The Underwater Piano:

A Resonance Theory of Cochlear Mechanics

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This thesis is my original work and has not been submitted, in whole or in part, for a degree at this or any other university. Nor does it contain, to the best of my knowledge and belief, any material published or written by any other person, except as acknowledged in the text. In particular, I acknowledge the contribution of Professor Neville H. Fletcher who wrote Appendix A of Bell & Fletcher (2004) [§R 5.6 *in this thesis*] *and who helped refine the text of that paper. Dr Ted Maddess provided the draft Matlab code used to perform the autocorrelation analysis reported in Chapter* R7. *Sharyn Wragg, RSBS Illustrator, drew some of the figures as noted.*

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My supervisors have contributed in large measure, and I am grateful to all of them. Professor Anthony W. Gummer of the University of Tübingen saw the potential of this work at an early stage, and I thank him for his initiative in opening the door to this PhD study and providing some support (a grant from the German Research Council, SFB 430, to A.W. Gummer). Professor Mandyam V. Srinivasan of this department immediately committed himself to supporting the enterprise and has not wavered in making it the best it could be. Professor Neville H. Fletcher of the Research School of Physical Sciences and Engineering at this university has contributed a depth of acoustic knowledge, quickly supplying prompts, questions, and criticisms which have all been aimed at making the thesis logically water-tight. Dr Ted Maddess, chair of the supervisory panel, has given freely of his time, interest, and programming skill and always kept the endpoint clearly in sight. Of course, my supervisors do not necessarily accept my assumptions, conclusions, and speculations. Indeed, it must be said that my efforts to pursue an unorthodox Helmholtz resonance model, rather than the standard Békésy traveling wave model, have not persuaded all of them; nevertheless, their constructive criticisms have served to sharpen my arguments and fill in some of the details.

My ideas have also been clarified by numerous email encounters with people in the field, and their time and perspectives are acknowledged. In particular, I thank members of the Auditory, Cochlea, and Blumschein discussion lists for their willingness to hear and discuss new approaches to how the ear works. Dr Paul Kolston has been a willing listener and persistent questioner. Along the way I have crossed paths with many others, and I am grateful for the leadings they have offered.

I regard experimentation on animals as ethically unsound, and in my view destroying living creatures is not a path to reliable knowledge. Francis Bacon saw the danger of "putting nature on the rack", as Goethe expressed the scientific enterprise. Bacon thought that "intemperate experimentation might elicit misleading or distorted responses from nature [in the same way as] torture is futile because it tends to elicit false or garbled confessions"[1]. My perspective is that hearing will only be understood by studying living, intact creatures, and in testing the ideas raised in this thesis I urge that experiments respect the lives of our kindred spirits, the animals.

I acknowledge the presence of the universal mind as a source of inspiration.

[1] As paraphrased by Pesic, P. (2000). *Labyrinth: A search for the hidden meaning of science*. (MIT Press: Cambridge, MA). [p. 27] Bacon, as Lord Chancellor, was qualified to judge.

Contents

Summary

This thesis takes a fresh approach to cochlear mechanics. Over the last quarter of a century, we have learnt that the cochlea is active and highly tuned, observations suggesting that something may be resonating. Rather than accepting the standard traveling wave interpretation, here I investigate whether a resonance theory of some kind can be applied to this remarkable behaviour.

A historical survey of resonance theories is first conducted, and advantages and drawbacks examined. A corresponding look at the traveling wave theory includes a listing of its short-comings.

A new model of the cochlea is put forward that exhibits inherently high tuning. The surface acoustic wave (SAW) model suggests that the three rows of outer hair cells (OHCs) interact in a similar way to the interdigital transducers of an electronic SAW device. Analytic equations are developed to describe the conjectured interactions between rows of active OHCs in which each cell is treated as a point source of expanding wavefronts. Motion of a cell launches a wave that is sensed by the stereocilia of neighbouring cells, producing positive feedback. Numerical calculations confirm that this arrangement provides sharp tuning when the feedback gain is set just below oscillation threshold.

