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Ray Meddis: A model scientist

Christian J. Sumner[1]

[1] Department of Psychology, Nottingham Trent University, Nottingham, UK

ABSTRACT

Ray was a scientist in the classical sense: a creative intellect who sought the truth. He was also someone who had a profound impact on the career of many hearing scientists. Ray believed that to understand hearing it was necessary to replicate its behavior in a computer model. His first major contribution in hearing was the "Meddis Haircell", and a series of papers exploring the adaptation of firing rate in auditory nerve fibers. These were accompanied by models of stream segregation, of pitch, of the segregation of concurrent vowels, numerous models of the processing of sound by neurons in the auditory brainstem, and a non-linear model of the basilar membrane. In later years, Ray became increasingly interested in hearing loss, and the role of the olivocochlear system. Technology also deserves a special mention: Ray's models were implemented in silicon, evaluated using automatic speech recognition, and even inspired a smart-phone based hearing aid. Ray lives on in his work, but also his colleagues: those of us that learnt from him, worked with him, disagreed with (yes!), were influenced by his work, and shared his passion for models of the auditory system.

Keywords: Ray Meddis, computational models, hearing

1. INTRODUCTION

Roll back to the 1980s (for me, at least): Live Aid, Dungeons and Dragons, and the BBC-microcomputer (32K, of course). But, though I didn't know it yet, another 80's classic, the Meddis Haircell (5), was going to be just as iconic and influential in my life.

Ray was the first hearing researcher I met. In the 1990s he was unique in the UK: a full time auditory modeler (not one of those experimentalists who dabbled with models). I visited his labs, first at the University of Loughborough and then the University of Essex. Like anyone else who showed a passion for hearing, and especially models of hearing, he welcomed me warmly from the first day. And like for many others, meeting Ray Meddis was a pivotal event in my career.

Ray's own career in research did not begin with hearing. His PhD was on the psychometrics of mood, in which he studied the factor structure and correlations between different ratings of mood. Following this he published several articles about rank methods in statistics, before beginning a program of research into sleep, including publishing a book on his theories (7).

Eventually, Ray discovered his calling: developing computer models of how we hear. For over 35 years, Ray developed computer models of the auditory system, ranging from cochlear filtering to auditory scene analysis. In this article, I will attempt to provide a review of some of his (early) work, and the work that has had the greatest influence on my own. It is not possible to discuss all his work, and I apologize for that which has been omitted. Neither is it possible to provide the complete context of related work by other authors of the time (more apologies). However, I will attempt to mention some of the developments that *followed* Ray's contributions, to indicate his influence.

Overall, I wish to convey his creativity. He was a scientist who generated many ideas, about an aspect of the world that fascinated him. His ideas were not always right, but they were always of great intellectual value and utility, and served to push forward our understanding of the auditory system.

2. THE PERIPHERY

Ray's work in hearing began with the auditory periphery, and this is the area of hearing in which he published the most papers (32 articles) and arguably had the most impact on the field (>2500 citations at the time of writing, according to Google Scholar).

[1] christian.sumner@ntu.ac.uk

2.1 The "Meddis Haircell"

The first publication in the field was a model of the inner haircell (IHC), and the adaptation of firing rate observed on the auditory nerve (5). The model simulated the sound driven release, and recycling of neurotransmitter at the IHC-auditory nerve synapse (Stage 5 in Figure 1). This model was remarkably successful in reproducing the firing properties of the auditory nerve.

Previous models (reviewed in 4) had introduced increasingly complex arrangements of neurotransmitter reservoirs, in order to account for observed adaptation characteristics. His model proposed a process consistent with physiological evidence at other synapses: the recycling of neurotransmitter. The limited supply rate of new transmitter, and the limited rates of reuptake and recycling, all contributed to the adaptation and saturation characteristics of firing rate at the synapse. It also had acceptable input-output non-linearity, rectification and phase-locking properties. This is a good example of Ray's modeling philosophy: that a model's properties should emerge naturally from faithful modelling of the mechanism, rather than by engineering-in each property explicitly.

