

I Introduction to Biological Hearing

The mystery of the ear inspires the psychologist, the physiologist, the otologist, and the physicist alike.
S. S. Stevens & H. Davis, 1938.

1.1 Introduction

No clear, comprehensive and internally consistent description of a theory of hearing has appeared in the literature to date. *The goal of this work is to provide a comprehensive and contiguous physiological description of hearing that includes both its acousto-mechanical (and hydraulic) and neural (electrolytic) dimensions.*

The depth and breadth of the presentation should be limited only by man's limited knowledge of the physical and biological world at the start of the 21st Century. This goal is not easily achieved between the covers of a book of practical size. Therefore, a new approach has been taken. A synopsis of this work will be available on the World Wide Web at www.hearingresearch.net. This source will be maintained for at least the next five years and is fully searchable. The website also contains a large glossary of terms uniquely defined to support discussions of the hearing modality. These alternate sources will be updated as the field continues to move forward.

Some of the technologies used in hearing have been only recently discovered. As a result, a comprehensive understanding of hearing has not been possible before the close of the 20th Century. One purpose of this work, and the supporting website site, is to describe these technologies in sufficient detail to be useful to the research biologist.

Critically important to any understanding of hearing has been the discovery of the active electrolytic semiconductor device, the Activa. This biological equivalent of the transistor, is the key to understanding the operation of the neural system. Its discovery has led to the Electrolytic Theory of the Neuron. This Electrolytic Theory of the Neuron replaces the earlier chemical theory of the neuron. The Electrolytic Theory of the Neuron provides detailed answers to questions that could not even be asked, with precision, under the now archaic chemical theory.

A brief glossary associated with hearing is presented in Appendix A. An updated and broader glossary is provided on the website.

1.1.1 The task of the biological sensory systems

Figure 1.1.1-1 attempts to show the high level of integration employed in the sensory neurological system. The sensory neurons of the peripheral nervous system (PNS) provide information concerning a wide variety of parameters to several different feature extraction engines of the cortex. The information extracted by these initial engines, primarily associated with the thalamus, is delivered to a common saliency map describing the environment of the animal in a form that can be accessed by the cognitive engines of the central nervous system (CNS). This form is largely independent of the original information. The form is most conveniently described as a group of analog signatures describing the original signal information. The signatures delivered to the saliency map from the major sensory modalities can be divided into two groups, those related to the awareness of the surrounding environment and those related to the analytical activity applicable to a particular object in the environment. The saliency map is

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not housed within a discrete portion of the CNS, but is distributed. It is most easily associated with the parietal lobe of the CNS. It is not clear at this time whether a distinct separation occurs between the current saliency database and a longer term memory database. This work will focus on the hearing modality. A companion work has presented a similar review of the vision modality¹.