A major requirement of the SAW model is that the waves carrying the feedback have slow speed (5–200 mm/s) and high dispersion. A wave type with the required properties is identified – a symmetric Lloyd–Redwood wave (or squirting wave) – and the physical properties of the organ of Corti are shown to well match those required by theory.

The squirting wave mechanism may provide a second filter for a primary traveling wave stimulus, or stand-alone tuning in a pure resonance model. In both, cyclic activity of squirting waves leads to standing waves, and this provides a physical rendering of the cochlear amplifier.

In keeping with pure resonance, this thesis proposes that OHCs react to the fast pressure wave rather than to bending of stereocilia induced by a traveling wave. Investigation of literature on OHC ultrastructure reveals anatomical features consistent with them being pressure detectors: they possess a cuticular pore (a small

compliant spot in an otherwise rigid cell body) and a spherical body within (Hensens body) that could be compressible. I conclude that OHCs are dual detectors, sensing displacement at high intensities and pressure at low. Thus, the conventional traveling wave could operate at high levels and resonance at levels dominated by the cochlear amplifier. The latter picture accords with the description due to Gold (1987) that the cochlea is an ‘underwater piano’ – a bank of strings that are highly tuned despite immersion in liquid.

An autocorrelation analysis of the distinctive outer hair cell geometry shows trends that support the SAW model. In particular, it explains why maximum distortion occurs at a ratio of the two primaries of about 1.2. This ratio also produces near-integer ratios in certain hair-cell alignments, suggesting that music may have a cochlear basis.

The thesis concludes with an evaluation and proposals to experimentally test its validity.

Prologue and outline of the thesis[2]

Sitting in the enveloping quietness of an anechoic chamber, or other quiet spot, you soon become aware that the ear makes its own distinctive sounds. Whistling, buzzing, hissing, perhaps a chiming chorus of many tones – such continuous sounds seem remarkably nonbiological to my perception, more in the realm of the electronic.

Even more remarkable, put a sensitive microphone in the ear canal and you will usually pick up an objective counterpart of that subjective experience. Now known in auditory science as spontaneous otoacoustic emission, the sound registered by the microphone is a clear message that the cochlea uses active processes to detect the phenomenally faint sounds – measured in micropascals – our ears routinely hear. If the ear were more sensitive, we would need to contend with the sound of air molecules raining upon our eardrums.

What is that process – the mechanical or electrical scheme that Hallowell Davis in 1983 called the 'cochlear amplifier'[3]– which energises the hazelnut-sized hearing organ buried in the solid bone of our skull?

That question has engaged my curiosity since the late 1970s, when English auditory physicist David Kemp[4] first put a microphone to an ear and discovered the telltale sounds of the cochlea at work. Siren-like, the sounds have drawn me into the theory and experiment of cochlear mechanics, first as a part-time MSc[5] and now this PhD. This thesis is a study of the micromechanics of this process and its aim is to see whether a resonance picture of some kind can be applied to the faint but mysterious sounds most cochleas emit.

Kemp's discoveries are rightly viewed as opening a fresh path to auditory science, and to the tools and techniques for diagnosing the functional status of the

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[2] Based on Bell, A. (2004). Hearing: travelling wave or resonance? *PLoS Biology* 2: e337.
[3] Davis, H. (1983). An active process in cochlear mechanics. *Hear. Res.* 9: 79-90.
[4] Kemp, D. T. (1978). Stimulated acoustic emissions from within the human auditory system. *J. Acoust. Soc. Am.* 64: 1386-1391.
[5] Bell, A. (1998). A study of frequency variations of spontaneous otoacoustic emissions from human ears. MSc thesis, Australian National University, Canberra.

cochlea. But in terms of fundamental understanding, I am indebted to a key paper by Thomas Gold more than half a century ago[6]. Still cited widely, this paper deals with the basic question of how the cochlea works to analyse sound into its component frequencies. Two prominent theories – sympathetic resonance, proposed by Hermann Helmholtz[7] in 1885, and traveling waves, proposed by Georg von Békésy[8] – need to be distinguished (Fig. 0.1). In brief, are there tiny, independently tuned elements in the cochlea, like the discrete strings of a piano, that are set into sympathetic vibration by incoming sound [**Chapters I 1 and I 2**], or is the continuously graded sensing surface of the cochlea hydrodynamically coupled so that, like flicking a rope, motion of the eardrum and middle ear bones causes a traveling wave to sweep from one end towards the other [**Chapter I 3**]?

