) using IHCs as the central detector.

(6) The speed of electromechanical ripples in a solid-state SAW resonator is about five orders of magnitude lower than the speed of the electrical signal in its input leads, a reduction that makes it possible to compactly store many cycles for signal analysis. In a similar way, the speed of the hypothetical squirting wave is 4–5 orders of magnitude lower than the speed of a sonic pressure wave in the surrounding cochlear fluids, some 1500 m s^{-1}.

4. Discussion

The structural parallels are suggestive, but does the cochlea really work that way? Earlier we pointed to some initial modelling results (Bell 2007a) indicating that, despite a tendency towards unrealistically sharp tuning (high Q values), the SAW model showed some attractive features, particularly in regard to phase responses. Because the feedback is wave mediated, phase jumps of 2π are a natural property of the model, whereas it is difficult to account for them on the standard travelling wave picture. However, more theoretical and experimental work is needed to clarify this aspect.

In terms of direct observations of the basilar membrane, we already have certain experimental results that can be interpreted along the lines suggested by the model. These results can be categorized according to two main predictions.

4.1. *Prediction A. Radial wave motion*

If the SAW model is valid, we would expect closely spaced phase changes across the partition. Relative phase changes of up to 180° between locations only 10 μm apart have been observed on the basilar membrane of a guinea pig (Nilsen and Russell 1999). At the same time, several workers have seen only small phase shifts (Nuttall *et al* 1999, Cooper and Rhode 1996, Recio *et al* 1998) and others have seen none (Cooper 2000, Ren *et al* 2003). We should note that a true standing wave system, such as a vibrating string, exhibits constant phase along its length, so these results do not, by themselves, constitute contradictory evidence.

Nevertheless, the Nilsen and Russell results are highly suggestive of short-wavelength activity. In interpreting findings reported in the literature, we need to keep in mind that phase delays presently attributed to a Békésy-style travelling wave could in fact all derive from local resonance-like activity between OHCs (so-called filter delays) and from true delays (propagation delays) between OHCs and IHCs.

More recently, Gummer *et al* (2006) found experimental evidence that in excised guinea pig cochleas there was a phase difference between the upper and lower surfaces of the subtectorial space, implying that the intervening fluid must be squeezed towards the IHCs. They used the theoretical framework of Hassan and Nagy (1997) to analyse the situation and concluded that 'a pulsating fluid motion' must be stimulating the IHCs.

4.2. *Prediction B. Inverted response of the middle row*

A distinctive feature of SAW devices is the alternating polarity of the interdigital electrodes. Translated to the cochlea, this means that the response of the middle row of OHCs should be in antiphase to the others.

A clear instance of in-phase and antiphase responses can be found in Karavitaki and Mountain (2000) who found that when an isolated gerbil cochlea was stimulated the nuclei from OHC1 and 3 moved out of phase with those from OHC2.

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. This work points to the existence of two distinct classes of OHCs, and the roughly 2:1 ratio is what one might expect from two outside rows and one middle row.

Reuter *et al* (1994) studied cochlear explants from bats and noted that when single OHCs became decoupled from the preparation they no longer moved in synchrony with the other cells and sometimes distinct antiphase movements were seen.

The work of Brundin and Russell (1993, 1994) is also suggestive. These workers used fluid jets to stimulate OHCs and found that they changed length, measured as both tonic (dc) and phasic (ac) changes. Long cells tended to shorten while short cells lengthened, although cells of intermediate length could do either. They supposed that the dc changes were due to rectification and amplification of the ac responses, in which case the intermediate cells were acting in one of two different phases. This conclusion is reinforced by the later (1994) work which showed that, depending on stimulation level, a single OHC could respond in phase or 180° out of phase.

These water-jet experiments confirm earlier work by Canlon *et al* (1988) and Canlon and Brundin (1991) where cells from the mid-frequency of the cochlea either expanded or contracted after stimulation. Similarly, Brundin *et al* (1989) showed tuning curves for six OHCs that lengthened upon water-jet stimulation whereas one shortened.