Numerous modelling studies in the 1990s, including Ray's, employed an initial bandpass filter to model the outer/middle ear transfer function, a linear Gammatone filterbank to model the mechanical filtering of the basilar membrane, and a haircell model. Often this was an array of "Meddis haircells", or a subsequent model proposed by Westerman and Smith which performed quite similarly but was analytically tractable (8, 9). Either way, the result was a computationally efficient, and remarkably functional "auditory frontend" which could be used as the input to models of subsequent processing.

These models were not without limitations. They did not capture the compressive nature of the cochlear filtering (due to the linear modelling of basilar membrane filtering). Nor could they account for the variation in firing rate as a function of level seen in different types of auditory nerve fibers. The Meddis haircell also phase-locked to higher frequencies that that of mammals. In 2002, Ray, myself, Lowel O'Mard and Enrique Lopez-Poveda published a revised IHC model (2) (Figure 1A). The incorporation of a biophysical model of the filtering by the haircell membrane (10) provided the further low-pass filtering to correctly model the phase locking seen both in the haircell itself and the auditory nerve.

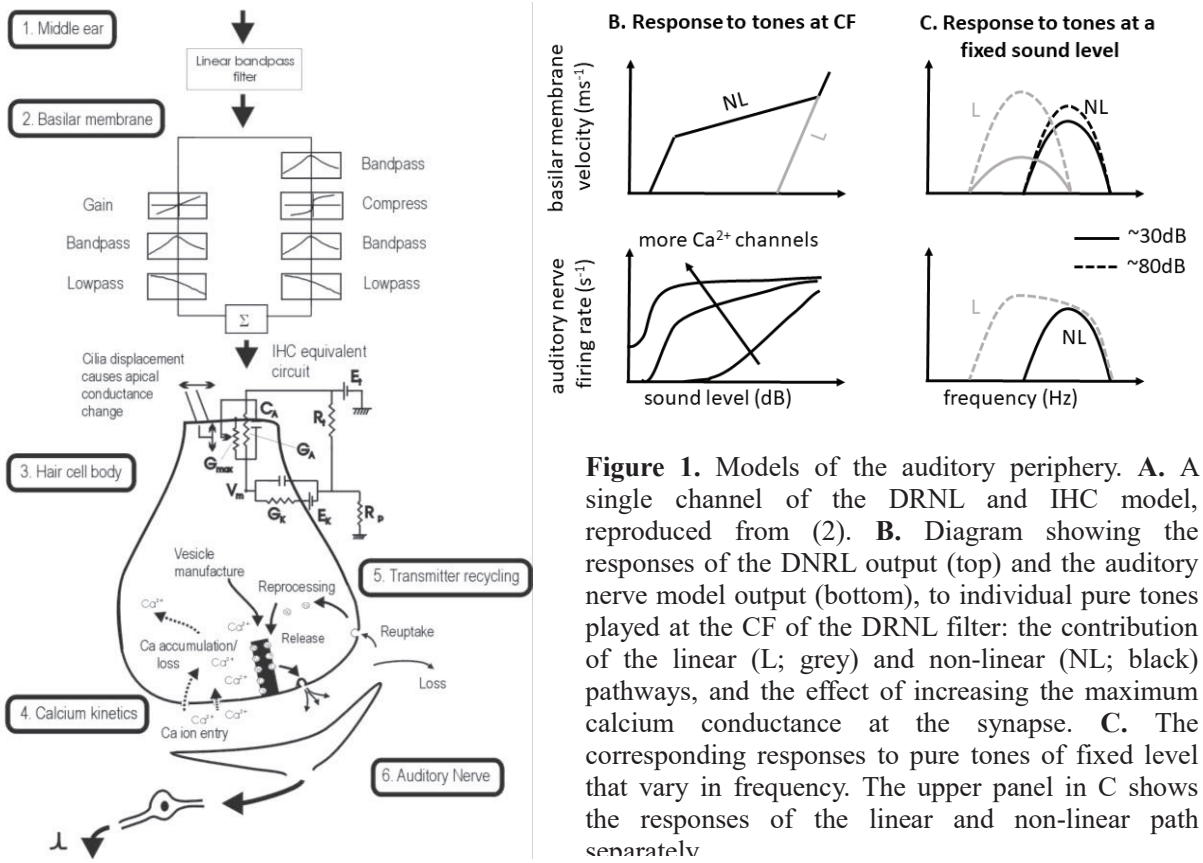

Figure 1. Models of the auditory periphery. **A.** A single channel of the DRNL and IHC model, reproduced from (2). **B.** Diagram showing the responses of the DNRL output (top) and the auditory nerve model output (bottom), to individual pure tones played at the CF of the DRNL filter: the contribution of the linear (L; grey) and non-linear (NL; black) pathways, and the effect of increasing the maximum calcium conductance at the synapse. **C.** The corresponding responses to pure tones of fixed level that vary in frequency. The upper panel in C shows the responses of the linear and non-linear path separately

The 2002 model also proposed that Calcium channels at each synapse might determine the auditory nerve fiber type. It is well established that, in all synapses, depolarization of the cell membrane (neuron or haircell) leads to the influx of Calcium, which in turn leads to the release of neurotransmitter (Figure 1A, stage 4). Scaling the overall amount of Calcium (the number of ion channels) at a synapse could act as a "gain" mechanism to determine the spontaneous rate. Simultaneously, this determined the window of dynamic range over which the synapse operated, determining the threshold of the nerve fiber and the shape of the rate-level function (Figure 1B).