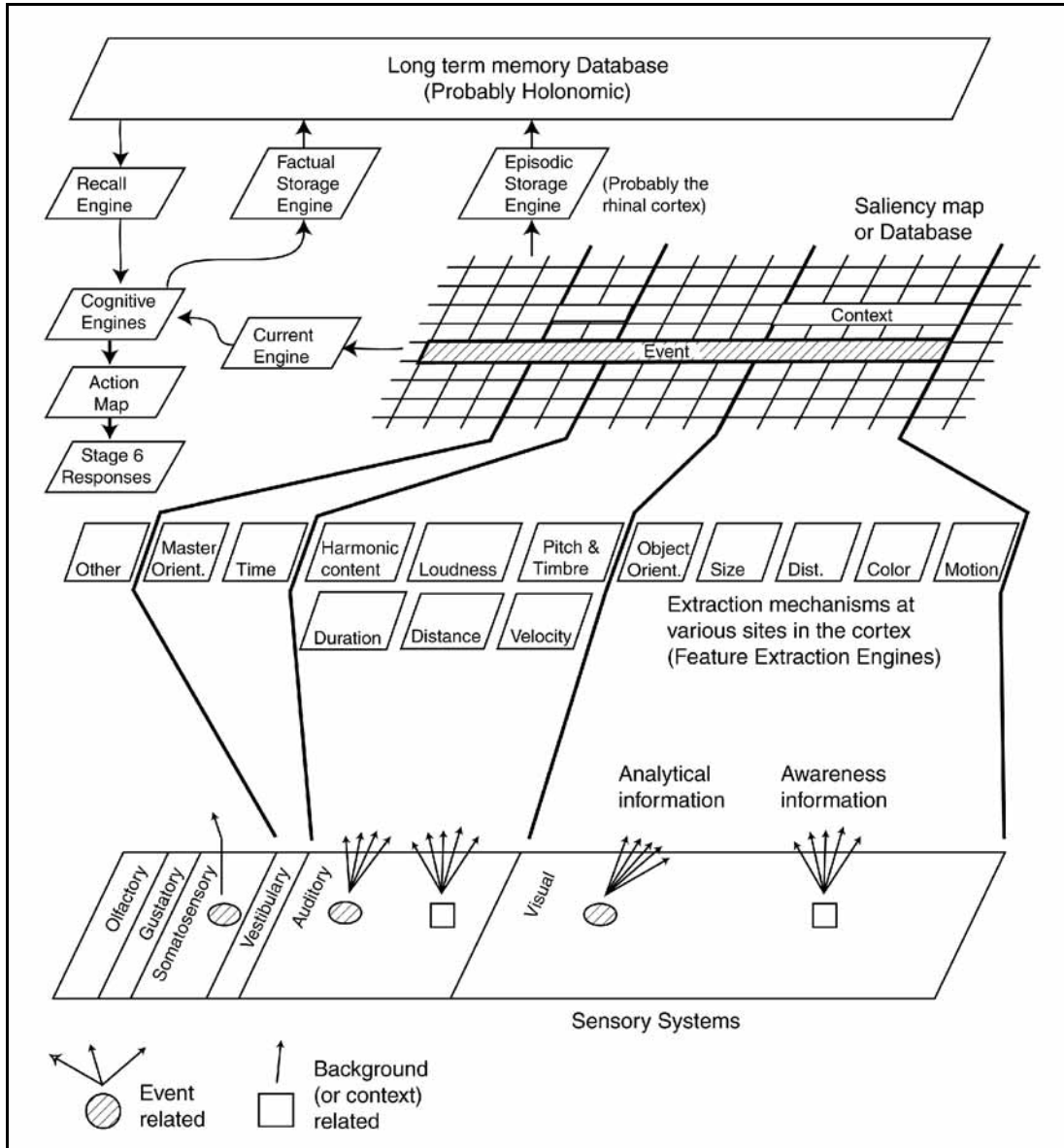


Figure 1.1.1-1 The saliency map as a point of convergence within the neural system of all animals. All of the sensory modalities feed information into the saliency map. The cognitive engines of stage 5 can access the map and other memory units prior to generating instructions to the superior colliculus to send commands to the stage 6 motor-glandular system.

1.1.2 The goal of this work

The task of this volume is a formidable one. It is best illustrated using Figure 1.1.2-1. The figure provides the spectrum of a very complex acoustic stimulus extending over only two and one-half seconds as well as the thought conveyed to a competent English speaker. The goal of this work is to explain how the hearing modality accepts this stimulus, processes the relevant signals, extracts the relevant information and presents the resultant perception to the cognitive portions of the brain for its consideration.

A complete theory and model of the auditory system should provide additional information concerning the message. This information includes the location of the source relative to the listener, and both the identification and mood of the speaker based on previous interactions. To keep this volume to a manageable size, the subjects of binaural source location and the characteristics of the source based on the timbre of the message will be postponed to a future work.

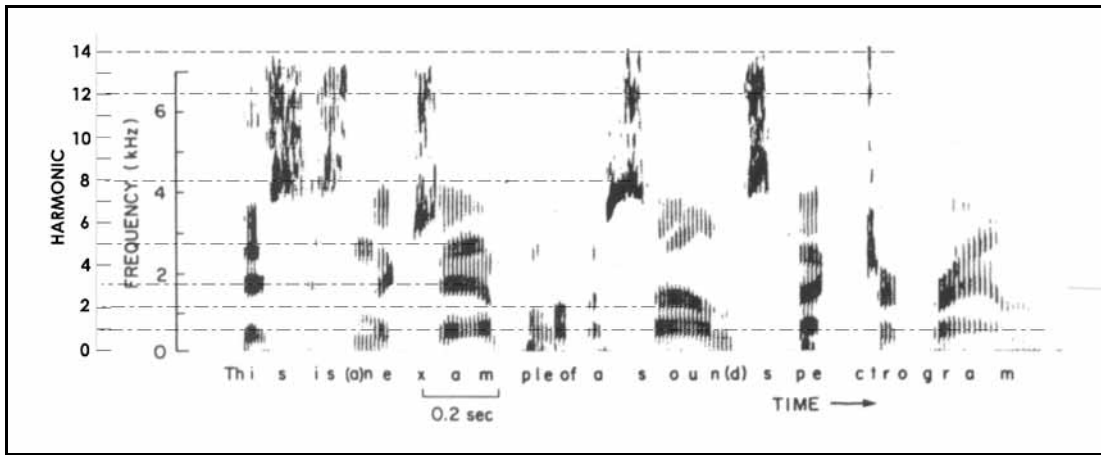


Figure 1.1.2-1 A spectrogram highlighting the features present in human audition. An overlay has been added to highlight the role of harmonics of the original tone formed by phonation. The frequency of phonation changes significantly as shown by deviations from the fundamental frequency (first harmonic). Modified from Stevens in Tower, 1975.

Understanding the precision with which the frequencies within the spectrogram can be determined is also a goal of this work. Similarly, defining the precision with which the timing of features can be obtained is also a goal. Determining the precision with which the amplitude of the signals, within the frequency and time constraints, can be determined is a third goal.

The sensory modalities of hearing and vision share many architectural similarities at the neural level (since they support a common central nervous system (CNS)). Section 1.3.1 includes a block diagram illustrating some of these similarities. Analogies between the two systems will be exploited in developing this theory of hearing.

1.1.3 A formal definition of hearing

Starting a book with a clear definition of the subject matter is important. However, for hearing this is not easy and has seldom been done. The hearing community has not placed a priority on describing the focus of their efforts. While this is understandable during the early days of exploratory research in a field, it is hardly an early day in hearing research. It is the author's position that it is well past the time to transition from largely unstructured exploratory research into a more organized applied research phase. A clear definition of hearing is needed as a basis for using a more structured Scientific Method, as required in applied research.

Webster hosted a meeting attempting to define this modality in 1990². The preferred definitions appear to have ranged between that of Bullock and a 1974 expression by Wever. This work needs a clearer and simultaneously broader functional definition of hearing from an operational perspective.

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Hearing is that sensory modality of the neurological system in animals tasked with characterizing the relevant external acoustic environment surrounding the animal. No limits are placed on the modality with respect to the intensity range, the temporal interval, or the frequency range, associated with hearing. These limitations are introduced in the evolutionary implementation of the modality in response to the specific needs of the animal. These needs are largely controlled by the ecological niche of the animal. Part of the external environment may be actively generated in support of echolocation.

While this definition includes the sensing of acoustic energy by the lateral line sensors of bony fish, the performance of this modality in fish will not be pursued here. Smith has provided a first level overview of that system that shows the similarity to the systems to be discussed here⁴.

