RESONANCE THEORIES OF HEARING – A HISTORY AND A FRESH APPROACH

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ABSTRACT. This paper provides an historical overview of how a powerful acoustical principle – sympathetic resonance – has been applied to our organ of hearing. It focuses on the principle's virtues, drawbacks, and varying fortunes. Why did Helmholtz's resonance theory of hearing in the 1850s fall from universal acceptance to near total disregard? What were the factors favouring travelling wave theories, most notably that of von Békésy in the mid 20th century? Post-Békésy, however, thinking on cochlear mechanics has been radically changed by findings that the cochlea is an active transducer, not a passive one as previously thought. As Kemp demonstrated in 1979, healthy cochleas are highly tuned and continuously emit narrow-band sound … prompting the thought that something seems to be resonating. Maybe, then, it is worth re-examining resonance, even though travelling waves remain the centre-piece of the standard cochlear model. A fresh resonance formulation is described.

1. INTRODUCTION

If the ear were more sensitive, we would have to contend with the noise of air molecules raining upon our ear drums. The core of our multi-stage sound transducer is the cochlea, a spiral-shaped organ the size of a hazelnut buried in the solid bone of the skull.

Operating close to theoretical limits, the cochlea has a 10-octave frequency response, operates over a signal power range of a million million times (120 dB), and exhibits a noise floor close to thermal noise. It's electrically powered using supplies of a fraction of a volt, and operates underwater (the cochlea is filled with watery liquid). And while we have broad ideas of how it works, there's still a long way to go.

Because the cochlea is inaccessible and delicate, its experimental study is difficult, and so auditory science has relied heavily on theory, informed by anatomy, psychophysics, and sometimes inconclusive direct probing on animals (experiments which, from my ethical perspective, are regrettable). There have been a multitude of theories, and progress has often been slow.

But in 1978 a new window into the cochlea suddenly opened. English auditory scientist David Kemp [1] discovered that the organ not only detects sound but produces it. He placed a microphone in his ear and picked up the faint but distinct sounds of the cochlea at work.

His discovery of "otoacoustic emissions" has revolutionised the field and led to new diagnostic tools and methods. Most human cochleas produce an echo in response to a click and, more remarkably, constantly emit faint, narrow-band tones. We now know much about these energetic phenomena, but still remain largely ignorant of how they are produced and how they relate to the fundamental process of sound transduction.

Here I give a broad outline of the two major theories of hearing – the accepted travelling wave theory and the now virtually outmoded resonance theory. Following Kemp's discoveries, the hearing field has generally been content to build active properties on top of the passive travelling wave, but I have misgivings. There are certain unsolved problems associated with travelling waves, and I think a resonance picture may provide a way around them.

Starting afresh, I have been endeavouring to construct a new resonance model of hearing. The following sections provide a historical perspective on the development of resonance theories, describe the general principles on which they operate, and argue for why resonance deserves reconsideration. As part of this, a summary is given of how the newly constructed model works.

2. HISTORY

For most of recorded history, people have turned to resonance as an explanation of how we hear. The ancient Greeks held that "like is perceived by like" so, in order for the inner soul to perceive a sound, Empedocles (5th century BCE) said there had to be direct contact. In other words, the ear must contain something of the same nature as the soul, and this was a highly refined substance particularly tenuous and pure called "implanted air", and it was this that resonated to incoming sound. "Hearing is by means of the ears," said Alcmaeon of Crotonia in 500 BCE, "because within them is an empty space, and this empty space resounds."[2] Aristotle concurred and said that when we hear "the air inside us is moved concurrently with the air outside." Empedocles introduced the notion that in the same way as the eye contains a lantern, the ear contains a bell or gong that the sound from without causes to ring [3]; perhaps he noticed the ringing sound in his own ears, an experience we now call tinnitus (Latin for "tinkling bell").

Renaissance science recognised the importance of resonance and Galileo formally treated the phenomenon in 1638 [4]. Observation of stringed musical instruments showed that they readily picked up vibrations in the air around them. Importantly, they responded in a discriminating way, becoming alive only to like frequencies and remaining insensitive to others.

The first scientifically based resonance theory of hearing was that of Bauhin [4] in 1605. It was successively refined by others, all considering air-filled spaces as the resonant elements. DuVerney in 1683 thought the cochlea's bony but thin spiral lamina vibrated – with high frequencies at one end and low at the other – and the notion of spectral analysis by sympathetic resonance had been born. Soon the idea of vibrating strings emerged, and by the 18th century people were using the analogy of the sensory membrane being composed of strings as in a stringed musical instrument.