Ray was passionate that wherever possible, the models should reflect mechanisms faithfully; that this would lead to more elegant models with more predictive power. At the time there was no experimental evidence to support the Calcium hypothesis for fiber type. Yet, recent data lend some support to this idea (11). This model also proposed that he number of vesicles of neurotransmitter ready for release at any one time was proposed to be small (~10), and this influenced the statistics of auditory nerve action potentials. Recent work has greatly expanded the range of spiking statistics that can be accounted for by models with as few as 4 quanta (12, 13).

2.2 Basilar membrane filtering

The Dual-Resonance Non-Linear (DRNL) filter, developed with Enrique Lopez-Poveda and Lowel O'Mard (14) to address the limitations of a linear filterbank, was a "non-linear bandpass" model (15). It proposed that the basilar membrane could be modeled as two parallel filter pathways (Figure 1A, Stage 2). The compressive pathway had a higher gain, and so determined the responses at low sound levels, producing the sensitive 'tip' of the tuning curve. The linear pathway was of lower gain, but because of the compression in the non-linear pathway, the output of the linear pathway dominated the overall output at high sound levels (Figure 1B). The linear-pathway produced the low-frequency tails of tuning curves, and led to a shift in center frequency with increasing sound levels (Figure 1C).

The DRNL was straightforward to fit to basilar membrane laser interferometry data (16); it produced suppression effects and distortion products (14). It could also account for masking data in human subjects (17). In keeping with Ray's modelling philosophy, several observed aspects of cochlear non-linearity, such as two-tone suppression and phase reversal, were emergent properties of the model. Furthermore, by changing a single parameter in the DRNL, one could control the gain of the "cochlear amplifier". Thus it could stimulate outer haircell damage, or the efferent control by the medial oliviocochlear system, which synapses on to outer haircells, and modulate the energy that they can impart to BM motion (18, 19).

The work of Ray, colleagues and others (20, 21) brought us the modern phenomenological cochlear model: capable of reproducing a great many of the known properties of the auditory periphery. In some instances such models can replace recordings from the auditory nerve, e.g.(22).