Fay has commented on the remarkable ability of the overall hearing system to perceive a wide variety of sound sources simultaneously and both differentiate between them and characterize each of them⁵. The ability of the system to isolate and continue to perceive speech in the presence of frequently overwhelming backgrounds is a remarkable feature of the system. The more the background resembles broadband noise, the easier for the system to discount it during conversation. The system relies upon structure in the analytical process.

1.1.4 State of the Hearing Research art

The current state of the art in hearing research is the result of a series of questionable intellectual turns taken over a long period of time. The first involved the description of the means of signal propagation within the neural system by Ludimar Hermann. He first published in 1854 and espoused a diffusion-based mechanism through the late 1890's. The second was the widely accepted position during the first half of the 20th Century that the cochlea contained a substantial number of resonant circuits providing the frequency discrimination required in hearing. The third was the assertion by Bekesy during the 1930's to 1970's, and supported by many others, that the basilar membrane was the principal signal transmission substrate within the cochlear partition. The fourth was the acceptance of the idea that the acoustic energy flowed along the basilar membrane according to the laws of fluid flow rather than acoustic flow related to a structured material. The fifth was the assertion by the dons of neuroscience during the 1950's that the means of signal transmission between neurons was fundamentally chemical. The most recent, beginning in the 1990's, has been the general acceptance of the idea that a mechanical feedback amplifier must exist in the cochlea. The reasoning being that an amplifier must be present to account for the larger amplitude of the motions of the cilia compared to the very small motions of the basilar membrane.

This work will show that all of these assumptions are unsupportable and that their rejection leads to a single comprehensive and consistent description and theory of hearing.

This work will provide a great number of citations to the literature. It should be understood that the citations are to the *data* in the material unless stated otherwise. As a general rule, the *concepts* of hearing included in the Introduction to the material are archaic and are not supported here. This assertion applies to even recent papers.

1.1.4.1 Historical background

Carterette⁵ and Schubert⁶ have provided a lengthy review of the history of hearing research beginning with the Babylonians. The road has been a long one and many first order concepts were defined long ago. Schubert, referenced an earlier quotation by Licklider, "There is no systematic overall theory of hearing." He went on to say in 1978, "This state of affairs has not changed during the ensuing nearly two decades of fairly vigorous research activity." He also noted that most of the books using "theory of hearing" in their title focused primarily on the operation of the cochlea. However, no viable theory of the operation of the cochlea has appeared to date. Davis summarized the poor state of hearing theory in 1984⁷. "In fact, peripheral auditory theory is in such a state of disarray that most of us are simply waiting for more experimental facts or perhaps the emergence of a coherent theory of the peripheral mechanism." Similar comments have been made as late as 1995 as noted in the preface.

Two volumes documenting recent international symposia have reviewed the state-of-the-art in hearing with an emphasis on the cochlea^{8,9}. Their titles stress the importance of models. The preface of the first volume contains the quotable assertion: "The bridge between experiment and theory is the model." However, no comprehensive physiological models are included in the papers. They are all floating models related to individual and very narrow

aspects of the cochlea, frequently the cochlea of surrogates (biological models) used to represent human hearing.

It is important to differentiate between the terms *physiological model* as used here and the term *biological model* as encountered in the biological literature. A biological model is an animal used as a surrogate in laboratory experiments. A physiological model is a physical description of the human (or other target) system from which a duplicate of the system could be assembled by man if both appropriate and adequate technology was available. Two other types of models need to be differentiated and defined. A *phenomenological model* is a model designed to properly emulate a hearing system in response to specific stimuli. It is not constrained to potential mechanisms compatible with neurology or biology. A *computational model* is entirely mathematical and claims no analogy to the physiological mechanisms within a subject species. A computational model frequently employs mathematical steps that cannot be accomplished within the neurological environment.

A recent volume edited by Malmierca & Irvine has described a series of phenomenological models and compared their performance¹⁰. While the volume provides a wealth of background and many references to the exploratory research, it offers little insight into the operation of hearing. The volume does not concern itself with the peripheral elements of the hearing modality. None of the eight models in Table 1 in that volume (pg 34), by Lopez-Poveda, explain the extremely rapid high frequency roll off observed at the output of the sensory neurons of mammalian hearing. Page 23 does contain a valuable list of various models by category.

It is asserted here that the state of technology known prior to 1960, and incorporated into the theories of hearing up to the year 2000, did not support a theoretical description of the hearing modality of the neural system of animals. Because of this situation, the admirable attempts by Bekesy, by Wever and by others to develop a theoretical foundation for hearing were necessarily inadequate. Because of this situation, most of the subsequent discussions of the operation of the hearing modality have attempted to build on their earlier incomplete foundations. As a result, the theories presented in the literature of the last half of the 20th Century have remained conceptual in character. There is little need to cite the theoretical literature of this earlier period. On the other hand, the empirical auditory performance data developed during the 20th Century, when combined with a variety of technologies from other fields, provides a broad base for the evolution of a new theory of hearing.

1.1.4.2 A brief technical background

When one speaks of the theory of hearing, the words of Bekesy in 1960 appear relevant to this day. "The words 'theory of hearing' as commonly used are misleading. We know little about the functioning of the auditory nerve and even less about the auditory cortex, and most of the theories of hearing do not make any statements about their functioning. Theories of hearing are usually concerned only with answering the question, how does the ear discriminate pitch?" Thus, for more than a century, the vibratory pattern of the elements within the cochlea has been the central problem of hearing. Bekesy noted, "Because for a century no numerical values concerning the mechanical properties of the cochlear partition (elements) were available, there was no restriction on the imagination, and probably every possible solution of the problem was proposed."