All of this thinking culminated in the immensely influential work of Helmholtz which he put forth in his landmark *Sensations of Tone* [5]. His resonance theory began as a public lecture in 1857 and within 20 years had gone on to become almost universally accepted. Helmholtz applied his scientific and mathematical skills to the simple analogy of the cochlea as a graded array of minute piano strings. Speak into a piano (with the dampers raised), said Helmholtz, and the strings will vibrate in sympathy, producing an audible echo; in like manner, the cochlea's arches of Corti will reverberate perceptibly in response to incoming sound. His presentation gave details of anatomy, number of resonators, and their degrees of coupling and damping, and it all seemed to fit nicely. He had to modify the theory to accommodate new anatomical findings, switching to the fibres of the basilar membrane as the preferred resonators, but the essence of his theory remained.

But then problems arose. The major one was a doubt that independently tuned stretched strings could exist in the basilar membrane. Anatomically, the structure shows a rather loose appearance and, since the fibres form a mesh, they must be closely coupled. It is therefore hard to see that the fibres could be finely tuned, that is, that they could have an appreciable quality factor, or Q, especially when the basilar membrane is immersed in liquid. And how could something no bigger than a nut have within it a structure able to resonate in sympathy with the throb of a double bass, for example?

The theory aims to explain how our keen pitch perception originates – we can easily detect changes in frequency of less than 1% – but if the Q of the fibres is low, this leads to the prediction that our pitch perception is correspondingly poor. On the other hand, if we nonetheless insist on retaining high Q, this invites another difficulty: a tone will take many cycles to build up and as many to decay, producing a hopeless blur of sound like a piano played with the sustain pedal always down. Something was amiss and the theory fell from favour.

Moreover, there were new alternatives. With the invention of the telephone, theories appeared likening the cochlea to a vibrating diaphragm. Some thought that the diaphragm was the basilar membrane; others thought the tectorial membrane a better choice.

3. TRAVELLING WAVE THEORIES

Towards the end of the 19th century another novel theory arose: that of a travelling wave [4]. It came in a succession of forms, the first being that of Hurst in 1894, who suggested a wave of displacement travelling down the basilar membrane (hence the name). Variants were put forward by Bonnier (1895), ter Kuile (1900), and Watt (1914). These theories made a positive virtue out of their low Q, explaining how sound perceptions could start and stop instantly. They also gave a useful role for the cochlear fluids, using hydrodynamics to help with propagation of the wave.

The wave is considered to travel along the basilar membrane like a wave in a flicked rope. Travelling wave theories are built on the idea that the cochlea is a coarse frequency analyser, leaving it to the nervous system (or perhaps some mechanical "second filter") to sharpen up the response.

The most famous travelling wave theory is due to Georg von Békésy who won a Nobel Prize for his decades-long efforts, beginning in 1928, to elucidate the mode of action of this wave. It is his name that we associate with the theory, for he was the first to actually observe a travelling wave in the cochlea, both in human cadavers and in animals, using intense sound stimulation and stroboscopic illumination [6]. He also built water-filled boxes divided by rubber membranes, and saw similar behaviour. He started his experiments expecting to rule out the basic place principle of Helmholtz [7] – that the sensing membrane in the cochlea maps frequency to distance along it – but was surprised to discover that, depending on the frequency of excitation, the peak of the wave shifted systematically from the base of the cochlea to its apex, offering a degree of frequency resolution. Again, the peak was supposed to be fine-tuned neurally so that, to quote Békésy [8] "very little mechanical frequency analysis is done by the inner ear."

As well as suitably low Q, the other attractive feature of his travelling waves was that they showed, in accord with observations, several cycles of delay between input and response. This seemed to be decisive evidence against the Helmholtz theory, for a simple resonator will give, at most, a phase delay of ±90° between driving force and displacement. By 1948 the travelling wave theory seemed incontrovertible.

4. GOLD'S RESONANCE IDEAS

But not quite. In 1946 a young Cambridge graduate accidentally landed into hearing research after doing war-time work on radar. Full of electronic signal-processing knowledge, Thomas Gold became focused on how the ear could attain such high sensitivity and frequency resolution. He was dissatisfied with the travelling wave picture because it cast an impossible burden onto the neural system: no matter how sharp its discrimination may be in theory, in practice noise enters all physical systems and will throw off attempts to precisely locate the peak. He became convinced that the basis of our acute frequency discrimination must reside in the ear. But how was that possible when cochlear fluids alone are sufficient to assure high damping?