Recent data has consolidated the view that human auditory filters are narrower than in typical experimental mammals (23). The controversy surrounding this arose in part because different psychophysical methods of estimating auditory filter widths give different estimates of cochlear tuning (24). To my knowledge, no model of the auditory periphery has yet successfully accounted for both ways of estimating cochlear tuning. Human models are necessarily are less constrained than those of animals; we do not know what human auditory nerve tuning curves look like. A well constrained model of the human periphery, which can account quantitatively for this difference, and for other data such as two-tone suppression, would surely be a valuable step in fully understanding how cochlear filtering influences human perception and communication.

3. PITCH

3.1 The autocorrelation model of pitch

In 1991, Michael Hewitt and Ray produced the definitive computational model of pitch processing (25) and his most cited work (>600 citations at the time of writing). Based on the original autocorrelation model proposed by Licklider (26), this model encapsulated the development of this and contemporary theories at the time (27) concerning the importance of temporal coding of periodicity in the auditory system for determining our perception of pitch.

The first stage of the model (Figure 2A) is a filterbank model of the auditory periphery similar to that already described. The autocorrelation stage then reveals the periodic variation in firing rate in each channel (Figure 2B, upper plot). These functions are pooled (i.e. averaged) across the filterbank

channels and a subsequent algorithm identifies the pitch from this pooled-autocorrelation function (Figure 2B, lower plot), often by finding the delay at which the highest peak occurs in the function. Several similar models were produced since from Ray and others, e.g. (28). Although addressing various limitations, a wide range of studies support that autocorrelation is a good model of pitch.

In the intervening years, there has been no evidence of autocorrelation being performed in any part of the auditory pathway. Numerous alternative mechanisms have been proposed e.g. (29), but the puzzle of pitch remains.

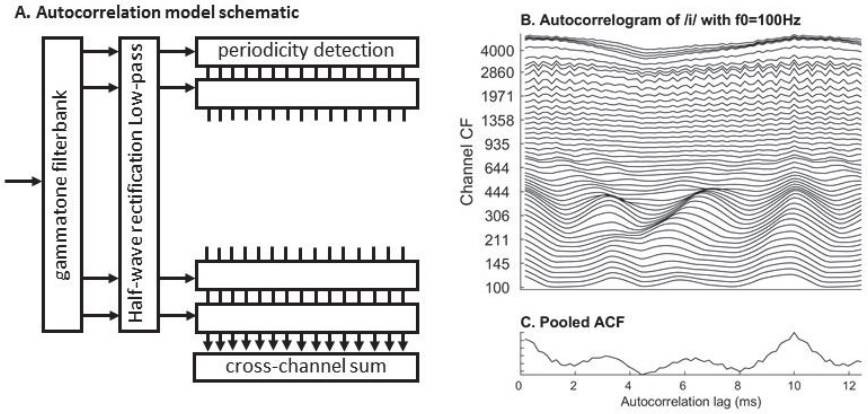

Figure 2. The autocorrelation model of pitch. **A.** Model schematic adapted from (1). **B.** Example autocorrelation output, based on the model from Smith et al. (4). C. Pooled ACF function.

4. BRAINSTEM AND MIDBRAIN NEURAL MODELS

Facilitated by their work on peripheral models, Ray and colleagues were well placed to study how the representation produced by the cochlea might be transformed by the brainstem and midbrain.

4.1 Cochlear nucleus cells

The cochlear nucleus (CN) is the first site of auditory processing in the central nervous system. To a crude approximation, the CN can be considered as a set of parallel processing pathways operating on the input from the auditory nerve. Knowledge of the connections, and understanding of the role of these connections within CN continues to grow. However, the responses of some CN neurons can be understood from the way that they integrate information across multiple auditory nerve fibers, and their intrinsic membrane properties. Stellate cells receive innervation from a number of auditory nerve fibers with similar CFs. Below threshold they act as comparatively linear leaky-integrators of their inputs. In response to a pure tone stimulus they exhibit particular precision in the timing of the first 2-3 action potentials. In a histogram of the timing of these spikes as a function of the time within the stimulus (a peri-stimulus time histogram; PSTH), this is visible as two or three distinct peaks at the beginning of the response (Figure 3B). Due to these peaks, these neurons are classified as 'choppers'.