The question of the determination of pitch has long been clouded by the difficulty of arriving at an adequate definition of pitch itself. The question of pitch became so heated in the 19th Century that an eminent researcher introduced the term "acoustical illusion" to bulwark his argument. Plomp even interrupted the initial paragraphs of his paper by providing a footnote recognizing this difficulty¹¹. Continuing the difficulty, he even offered two definitions. "To avoid any misunderstanding, by *pitch* is meant, in this paper, that attribute of auditory sensation in terms of which sounds may be ordered on a *musical scale*, [or, otherwise stated] that attribute that constitutes *melody*." The brackets are added to emphasize the dichotomy. While this author can support his first definition, the second one appears less appropriate. Perhaps he meant that attribute that contributes to a melodious sensation. In this work any series of chords separated by time intervals will be defined as a melody, whether melodious to the ear or not. The Plomp paper contains an excellent historical review of the pitch problem.

Wever & Lawrence reviewed all of the conceptual theories of pitch sensing proposed during the first half of the 20th Century in as much detail as the individual theories allowed¹². They also evaluated them against the extensive range of available exploratory research. They divided the various conceptual theories into three categories, the early Helmholtz "resonance" theory of cochlear operation, the subsequent standing wave-based theories and finally, the traveling wave theories. They describe twelve different traveling wave theories and two different standing wave

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theories. A major reason for the number of traveling wave theories was the lack of a realistic theory based on the knowledge of the day previously obtained by exploratory research. The primary reason was more fundamental. The technological base of the day did not provide realistic alternatives.

Glick, Gescheider & Frisina have provided the latest truly comprehensive review of hearing, including the operation of the cochlea¹³. Their review of the theories of the frequency selection process includes both the pros and substantive criticisms associated with each, to the extent available from their perspective. It is by far the most lucid review available. Their discussion is noticeably lacking in any discussion of the geometry of the inner and outer hair cells presumed to be the sensory neurons of hearing. In addition, the analyses do not address or place sufficient emphasis on the requirement that the basilar membrane support a traveling wave velocity of less than a few meters/second. This is a well recognized and critical requirement. It is not achievable by a material with the structural features of the basilar membrane.

In 2001, Allen presented a chapter in the 2nd Edition of *Physiology of the Ear* where he made two major contributions¹⁴. First, he cautioned the reader in an unusual way.

"A warning to the reader: Due to experimental uncertainty there is diverse opinion in the literature about certain critical issues. For example, (a) it is very difficult to experimentally observe the motion of the basilar membrane in a fully functional cochlea; (b) questions regarding the relative motion of the tectorial membrane to other adjacent structures are largely a matter of conjecture."

Second, he summarized many outstanding problems related to hearing from his broad perspective. They included (in the order presented):

1. "The fundamental question in cochlear research today is: *What is the role of the outer hair cell (OHC) in cochlear mechanics?*"
2. "The obvious question arises; *How can the basic cochlear detectors (the IHCs) have a dynamic range of less than 65 dB, and yet the auditory system has a dynamic range of 120 dB?*"
3. "The key question before us is: *What is the chain of events that leads to the stimulus compression seen by the IHCs?*"

The italics were in the original work. This work will provide a theoretical answer to all these questions along with the data to support the answers. It will also go far beyond these fundamental questions to present detailed comprehensive models, detailed sub-models, and very detailed circuits and methods of operation. It will provide the first published work describing the actual frequency selection mechanism used within the cochlea of the inner ear.

Allen reached an interesting conclusion regarding item one. "We conclude that *there must be nonlinear compression (level-dependent gain) built into the mechanics of the cochlea* to account for the large acoustic dynamic range." This work will show that the situation is more complex, and more elegant than he envisioned.

Allen's analysis regarding item two led to item three. This work will redefine these items in greater detail. By showing the premise within item two is inappropriate, item three takes on a different perspective.

1.1.4.3 Major impediments to advancing the theory of hearing

Geisler & Cai highlighted the primary impediment to advancing the theory of hearing in 1996¹⁵. "Thus, it is somewhat surprising to realize that we still have, a full half-century after Beke's pioneering work, *direct* measurements on only a small portion of the mechanical vibration patterns produced in the living cochlea by various sounds." The problem is actually worse. Very little data is available by direct measurement from the sensory neurons known as the outer hair cells, OHC. Virtually no direct data has been reported from the sensory neurons known as the inner hair cells, IHC. Without this data, separating the performance parameters associated with each element in a nonlinear system properly is difficult for analysts. Lacking this knowledge, concatenating the performance parameters to obtain a composite performance estimate based on a contiguous model is difficult and prone to serious errors.

Lacking detailed knowledge of the signals present at the axons of the sensory neurons, little data has been available to guide interpretation of how the elements of the Organ of Corti perform.

An equally severe limitation is the fact that no detailed explanation of the signaling mechanisms used within the individual neurons of the nervous system has appeared. Lacking this information, describing the operation of the hearing system, and also other sensory system modalities, is essentially impossible. This problem has recently been resolved with the exposition of the Electrolytic Theory of the Neuron¹⁰. Chapter three of this work will summarize the Electrolytic Theory of the Neuron.

1.1.4.4 Other theories of frequency discrimination within the cochlea

Many readers will be startled by the above difference in interpretation of how the auditory system works and will cite the extensive work of Bekeşy. However, the reader is encouraged to review the volume by Bekeşy summarizing his work in auditory science¹⁷. The primary point to note is he did not include the tectorial membrane in most of his models. The technical problems with his proposals are severe in the light of later knowledge. Even his latest model of the cochlea was completely inadequate to the task. It did not provide a viable foundation for a new theory.