During a boring seminar, inspiration hit: if the ear employed *positive feedback*, he realised, these problems could disappear [9]. He knew all about regenerative receivers, which were simple circuits that used positive feedback to amplify a radio signal before it was detected, thereby achieving high sensitivity and narrow bandwidth. He reasoned 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 system", and so proposed that the ear must be an active system – not a passive one as everybody had previously thought – and that it worked like a regenerative receiver. In this way, damping could be counteracted by positive feedback, and, given just the right level of feedback gain, the bandwidth could be made arbitrarily narrow.

Gold later framed the problem confronting the cochlea in terms of an evocative analogy [10]: the cochlea's strings – whatever they may be – are immersed in liquid, so making them resonate is as difficult as sounding a piano submerged in water. But if we were to add sensors and actuators to every string, and apply positive feedback, the "underwater piano" could work again.

He and Pumphrey, his colleague, designed experiments to test the hypothesis that there must be high-Q resonators in the ear. There were two ground-breaking experiments in 1948 [11,12], the first of which involved testing the hearing thresholds of listeners first to continuous tones and then to increasingly briefer versions. If hearing depends on resonators building up strength, like pushing a child on a swing, the threshold should depend in a predictable way on the number of pushes, or cycles. Their results accorded with this picture, and they calculated that the Q of the resonators must be between 32 and 300, depending on frequency.

Flowing from Gold's model was a startling prediction: if the ear were in fact using positive feedback, then if the gain were set a little too high, it would continuously squeal, as regenerative receivers (and PA systems) are prone to do. Daringly, he equated this state of affairs with the common phenomenon of ringing in the ear, or tinnitus. He caused his ears to ring by taking aspirin, placed a microphone in his ear, and tried to pick up a sound. The conditions and equipment weren't right, and the experiment failed.

Gold and Pumphrey remained convinced that Helmholtz was correct, and the abstract of their 1948 paper declares "previous theories of hearing are considered, and it is shown that only the resonance hypothesis of Helmholtz... is consistent with observation"[13]. Gold paid a visit to Békésy in Harvard and tried to convince him of the impossibility of relying on neural discrimination. He also pointed out the scaling errors that Békésy introduced by building a cochlear model many times actual size, but each side stuck to their views, and for many years – until Kemp's momentous discoveries – Békésy's ideas prevailed [14]. People just assumed that the high Qs that Gold and Pumphrey had found must have a neural origin, and the loop-hole in their second experiment (the extra cue) was leapt upon.

With Gold's ideas falling on deaf ears, he left the field and made a name in cosmology instead.

5. DISTINGUISHING TRAVELLING WAVE AND RESONANCE

Békésy made many mechanical models demonstrating how a travelling wave works, and he did important work clarifying the fundamental differences between travelling waves and resonance. To model the cochlea he built arrays of pendulums – bobs on strings of varying length – suspended from a common rod.

First he demonstrated that a bank of resonators (the pendulums) could behave like a travelling wave. If there were coupling between the resonators – such as by threading rubber strands between the strings – then after exciting the shortest pendulum, a wave motion would be seen progressing from this pendulum to the longest. If the coupling is light, then the wave progresses very slowly, giving large delays.

The other way of exciting what looks like a travelling wave is to suddenly jerk the rod. Even with no coupling, an apparent wave will be seen to move from the shortest pendulum towards the longest. In this case the wave carries no energy; it is just an illusion, an epiphenomenon, reflecting the fact that the shortest pendulum will accumulate phase faster than the longer ones. It's rather like the blinking lights outside a theatre which give the impression of movement.

It is important for later discussion to recognise that although they can give a similar result, there are fundamentally different physical processes driving them. In terms of physical understanding, we need to clearly distinguish these two mechanisms, for one marks a travelling wave theory and the other a resonance theory.

Travelling wave. The essence of a travelling wave theory is that the signal path through the resonators is *in series*. That is, the input to the system is via the high frequency resonator and the energy is passed sequentially (via coupling) to lower frequency resonators. The Q of the individual resonators can be high or low, but the key is that the signal energy is injected into the high frequency end, just as what happens in a tapered transmission line. Likewise, the classic travelling wave theory of Békésy is that the input applied to the stapes causes an immediate deflection of the basilar membrane at the high frequency end and this is then coupled (hydrodynamically and materially) to neighbouring sections until a peak is reached at the characteristic place (after which motion quickly decays).