Interestingly, these biphasic responses from water-jet experiments have only been seen when the OHCs were electrically floating. They have not been seen when the cells are voltage-clamped and electrically stimulated (e.g., Frank *et al* 1999 and references therein). Clamp studies indicate that OHC electromotility has a constant phase: depolarization invariably shortens a cell and hyperpolarization lengthens it (Evans and Dallos 1993). This no-clamping requirement suggests that transient voltage-sensitive currents may be operating in unperturbed cells.

As a general perspective, requiring that responses should alternate from row to row could be most easily realized by calling on the resting membrane potentials of the rows to be alternately hyperpolarized and depolarized. The work of Tanaka *et al* (1980) points this way, and in a related finding Jia and He (2004) found that a potassium current that regulates resting membrane potential varied systematically in the required direction (radially). However, it is clear that more work is needed to test this prediction.

4.3. *Biomimetics*

Many efforts have been made to construct artificial cochleas, either in electrical or micromachined form (see Chen *et al* 2006 and its references). All have been based on the classic travelling wave picture of a thin membrane of graded stiffness and width separating fluid-filled channels. The aim has been either to understand the cochlea or to make a robust frequency-analysing device. In the case of physical implementations, all designs have had poor frequency-resolution, extremely limited frequency range, and very low sensitivity.

In terms of sensitivity, for example, the live cochlea responds with a figure of roughly 10 000 to 15 000 nm Pa^{-1}, whereas manufactured counterparts typically provide responses four of five orders of magnitude less. Even the dead cochlea provides better performance than any existing physical model, even when the models artificially enhance responses by having air on one side of the membrane. To boost responses further by adding active electromechanical devices to such 'basilar membranes' appears difficult, since the mechanism behind the cochlear amplifier remains obscure.

Given this difficulty, building a sensitive biomimetic cochlea based on the SAW resonator model may be more straight forward. The design could use a set of discrete sensors and actuators arrayed as interdigital electrodes and coupled back to each other with a suitable time delay (here, a two-port system may be simpler than a single-port one). Electrical delays may be easier to implement than physical wave delays: at this stage, the use of fluid coupling and squirting waves, as supposedly employed by the cochlea, might complicate matters. The end result may be a physically realized audiofrequency spectrum analyser with narrow tuning, wide range and adequate sensitivity.

Perhaps in copying the travelling wave phenomenon to build frequency analysers we have been trying to mimic the wrong thing—the inefficient passive mechanics and not the potentially more efficient active process. It returns us to the question of what is the adequate (or primary) stimulus in the cochlea: displacement of the basilar membrane due to differential pressure, which creates a travelling wave, or common-mode pressure due to the fast pressure wave (Bell 2007b). Either, or both, may feed into the SAW mechanism; even if the travelling wave is the actual primary stimulus, the SAW mechanism could act as a fine-tuning mechanism or 'second filter'.

There are a number of other sensory systems where cells are symmetrically placed facing each other—in balance organs, or example (see figure 10.6 of Friedmann and Ballantyne 1984)—and this arrangement could comprise a mechanical filter. Indeed, the general concept of shuttling coherent energy between cells seems to offer wide scope for information processing in biological, and human-made systems. Importantly, it brings the SAW topology down from the megahertz and gigahertz realm, where it has made its mark, to the familiar world of the sonic and subsonic occupied by most living creatures.

5. Conclusion

Describing the cochlea in terms of a SAW device provides an elegant, physical realization of the cochlear amplifier. Anatomically, the cochlea seems well designed for conveying positive feedback between rows of OHCs. By making use of the distinctive properties of squirting waves, the scheme could realistically provide sharp resonance frequencies varying from 20 kHz at the basal end to 20 Hz at the apex.

The SAW model supports the earlier work of Gold, who interpreted his findings in terms of Helmholtz's resonance theory of hearing. In pointing to strong local resonances, the model also aligns with the Helmholtz picture and, if confirmed, would breathe new life into his key idea. There also appear to be several potential advantages in using the SAW topology to construct an artificial cochlea, and this possibility deserves exploration.

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