The original resonance theory of Helmholtz is sometimes described as “probably the most elegant of all theories of hearing¹⁸.” However, that is partly because of its precedence. It calls for the (largely uncharacterized, based on the technology of the day) transverse fibers of the basilar membrane to act as tiny resonators, each tuned to a different frequency. As even Bekeşy noted as early as 1928, “The principal difficulty with this theory comes from the magnitude of the damping of the individual resonators” (Bekeşy, page 404). The observed selectivity of the system requires a very high sharpness of resonance (defined by the quality factor Q). The materials forming the basilar membrane suggest a much lower Q than proposed by Helmholtz. No suitable compromise has ever been proposed to satisfy this fundamental conflict in this early theory.

Most of the alternate theories since that of Helmholtz have arisen because of the limitations imposed by the required Q's in the resonance model. These theories have generally involved either traveling wave or standing wave models. “In these theories, the speed of conduction in the cochlea assumes a critical importance, as we shall see” (Wever & Lawrence, page 247).

Most previous theories contain a paradox. They are unable to explain how a traveling wave in a fluid could be reduced to velocities of less than one-three-hundredth to one-five-hundredth of the velocity of normal longitudinal waves in water. Nearly all of those proponents of a conceptual theory noted this problem and based their theory on some unknown mechanism providing this capability (frequently as a variable along the length of the cochlea). Wever & Lawrence provide a table of the propagation velocities required by the different traveling wave theories. A casual perusal of this table suggests the lack of a fundamental, plausible, theory among the group. The standing wave theories face a similar challenge regarding the propagation velocity. However, since these theories rely upon the interference of two traveling waves, they require a round trip travel time roughly equivalent to the one way travel time of the traveling wave theories. They focus on a speed of transmission in the 0.64 meters per second region (one-two-thousandth the speed of sound in water).

Wever & Lawrence dismiss the standing wave theories as inconsistent with their extensive experiments and database (page 293).

No major theories relating to the operation of the cochlea have emerged since the 1960's. Recent writings have focused on two areas. First, more sophisticated tools have been used to develop more detailed models of the basilar membrane as a transmission line (in one, two, and three dimensions). Allen, writing in the 2nd edition of Jahn & Santo-Sacchi has described these efforts and provided references¹⁹. He describes the shortcomings of the one-dimensional model as a lead-in to the discussion of multidimensional models. They remain floating models that do not incorporate the unique structural arrangements within the Organ of Corti. Allen concluded his discussion in 2001 by noting the following. “A theory (a computational model) was desperately needed to tie all these results together (as it is today).” Rauschecker & Tian repeated this claim in 2005²⁰. The discovery of the properties of the curving dielectric waveguide in fiber-optics in 1969 provides the answer to the above dilemma (Section 4.4.2).

Second, efforts have been made to introduce a plausible feedback mechanism between the inner and outer hair cells. This mechanism would satisfy the need for different circuit Q's under different operating conditions and thereby

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salvage a version of the Helmholtz theory based on resonance. Neither the transmission line models nor proposed feedback circuits are satisfying or useful in a broader model of the Organ of Corti or the cochlea as an integral functioning unit.

While manipulating various electrical analogs of the putative transmission line formed by the basilar membrane, the investigators had not provided reasonable mechanical parameters for the membrane base on the mathematical analogy. Lacking such values, considering the analogy valid is difficult. The problem focuses on the elasticity of the basilar membrane on the assumption that the signal is propagated as a compression wave, or on the surface tension of some part of the membrane if a Rayleigh wave is assumed. Associating a surface wave with either surface of the basilar membrane is difficult due to its complex structure. As Allen noted in 2001 (Jahn & Santos-Sacchi, 2nd, pg 404), "The discrepancy in frequency selectivity between the basilar membrane and neural responses has always been, and still is, the most serious problem for the cochlear modeling community. *In my view, this discrepancy is one of the most basic unsolved problems of cochlear modeling.*" [The italics are in the original]

1.1.4.5 Categorizing prior frequency discrimination proposals

Descriptions of the signal conditioning performed within the inner ear have historically fallen into what de Boer describes as two classes, the classical and the non-classical²¹. All of these involve linear operation of the mechanical portions of the inner ear, which has been largely limited to the basilar membrane. He defines the classical class as depending on only one parameter, the distance x from one end of the basilar membrane. His non-classical class has involved more complex models where the response is controlled by parameters that are distributed over space. He asserts that all non-classical models can be reduced to the classical model. However, this assertion appears based on the assumption that the basilar membrane is key to both classes of models.

Robles & Ruggero have provided the most recent review of the classical concept of cochlear partition operation²². It continues to focus on the basilar membrane as a primary functional element. However, the long review does not show any detailed morphology of the inner ear that accounts for the flow of energy from the oval window to both the inner and outer hair cells, the sensory neurons of hearing. While the review lists over 400 references, it does not describe the operational details associated with the cochlea. The sections related to micromechanics, cochlear frequency filtering and the "Cochlear Amplifier" rely heavily on the transitive verb presumed. They make an interesting opening statement to their Section X. "Although, the existence of an organ of Corti mechanical feedback upon the BM is now well established, the nature of the feedback, including the question of whether it involves expenditure of biological energy, remains uncertain. In strict terms, the existence of amplification has been addressed directly only by analyses of power fluxes." It appears clear from their statement that the existence of such mechanical feedback is far from established. No substantive material is provided on the location, characteristics or performance (such as a Bode Diagram) of the cochlear amplifier. They note a recent, but much shorter, review in a similar publication that is not compatible with their position²³.

This work introduces a separate non-classical class, not envisioned by de Boer. It does not support the views expressed by Robles & Ruggero. In this class, the basilar membrane does not play a key role in the process of signal conditioning (except as an inertial mass). This new class still involves linear operation of the acousto-mechanical portion of the cochlear partition. However, the gel surface of the tectorial membrane is the active element supporting acoustic energy propagation. See Figure 4.3.2-2.