Resonance. By way of contrast, what distinguishes a resonance theory of excitation is that the signal energy is applied to the system *in parallel*. Thus, when we jerk the rod suspending the pendulums, or lift the lid on a piano and yell into it, the excitation is applied to all the resonant elements virtually simultaneously. In the same way, Helmholtz called for an array of independent resonators that were excited by sound passing through the cochlear fluids. It is this idea that I want to reconsider.

The advantage of the pure resonance approach is that only that resonator with matching frequency receives energy (provided the Q is sufficiently high). Moreover, weak signals can, cycle by cycle, cause a resonator to build up an appreciable in-phase motion, like a child pumping a swing. In this way the cochlea would be able to hear sounds just above thermal noise.

The question, then, is can a resonance mechanism operate in conjunction with the travelling wave one? Perhaps the ear uses a hybrid of travelling wave and resonance to optimise performance. No one yet believes they have the perfect cochlear model, and maybe persistent anomalies in travelling wave models can be resolved by introducing resonance effects. Whatever the answer, it must accommodate the range of cellular-powered phenomena discovered by Kemp.

6. KEMP AND THE ACTIVE COCHLEA

David Kemp's experiments gave a clear demonstration that Gold was heading in the right direction and have changed the face of auditory science. In the same way as faint radio signals have opened an unsuspected window on outer space, his otoacoustic emissions have limned a new horizon into inner space. In 1978 he placed a microphone in his ear and picked up the faint signal that Gold had been searching for 30 years earlier. His equipment was better, and you didn't need to induce tinnitus to pick up a ringing sound.

We now recognise broad classes of acoustic emissions. As well as the striking spontaneous emissions, other continuous signals of cochlear origin can be detected: stimulus frequency emissions (where the sound coming out is at the same frequency as that going in) and distortion product emissions (where the modulation products of two input stimuli are detected). The most widely employed tools for diagnosis of cochlear function use transient stimuli: in response to a click, an echo will come back from the cochlea – Kemp's original experiment – and similarly a tone burst of a set frequency will lead to a similar answering echo.

These 'active' properties reflect the operation of a so-called 'cochlear amplifier' and they fade away once sound intensities reach 60–80 dB SPL. The active cochlea is highly tuned, and the relative bandwidth of spontaneous emissions, which show very stable frequencies, can be less than 1 in 1000.

When I first read a report of Kemp's findings in 1979, I was astonished. Surely travelling wave theory couldn't be right: how could a more or less slack membrane immersed in fluid sing? Helmholtz must be closer to the mark, I thought, and I have been intrigued by the cochlea and its micromechanics ever since. I have been searching for an explanation of spontaneous emissions: if something is constantly ringing, what are the resonating elements? Gathering clues to their origin, I studied the stability of these tones [15], and am now currently engaged in PhD research at the Australian National University investigating whether a resonance model of the cochlea is possible.

The auditory community has interpreted Kemp's work in terms of a travelling wave but with additional parameters. People accept Gold's incisive idea of an active cochlear process, but resist his call to reinstate simple resonance. Thus, the delay of the cochlear echo has been seen as the delay of the travelling wave as it propagates from the stapes to its characteristic place and then, by means of a "reverse travelling wave", returns to its place of origin. If the stimulus recirculates, the travel time for the loop defines the period of a spontaneous emission. To counter propagation losses, the basilar membrane has been ascribed negative resistance, a state of affairs presumed possible by some (unknown) sensing action of the outer hair cells – which are pretty certain to be the source of the mechanical activity detected by Kemp. We now know, for example, that when an outer hair cell is stimulated, it changes length cycle by cycle in step with the stimulus [16]. In other words, these cells are effectors as well as sensors.

7. TRAVELLING WAVES AND RESONANCE

This all adds up to a system that can be described by travelling wave equations and which mimics what happens in a tapered transmission line (provided the line also contains a travelling wave amplifier and can operate in reverse). There is no doubt that this class of model comes close to describing the measured responses of the cochlea. However, I think a resonance mechanism may play a significant, if not dominant, part at low sound levels.