The first option, sympathetic resonance, has the advantage of allowing vanishingly small energies to build up, cycle by cycle, into an appreciable motion – like boosting a child on a swing. The second, traveling wave, has the weight of von Békésy's extensive experiments and a huge amount of theoretical analysis behind it. At the same time, one of the drawbacks of the traveling wave theory is the difficulty of accounting for the ear's exquisite fine tuning: trained musicians can easily detect tuning differences of less than 0.2%. Even von Békésy himself notes that 'the resonance theory of hearing is probably the most elegant of all theories of hearing'[9].

Gold's work, done in collaboration with R. J. Pumphrey[10], was the first to consider that the ear cannot act passively, as both Helmholtz and von Békésy had thought, but must be an active detector. Gold was a physicist who had done wartime work on radar, and he brought his signal-processing knowledge to bear on how the cochlea works. He knew that, to preserve signal-to-noise ratio, a signal had to be amplified before the detector, and that 'surely nature can't be as stupid as to go and put a nerve fibre – that is a detector – right at the front end of the sensitivity of the

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[6] Gold, T. (1948). Hearing. II. The physical basis of the action of the cochlea. *Proc. Roy. Soc. Lond. B* 135: 492-498.
[7] Helmholtz, H. L. F. v. (1875). *On the Sensations of Tone as a Physiological Basis for the Theory of Music*. (Longmans, Green: London).
[8] Békésy, G. v. (1960). *Experiments in Hearing*. (McGraw-Hill: New York).
[9] Ibid. p. 404.
[10] Gold, T. and R. J. Pumphrey (1948). Hearing. I. The cochlea as a frequency analyzer. *Proc. Roy. Soc. Lond. B* 135: 462-491.

system'[11]. He therefore proposed that the ear operated like a regenerative receiver, much like some radio receivers of the time that used positive feedback to amplify a signal before it was detected.

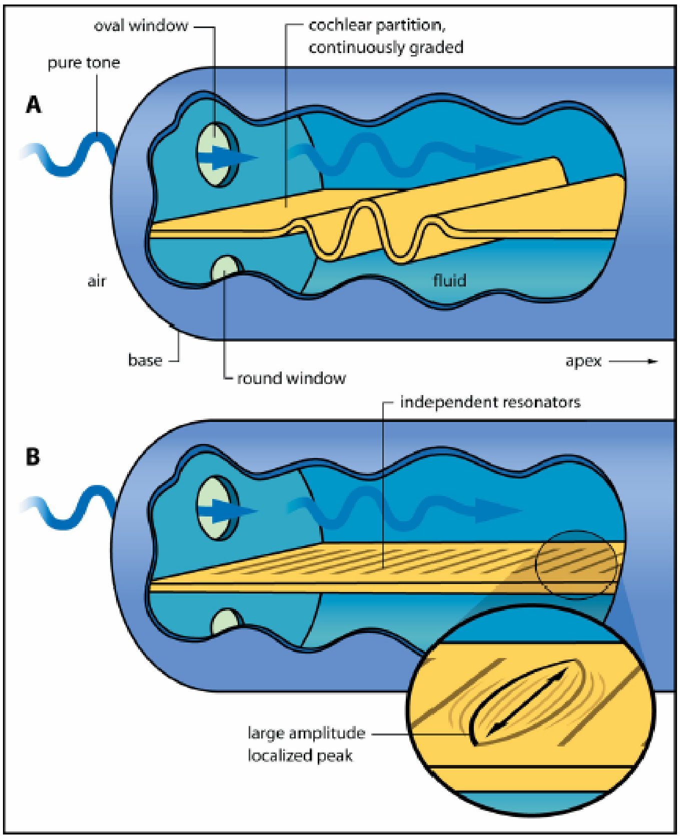

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Fig. 0.1. Two Views of Cochlear Mechanics. The cochlea, shown uncoiled, is filled with liquid. In the accepted traveling wave picture (A), the partition vibrates up and down like a flicked rope, and a wave of displacement sweeps from base (high frequencies) to apex (low frequencies). Where the wave broadly peaks depends on frequency. An alternative resonance view (B) is that independent elements on the partition can vibrate side to side in sympathy with incoming sound. It remains open whether the resonant elements are set off by a traveling wave (giving a hybrid picture) or directly by sound pressure in the liquid (resonance alone).