The cochlear partition described here can best be distinguished from earlier works by avoiding the descriptive term, Organ of Corti. While this early researcher deserves the honor, his name has become associated with a conceptual mode of auditory operation, based on basilar membrane motions, not supported here.

While investigations during the last 50 years have focused on locating the resonating elements within the cochlea, the efforts have been fruitless. As will be shown in detail in Section 4.3, no resonant circuits, either mechanical or electrical exist within the cochlea. The method of frequency selection relies upon dispersion (analogous to light through a prism) and not the presence of large numbers of progressively tuned resonant circuits.

1.1.5 The acoustic environment

The acoustic environment of interest in hearing assumes two drastically different forms. The acoustic environment external to the subject is a highly complex mixture of compression type acoustic waves traveling through the air (or water) from a multitude of individual sources. At the tympanic membrane, this multidimensional acoustic environment is converted into a single dimension acousto-mechanical environment for transfer by mechanical means to the oval window, the exterior functional surface of the structure known as the labyrinth. The labyrinth is a highly optimized structure that combines the elements of the vestibular system and the auditory components of the "inner ear," most obviously the cochlea.

Within the vestibule of the labyrinth, the acoustic energy destined for the cochlea is transformed into a unique mode of propagation first explored by Lord Rayleigh in the 19th Century and known as a surface acoustic wave. A special type of "modified Rayleigh wave" can be propagated along the surface of two materials of different density if the surface between the two media is not excessively curved. Both the normal and modified Rayleigh waves consist of energy exhibiting an amplitude that is normal to the surface and perpendicular to the direction of energy propagation.

While not widely noted in the literature, acoustic energy propagation is a vectorial process. As such, the energy generally travels in a straight line from a source, frequently radiating spherically from a point source. As a vectorial mechanism, it is subject to all the processes associated with a vectorial quantity. It participates in interference, dispersion, diffraction and refraction. All of these phenomena play significant roles in hearing.

Figure 1.1.5-1 shows the power levels usually found in human hearing environments along with annotation helping interpret this data. It should be noted, the power levels listed are more correctly described as power *density* levels. The power density level of the acoustic environment adjacent to a subject is usually described relative to an absolute reference. The acoustic reference is P_0 , equal to 10^{-16} Watts per square centimeter in air. This is equivalent to an RMS pressure of 2×10^{-5} Newtons per square meter or 0.0002 dynes per square centimeter at a frequency of 1000 Hertz. One Newton per square meter has been defined as equal to one Pascal. Therefore the reference RMS pressure is usually described as 20 micropascals and called the Specific Pressure Level, SPL in air. Section 1.2.2 will address these units in more detail.

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Range		Sound Level dB SPL	Power ratio P/P_0	Pressure ratio, @ same impedance	Typical Example
Inst.	Oper. Level				
↑ ↓	hyper-	180	10^{18}	10^9	Saturn rocket from 50 meters
		140	10^{14}	107	Loud rock group
	phono-	100	10^{10}	10^5	Shouting at close range
		80	10^8	10^4	Busy street
	meso-	70	10^7	3.2×10^3	Normal conversation
		50	10^5	316	Quiet conversation
	kaumo-	30	10^3	31.6	Soft whisper
		20	10^2	10	Country area at night
		6.5	4.5	2.1	Mean threshold at 1 kHz
		3	2	1.4	
	0	1	1	Pressure Reference 20 μ Pa	

Figure 1.1.5-1 The sound environment relative to human hearing. The main table shows the levels and ratios normally found in hearing. The scales are not equally spaced. Left; annotation describing the regimes of human hearing and the instantaneous dynamic range (heavy bar) of hearing within the overall range (dashed line). A reduction of 60 dB in sound level is a reduction of one million to one in power level but only one thousand to one in pressure amplitude.

Besides relating power levels to the local environment, the table attempts to relate them to human hearing. Normal hearing operations can be described based on four distinct operating regimes. These are the nominal phonotopic regime, the mesotopic regime below it and two marginal regimes. As shown, the kaumotopic regime is found below the mesotopic regime. The hypertopic regime is found above the phonotopic regime. It will also be shown that human hearing has an instantaneous operating range of about 200:1, or 46 dB. To accommodate the much larger external environment, a mechanism (recognized externally as a phenomenon) called adaptation is built into the system. The narrow instantaneous range explains why someone must shout in a noisy environment to be understood by a listener. The power level of the voice must be brought into the same range as the background level if it is to be processed effectively within the instantaneous dynamic range of the hearing system.

1.1.5.1 Compression (or bulk) wave propagation

The acoustic environment surrounding a subject can be very complex. To describe the acoustic environment realistically, the use of a multidimensional graphical space is required. The coordinates of this space are typically, the intensity of the acoustic energy (at an unstated impedance level), the frequency spectrum of the energy, the temporal characteristics of that energy and the spatial coordinates of the source. In the case of binaural hearing, the temporal difference in arrival time of the intensity waveform at the two ears can be computed.

Acoustic energy is normally propagated as a compression wave in a bulk medium. The maximum frequency associated with that propagation is determined largely by the bulk parameters of that medium. This frequency can be quite high in common solid media. Acoustic frequencies, extending into the giga-Hertz (10^9 Hertz) range, are frequently used in modern engineering applications. In biological systems, hearing is usually limited to processing acoustic energy at frequencies below 150,000 Hertz. In human adults, it is typically limited to frequencies below 15,000 Hertz (18-20,000 Hertz maximum in the young) by operational requirements discussed in Chapter 2.