But first, one should realise that there are two different, although related, signals in the cochlea. One is the usual acoustic pressure wave that, following back-and-forth vibration of the stapes, is communicated to the cochlear fluids at the speed of sound in water (1500 m/s). This wave creates, nearly instantaneously, a hydraulic pressure field, the size of the pressure being controlled largely by the compliance of the round window (which is the major point of pressure relief) since the rest of the cochlea, mostly water, is nearly incompressible. This hydraulic pressure is sometimes called common-mode pressure, for it occurs, in phase, on both sides of the sensory partition.

The second signal is the differential pressure, the difference in pressure between the upper gallery (scala vestibuli) and the lower gallery (scala tympani) caused by the presence of the partition itself. It is the differential pressure that causes a slow travelling wave of displacement to propagate from base to apex (because of the graded acoustic stiffness of the partition), and this motion is presumed to bend stereocilia and stimulate the firing of hair cells. The common-mode pressure has been thought to have no sensible effect on the cells and has been disregarded (after all, hair cells do bear distinctive stereocilia).

My idea is that this neglected compressional wave could stimulate outer hair cells – without requiring a travelling wave to bend stereocilia. This possibility fits in with how some water-dwelling animals hear: they need to detect the long-range (far-field) pressure component of an underwater sound, not the short-range (near-field) displacement component which rapidly fades. Sharks, for example, pick up distress calls over hundreds of metres (when displacements have shrunk to 10^{-12} m). Sharks have no swim bladder, and the auditory cells in their macula neglecta carry no otoliths, so how do they detect long-range pressure? Anatomy gives a clue: their auditory cells house many 'vacuities' within the cell body itself [17], suggesting they use an enclosed bubble to perform 'on the spot' pressure-to-displacement conversion.

In a similar way, I suspect that mammalian outer hair cells detect acoustic pressure. The direct pressure signal is fast and phase coherent, making a clean and clear signal for an organism to feed into a cochlear amplifier.

Such an arrangement may be able to explain behaviour that the travelling wave cannot. For example, cochlear echoes show a similar waveform as input signal strength is raised. Active travelling wave models have not yet replicated this behaviour and a recent paper announced in its abstract that this behaviour "contradicts many, if not most, cochlear models"[18]. Another prominent modeller noted the difficulty

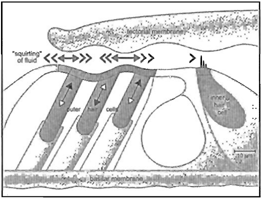

Figure 1. Strings of an underwater piano? The cochlea's resonant elements could be tiny parcels of liquid oscillating in a positive feedback loop between rows of outer hair cells. Outer hair cells moving up and down (in response to intracochlear pressure) could create 'squirting waves' in the fluid gap above. The waves could in turn bend stereocilia (for clarity, not shown), creating positive feedback and a standing wave. Wave energy escapes to the inner hair cell's stereocilia, and we hear.

of formulating a satisfactory time-domain model and suggested that "non-causal" factors must be at work [19]. In addition, people with blocked round windows can still hear, as can those who have lost middle ears to disease – observations difficult to square with a travelling wave model.

If a pressure wave is the exciting stimulus in these cases, it raises the possibility of parallel excitation of a resonant system. But what, then, are the resonating elements? As set out below, candidates for the piano strings can be identified and they appear to have the necessary pressure sensitivity [20], allowing construction of a fully resonant model of the active cochlea.

8. A NEW RESONANCE MODEL OF THE COCHLEA

My conceptual resonance model takes as its starting point the special nature of spontaneous otoacoustic emissions. It sees these stable and narrow-band signals as the cochlea's intrinsic resonant elements – its piano strings – and not as by-products of over-active forward and reverse travelling waves in a recirculating loop. That implies we have an array of highly tuned generators, exquisitely sensitive to sound, disposed from base (high frequency) to apex (low). Each string has its distinct place on the membrane, as required by Helmholtz's place principle.

We know that outer hair cells are active elements responsible for the so-called "cochlear amplifier" [21], so each string must somehow involve these cells. The inspiration for this work is that a string can form in the *space* between cells. Outer hair cells are precisely arranged in three distinct rows, and because the cells are, as mentioned earlier, both sensors and effectors, it is possible for positive feedback to occur between the motor element of one cell (its cell body) and the sensing element of a neighbour (its stereocilia). The result is stable oscillation, and this, I suggest, is the cochlea's elusive tuning element.