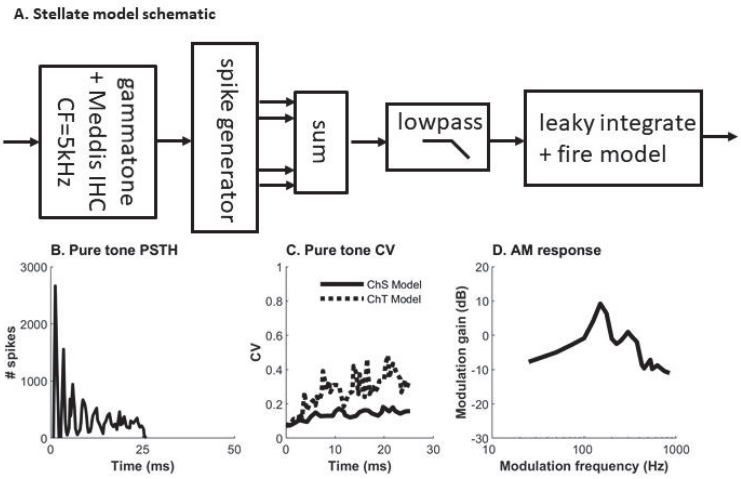

Figure 3. Stellate cell model. **A.** Model Schematic (adapted from 3). **B.** Example of a sustained chopper (ChS) response from (adapted from 3). **C.** Coefficient of variation (CV) of the response in **B** and of a less regular transient chopper model adapted from (3). **D.** Phase-locking in a sustained chopper model to the frequency of a sinusoidally amplitude modulated tone, expressed as gain relative to the modulation in the stimulus waveform adapted from (6).

Chopper neurons vary in the degree to which the regularity of this spiking continues throughout the response to a pure tone. Evidence suggested that inhibition played a key role in determining this (30). Hewitt and Meddis (3) demonstrated further, that a single 'integrate-and-fire' type model neuron (Figure 3A) with no inhibition could reproduce this behavior, and regularity was dependent on the number of auditory nerve fibers innervating the neuron, the threshold and the current magnitude of the individual inputs.

A further interesting property of this cell type was the way that it encoded the acoustic envelope. The mean firing rate of neurons in CN is generally insensitive to frequency of amplitude modulation (AM). Rather, information about any modulation is encoded in the timing of spikes. This is not dissimilar to the way that auditory nerve fibers 'phase-lock' to low frequency carriers and AM. However, unlike the auditory nerve, phase-locking in individual chopper neurons is 'tuned' to specific modulation frequencies (31). Thus a logical hypothesis was that these neurons formed the first stage in an envelope extraction process in the brain, with different neurons being tuned to different modulation frequencies. Meddis and Hewitt (32) demonstrated that their simple stellate neuron model demonstrated similar phase-locking to the envelope as that observed in vivo.

Computer models have continued to contribute to our understanding of processing in the CN. For example, models have shown how auditory nerve innervation contributes to the responses of onset and primary-like neurons (33, 34), and have been instrumental in synthesizing how different membrane currents contribute to response properties (35-37). Models of stellate-cells also successfully predicted the existence of mode-locked (more complex patterns of synchronization to envelopes) spike trains in these neurons (38). Such models are now informing our understanding about the consequences of synaptopathy (39).