As points of reference, the propagation velocity of compression waves in water approximates 1500 meters/sec. In air, the propagation velocity of compression waves is 344 meters/sec at 20 Celsius. Within the functional portion of the cochlea, the propagation velocity of the surface acoustic wave is only 6+ meters/sec (less than 1/2 of one percent of its velocity in water). This drastic slowing of the propagation velocity is key to the operation of the auditory modality. The discussion of acoustic wave propagation will be expanded in Section 4.1.

1.1.6 Scope, Theory, and findings of this work

The time has arrived to address the theory-poor state of hearing research noted by Kiang (See Preface). Major advances in the available technologies have occurred in the last half century and they are available to support such an effort. This text is designed to summarize the new theory, show how it is consistent with most of the relevant data in the literature and act as a guide for planning new investigations (the essence of the scientific method).

To achieve Kiang's goal and satisfy Allen's requirements requires a major paradigm shift relative to the conventional wisdom reflected in the literature. To achieve this goal, a holistic approach not subject to any prior conditions was instituted to arrive at a comprehensive description of the sensory modality known as hearing. The result is a single comprehensive and consistent description of the hearing modality. Unfortunately, it does not support many earlier conceptual theories and assertions. In brief, prior concepts of energy flow within the fluids or the basilar membrane of the cochlea are discarded and prior concepts of the signaling portion of the neuron as a chemistry-based are also discarded.

A requirement of a new theory is that it is comprehensive, adequately detailed, properly parsed, and uses specifically defined terminology. Because of the scope of the investigation, the new theory of hearing is difficult to describe in only a few words. The following is a long-form description of the theory. "The Multi-Channel Theory of Biological Hearing based on a Surface Acoustic Wave (SAW) Filter, on an active liquid-crystalline Electrolytic Semiconductor Device within the Neuron and on Holonomic Cognition using Associative Memory Techniques." A short-form description will be used. "The Multi-Channel SAW-based Electrolytic Theory of Hearing."

The proposed theory calls for the propagation of acoustic energy within the cochlear partition as a slow surface acoustic wave along Hensen's stripe. Hensen's stripe is a unique morphological feature of the gelatinous (liquid-crystalline) surface of the tectorial membrane facing the basilar membrane. It also calls for the separation of the acoustic stimulus into a broad fan of spectrally narrow signaling channels. This frequency band isolation is performed by means of the mechanism of dispersion, rather than resonance, within the cochlear partition. The degree of dispersion is controlled by the curvature of the cochlear partition. A specific direct (and crucial) functional role for the outer hair cells is also described. Finally, the theory defines the active portion of each neuron as an electrolytic circuit incorporating at least one active semiconductor device analogous to the transistor and called an Activa.

This book is organized as a guide to this new theory. The morphology of hearing is discussed briefly in Chapter 2 as a means of orientation and for reference. However, new structural relationships have been illuminated based on this work. The primary goal of the overall work is to provide a comprehensive theory and model of the biological hearing mechanism from a physiological perspective (Chapter 4). The emphasis is primarily on human hearing. However, other species will be discussed when such discussion provides additional insight into the human hearing system. The second goal of this work is to provide an entirely deterministic explanation, model, and set of circuit diagrams associated with that theory (at least before the cognition stage). These are presented in Chapters 5 to 8. The third goal is to show that this framework explains the primary characteristics of the auditory system under all previously explored conditions (Chapter 9). Chapter 10 will touch on a few abnormalities encountered in hearing.

An introduction to the Electrolytic Theory of the Neuron in this work will be postponed until an adequate foundation has been created in Chapter 3. That chapter presents an entirely new theory of the operation of the neuron that is a cornerstone of this work. It is based on the structure and arrangement of specialized liquid-crystalline cell membranes as elucidated via the electron microscope. It replaces essentially all earlier work where the operation of the neuron was assumed to be chemistry-based. The introduction will lead to the detailed definition of the circuits, operation and performance of the neuron, as well as the synapse in a variety of roles based entirely on electrolytics. It will also lead to a detailed description of how an action potential is generated entirely by conventional, and well understood, electrolytic means.

The Theory of the Neuron has also been published in the earlier companion volume, "Biological Vision: A 21st

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Century Tutorial²⁴ and its associated online manuscript, "Processes in Biological Vision²⁵." When cited later in this work, these two documents will be cited as (BV, §x.x.x) or (PBV, §y.y.y) where the first digit of the citation is the chapter number of the document. PBV is available on line at www.sightresearch.net. BV is published and available in libraries, from the website or from book sellers.

This work will invoke, and rely upon, the proposition that the signals of hearing become less cochle-o-topic and become more abstract as they ascend the signal path to the brain. As the auditory signals are processed by the thalamus and beyond, the data can no longer be associated directly with signals from a single position along the cochlea or in the external environment. Conversely, the signals at a given point in the ascending system may exhibit a *receptive field* including many individual positions along the cochlea. However, the complexity of the data at these points is best defined within the psychological concepts of interps and percepts. The psychophysical responses of a subject are based on these interps and percepts.

The contribution to hearing performance due to binaural operation is small except with regard to source location. This contribution will be discussed in Chapter 8. The contribution of binaural hearing to the awareness and analytical modalities of hearing will not be discussed in this work.

1.1.6.1 The basic premise of this work

This is the first presentation of a complete, contiguous and consistent theory of the organization and operation of the auditory system. It is complete down to the individual circuit (conexus) found within each neuron. The Theory is also able to describe the interconnections (synapses) between nearly all circuits outside the CNS, and provides the general architecture of the system within the CNS. While the volume of reported exploratory hearing research is immense, this work and the accompanying manuscript will show that the Theory is consistent with all of the major results found in the literature.