Oscillation occurs in a direction across the partition, not up and down as the travelling wave theory supposes. This bypasses the requirement for the mechanics of the partition to be governed by differential pressures and travelling waves. However, it introduces its own tuning problem: how can the space between the rows be tuned over 3 decades of frequency? If we require a single wavelength between the rows – a distance of about 30 micrometres – this calls for a very slow wave. For example, a 1 kHz wave shuttling between the rows will need to travel 30 μm in 1 ms, or just 30 mm/s.

Happily, such waves do exist. They are known in ultrasonics as symmetric Lloyd–Redwood waves, or "squirting waves", and propagate in the thin gap between two compliant plates immersed in water – just the arrangement we find in the space occupied by the hair cell stereocilia (Fig. 1). A recent paper [22] shows how the slow speed and high dispersion of these waves allows the "strings" to be tuned over the full range of human hearing. The standing wave produced by the squirting wave provides a natural explanation for the cochlear amplifier: it is a positive feedback system that amplifies the input signal before passing it to the inner hair cells (which finally transduce the signal into nerve pulses and send it to the brain). In other words we have a regenerative receiver performing amplification before detection, just as Gold required. The system is like his "underwater piano": it uses a system of sensors and actuators in a positive feedback loop to overcome the effects of viscosity and produce high Q.

We have the piano strings, but for a true resonant system we need the bank of resonators to be excited in parallel (that is, simultaneously). As foreshadowed, that could happen if outer hair cells are sensitive to the fast pressure wave. Outer hair cells are constructed like pressure sensors and are in continuous hydraulic connection with the cochlea's entire fluid contents – anatomically, they are, unlike inner hair cells, surrounded by fluid spaces, not other cells. Intracochlear fluid pressure could therefore be an important stimulus.

This new resonant scheme, unlike a bank of pendulums, is not limited to phase variations of ±90°. This is because the wavelengths involved are small compared to the width of the basilar membrane, and so phase delays can accumulate in the supporting structure before they are communicated to the basilar membrane where observations are finally made.

Like all pianos, the cochlear version has that essential component, dampers. The dampers are the efferent system, which is able to electrically adjust the gain of each of the outer hair cell triplets. The mechanical gain from positive feedback depends on having a differential response between the three rows, so by adjusting the resting membrane potentials between rows, the efferent nerves could quickly raise or lower the gain.

The evidence that outer hair cells react to pressure stimuli [23] is scattered and indirect, but prevalent. Naturally, if the cells are pressure detectors, they will have some compressibility. Imagine what would happen if the stapes pushed in on the nearly incompressible fluids of a cochlea surrounded by solid bone: the energy would be funnelled directly to the most compressible parts – in particular, I suggest, the outer hair cells. These cells are well designed to be pressure sensors: they are constructed like rigid test tubes with a small compliant spot (the cuticular pore) at the top. Significantly, this pore is a vestige of where, during development, a sensory apparatus (the kinocilium) used to be. Thus, the biochemical signalling could still be in place to register movement of the cuticular pore created by pressure differences between the cell interior and the cochlear fluid.

For efficient operation, outer hair cells would need to contain a very compressible material. Air would be a good choice, and these cells do contain a peculiar spherically layered structure – Hensens body – whose function could be to generate an air bubble, much like the swim bladder cells of fish do and, even more so, like the hearing cells of sharks and their 'vacuities'. The compressibility is possibly part of a positive feedback loop of its own in that when a cell changes length in response to stimulation it is difficult for it not to change volume too. If so, outer hair cells could appear much more compressible than air itself – rarefied air, if you will.

If this begins to sound like "implanted air", one can only respect the insight of those ancient Greek philosophers and wonder again whether they, and Helmholtz and Gold, might have been right.

9. CONCLUDING REMARKS

"The resonance theory of Helmholtz is probably the most elegant of all theories of hearing", said Békésy [24], and I agree. The travelling wave theory strikes me as failing to meet the cochlea's requirement for utmost finesse. It is based on the assumption that up and down motion of the basilar membrane always drives the outer hair cells, when it could be that, at low sound levels, it's the other way round. In a living system, common-mode pressure could resonantly stimulate outer hair cell motion in a direction across the partition; in this way we could escape the long-assumed need for differential pressure to be the sole driving force in the cochlea.

The cochlea could make the best of both worlds, using resonance at low sound levels and a travelling wave at higher ones. This division of labour might underlie the cochlea's astounding dynamic range. Whatever the case, I think there must be a major role for resonance. Sympathetic resonance is a principle behind everything from quarks to quasars, and must surely have a place in the raison d'etre of acoustics – the ear.

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