4.2 Comodulation masking release

Although many properties of cochlear nucleus cells appear to arise from their intrinsic membrane properties and their innervation via the auditory nerve, the importance of network processing in the CN is becoming increasingly clear (40). One of the best established sources of local connections in the VCN are the inhibitory connections provided by the D-stellates which are associated with 'onset-chopper' responses. Ray and colleagues proposed that this wideband inhibitory circuit could enhance signals in noise, by providing inhibition which was time locked to wide-band envelope fluctuations, suppressing the response to the masker in conditions where a masker's spectral energy was co-modulated across a wide frequency range. This lead to an effect similar to the psychophysical phenomenon known as co-modulation masking release (41, 42). This work highlighted how models of the VCN could yield meaningful predictions about circuit processing, as has been more frequently demonstrated in the dorsal region of CN, e.g. (43). Evidence continues to accumulate of circuitry in VCN, e.g. (44). Perhaps the next frontier is to bring these models together at a large scale, e.g.(40). With ever more computational power, simulating the entire cochlear nucleus may be sight.

4.3 Coincidence detection in the midbrain

One of the most controversial debates in the encoding of modulation has been the topographical (or periodotopic) arrangement of neurons in the inferior colliculus (IC) which, unlike in the CN, show rate-tuning to modulation frequency (45). The contribution of Hewitt and Meddis (32) was to show a possible way in which this firing rate sensitivity might arise from temporal modulation tuning of cochlear nucleus stellate cells, which project to the IC. In this model, the firing rate-tuning is determined by the temporal tuning of a number of CN neurons converging onto one IC neuron. The converging CN neurons have similar temporal tuning. Their locking to the envelope is most coincident when stimulated with modulation frequencies close to the peak in the tMTFs of the CN model neurons. Thus, the firing rate of the IC neuron increases close to the tMTF peaks in the CN stellate cells projecting to it. The model was effective at reproducing the rate-sensitivity of IC neurons, and the effects of sound level on those functions (45). It is clear, e.g. (46, 47) that several other factors can also influence modulation tuning in the IC. Nevertheless this model demonstrated that it was relatively simple to transform the temporal coding in the brainstem into a rate code in the midbrain.

4.4 A chopper neuron based pitch model

The possible role of cochlear nucleus stellate cells and coincidence detection in the IC for pitch processing was subsequently investigated by Weigrebe and Meddis (48) and Meddis and O'Mard (49). Their model was proposed as a physiologically plausible equivalent of the previous autocorrelation model, with a similar overall architecture, but with different individual components. In place of an

autocorrelation operation, for each frequency channel of the cochlear filterbank there was an array of cochlear nucleus stellate cells. This was followed by a layer of inferior colliculus coincidence detectors, individually tuned to the range of pitch periods required. Duplicated across the frequency range of the cochlea, this created a two-dimensional 'correlogram-like' map of the periodicities present in each frequency range. A subsequent set of across-frequency integrators for each delay tuning, also presumed to be in the IC, formed the equivalent of the pooled-autocorrelation function from which pitch judgements were to be made. This stellate cell model and the subsequent stages in the IC demonstrated sensitivity to variations in stimuli consistent with pitch, such as the ability to extract the pitch from a harmonic complex with a missing fundamental or sensitivity to linearly shifted (i.e. inharmonic) components. This study stands as a valuable addendum to autocorrelation models of pitch: the brain *does* have the computational facility to process the cues for pitch. The potential of coincidence detection for processing pitch has now been demonstrated several times, e.g. (50-52).

5. FINAL REMARKS

This short article has focused on a subset of Ray's work. It omits many other contributions by him, his colleagues, and does a poor service to many other scientists who shared his passion and inspired him. Ray had a tremendous influence on not only the research but the lives of individuals. He cared deeply not only about the topic but also the people he worked with, mentored, and his colleagues in the wider community. One last point: Ray began his work in hearing, creating models of the auditory system was a relative rarity. Today, complex numerical methods and computational models are indispensable and standard tools. This means there are more opportunities for the next generation of auditory modelers to follow in the footsteps of Ray. I'm pretty sure he would be happy about that.

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