Regenerative receivers were simple – one could be built with a single vacuum tube – and they provided high sensitivity and narrow bandwidth. A drawback, however, was that, if provoked, the circuit could 'take off', producing an unwanted whistle. Gold connected this with the perception of ringing in the ear (tinnitus), and daringly suggested that if a microphone were put next to the ear, a corresponding

[11] Gold, T. (1989). Historical background to the proposal, 40 years ago, of an active model for cochlear frequency analysis. In: *Cochlear Mechanisms: Structure, Function, and Models*, edited by J. P. Wilson and D. T. Kemp (Plenum: New York), 299-305.

sound might be picked up. He experimented, placing a microphone in his ear after inducing temporary tinnitus with overly loud sound. The technology wasn't up to the job – in 1948 microphones weren't sensitive enough – and the experiment, sadly, failed.

Gold's pioneering work is now acknowledged to be a harbinger of Kemp's discoveries. But there is one aspect of Gold's paper that is not so widely considered: The experiments of Gold and Pumphrey led them to favour a resonance theory of hearing. In fact, the abstract of their 1948 paper declares that 'previous theories of hearing are considered, and it is shown that only the resonance theory of Helmholtz… is consistent with observation'.

I think the resonance theory deserves reconsideration. The evidence of my ears tells me that the cochlea is very highly tuned, and an active resonance theory of some sort seems to provide the most satisfying explanation. Furthermore, as well as Gold's neglected experiment, we now know from studies of acoustic emissions that the relative bandwidth of spontaneously emitted sound from the cochlea can be 1/1000 of the emission's frequency, or less. This thesis, begun initially with Professor A. W. Gummer and continued under the guidance of Professors M. V. Srinivasan and N. H. Fletcher and Dr T. Maddess, has centred on finding an answer to that most fundamental question: if the cochlea is resonating, what are the resonant elements?

A point of inspiration for me is Gold's later discussion[12] of cochlear function – some nine years after Kemp's discoveries had been made. Gold draws a striking analogy for the problem confronting the cochlea, whose resonant elements – whatever they are – sit immersed in fluid (the aqueous lymph that fills the organ). To make these elements resonate is difficult, says Gold, because they are damped by surrounding fluid, just like the strings of a piano submerged in water would be. He concludes that, to make 'an underwater piano' work, we would have to add sensors and actuators to every string so that once a string is sounded the damping is counteracted by positive feedback. 'If we now supplied each string with a correctly designed feedback circuit,' he surmises, 'then the underwater piano would work again.'[13]

[12] Gold, T. (1987). The theory of hearing. In: *Highlights in Science*, edited by H. Messel (Pergamon: Sydney), 149-157.
[13] Ibid, p.155.

This research includes an investigation of what Gold's underwater piano strings might be. A prime candidate has been found and its identity – squirting waves between rows of outer hair cells – put forward in a recent paper[14] and elaborated in **Chapter R 5**. Outer hair cells are both effectors (they change length when stimulated) and sensors (their stereocilia detect minute displacements), so in this way a positive feedback network can form that sets up resonance between one row of cells and its neighbour. The key is to transmit the feedback with the correct phase delay, and the thesis describes how this can be done using the analogy of surface acoustic wave (SAW) resonators [**Chapter M 4**] in which squirting waves carry the wave energy in the gap occupied by the outer hair cell stereocilia [**Chapter R 5**]. The paper suggests that the outer hair cells create a standing wave resonance, from which energy is delivered to inner hair cells, a picture depicted schematically in Fig. 0.2 below. In this way, the input signal is amplified before it is detected – an active system functioning just like Gold's regenerative receiver – and which is modelled using Matlab in **Chapter R 6**.

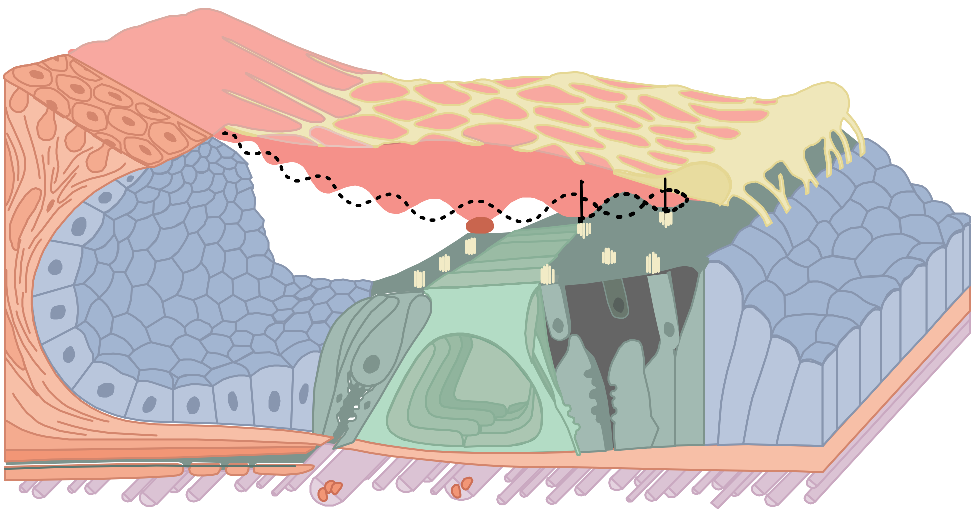

Fig. 0.2. A perspective view showing how a standing wave could form in the cochlea. The arrangement is similar to that of a surface acoustic wave (SAW) resonator, and is driven by positive feedback between rows of outer hair cells, which have both sensory and motor properties. [Adapted from Lim 1980, *J. Acoust. Soc. Am.* **67**, p. 1686, with permission of the author and the Acoustical Society of America]

[14] Bell, A. and N. H. Fletcher (2004). The cochlear amplifier as a standing wave: "squirting" waves between rows of outer hair cells? *J. Acoust. Soc. Am.* 116: 1016-1024.

With a prime candidate in place for the resonating elements, this should, I think, prompt us to re-evaluate resonance theories of hearing, which were first put forward by the ancient Greeks and which, irrepressibly, keep resurfacing. The best-known resonance theory was that formulated by Helmholtz, but at that time no satisfactory resonating elements could be identified, and it lapsed until Gold's attempt to revive it.

Chapter R 7 uses an autocorrelation technique to examine the distinctive pattern in which OHCs appear. It finds that the OHC unit cell has a geometry which may explain why distortion products in the ear reach a maximum at ratios of the primaries of about 1.2. Moreover, that same geometry produces distances between nearby cells that at times correspond to those produced by simple integer ratios of frequencies – that is, that the cochlear geometry may be designed for detection of harmonics. Here we find a possible cochlear basis for the origin of music. Pythagoras would be pleased.

There are other difficulties in reviving a resonance theory of hearing, and a major one is seeing how the outer hair cells can act as detectors of intracochlear pressure. **Chapter D 8** describes how this may occur by making use of a compressible element inside the body of the cell, a feature that also gives a natural explanation for kinocilia and the cuticular pore. **Chapter D 9** provides an electrophysiological basis for this detection scheme and suggests that the so-called 'silent current' in outer hair cells is, at sound pressure levels below about 60 dB SPL, modulated by intracochlear pressure.

It is conceivable that motion of the conventional traveling wave sets off the resonant elements, in which case we have an interesting hybrid of traveling wave and resonance. The other possibility, which this thesis argues the case for, is that outer hair cells are stimulated by the fast pressure wave that sweeps through all of the cochlear fluid at the speed of sound in water (1500 m/s). If that is so, and outer hair cells are sensitive pressure sensors, not displacement detectors, then the ear is a fully resonant, pressure-driven system, a conclusion set out in **Chapter D 10** along with predictions and suggestions for further investigation. The end point of the thesis is that it is not out of the question that the cochlea could function on resonance principles. Conceivably, Helmholtz, and Gold after him, could have been right.