The extent and complexity of the auditory system have led many authors to define various functional dichotomies and associate them with a "dual channel" characteristic or "duplex theory." Unfortunately, such descriptions lead to floating models of only specific parts of the system that are difficult to rationalize with the overall system. The practice will be avoided here. The beauty and sophistication of the overall system are in its multiple path interactions.

Discussions relating to the linearity or nonlinearity of the auditory system have historically been imprecise. The Electrolytic Theory of the Neuron shows operation of the sensory neurons are fundamentally nonlinear. Their output circuit exhibits a logarithmic conversion of current to voltage which is nonlinear by definition. The adaptation circuit operates as a nonlinear amplifier when subjected to "large signals." Because of these circuit features, the auditory system can only be considered as linear for small signals, typically below 45 dB SPL. The system is nonlinear by design over the phonotopic operating regime.

The method of frequency selection employed within the cochlea is based on the spatial dispersion of acoustic energy as a function of its frequency and the curvature of the propagating structure. The mechanism is equivalent to that of light escaping from a curved fiber-optic cable as a function of the cable's curvature. Resonant phenomena play no role in the operation of the cochlea.

Following spectral separation by dispersion, the individual signals are intercepted by the outer hair cells mounted on the basilar membrane. In this context, the bulk and structure of both the tectorial and basilar membranes are considered inertial masses. While this position may be considered radical, it does explain the operation of the auditory system. This is in contrast to various resonant approaches which after more than 100 years of investigation, do not.

This work will not dwell on the wide variety of equations in the literature developed from computational analyses lacking any physical model supporting them. Hellman & Hellman have provided references to a great variety of computational models that will not be addressed explicitly here²⁶. Sumner et al. have provided a more recent conceptual description of the inner hair and auditory-nerve complex and provided a separate summary of previous models²⁷. These are frequently described as phenomenological models, sometimes as kinetic models. In general, they are extraneous models.

The key finding of this work is that the neurological system cannot perform transcendental mathematics (trigonometric conversions, Fourier transforms, etc.) beyond those associated with the natural logarithm and exponentiation. Instead, it uses lookup tables resulting from learning.

This work will not dwell on test protocols and methodology, except where the protocols or methods adopted previously have impacted the precise interpretation of the resultant data. Unfortunately, exploratory research is plagued by not knowing the important parameters to control before starting the investigation. As a result, the investigator must be careful to describe his procedures and limit the applicability of his finding accordingly. Rosenblith discussed this point in some detail²⁸. Rosenblith also noted an important feature of auditory research. Data acquired by different investigators and data acquired by one researcher involving several subjects frequently differ numerically by an order of magnitude. This situation is a serious impediment to the extraction of the "truth" from a search of the hearing literature. It is particularly difficult if no comprehensive model of hearing is available.

1.1.6.2 Compatibility with the prior literature

The model presented here is *not* compatible with what has previously been taught in schools. It is left to the older reader to decide whether the new understanding is strong enough to overcome many premises they were taught in their youth. For the younger reader, the material is left to speak for itself.

A fundamental premise of this work is that the cochlear partition within the cochlea must be in its coiled form to operate effectively. Any prior investigations based on an uncoiled cochlear partition, either real or in analog form, must be discarded based on this fundamental premise. The justification for this position is provided in detail in Section 4.4.

The vibrational modes of a coiled cochlear partition do not even remotely resemble the modes of an uncoiled equivalent.

The architecture and neural operation of the auditory system will be compared with the similar elements of the visual system. The functional characteristics of the visual system, and many of its other features were recently presented in a companion work, as noted above.

1.1.6.3 Fundamental findings of this work

As a result of this work, a number of fundamental facts need to be introduced into future research into the auditory system of both humans and other animals. These facts are enumerated below to prepare the reader for the material to follow.

- After a long progression of focusing on the role of the cochlea, then the role of the cochlear partition, and then the basilar membrane, it is time to make the next step and focus on the real active mechanical element within the cochlea—the gelatinous surface of the tectorial membrane. Recent work has shown that the basilar membrane is in fact, as its name implies, a foundation structure in the form of a well supported inertial mass. It plays no direct role in the auditory mechanism. On the other hand, the gel surface of the tectorial membrane supports a slow temporally non-dispersive traveling wave that is found in two forms. The energy of the acoustic stimulus travels longitudinally along Hensen's stripe as a slow non-dispersive traveling wave for all frequencies below a critical value. At a critical location, the energy of the stimulus at the equivalent frequency is caused to disperse spatially, moving approximately orthogonally to Hensen's stripe. This spatial dispersion as a function of place along the length of the tectorial membrane is the fundamental mechanism of frequency selection in hearing.
- The sensory neurons are mounted rigidly to the basilar membrane (via the Deiters cells) with their cilia in contact with either Hensen's stripe or the broad surface of the gel coating sometimes described as Kimura's membrane. It is the motion of the gel coating within the immediate vicinity of the sensory neurons that causes energy to be transferred to the piezoelectric portion of the sensory neurons. The excitation of the neural portion of the auditory system follows from the conversion of this energy to an electrical signal.
- Elimination of the basilar membrane as an active element in hearing removes the requirement for any amplifier mechanism supporting higher amplitude cilia motions than observed for either the basilar membrane or the bulk of the tectorial membrane. The paradox involving basilar membrane motions with amplitudes much smaller than the

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diameter of an atom is resolved successfully.

- The sensory neurons are divided into two distinct classes with distinct functional roles. The inner sensory neurons (generally described as the Inner Hair Cells) are in contact with and are excited by the bulk (wideband) energy traveling along Hensen's stripe. These neurons are the source of wideband electrical signals that are processed by the neural system. The outer sensory neurons (generally described as the Outer Hair Cells) are in contact with and are excited by the tonal (narrowband) energy traveling across the gel surface at the location of the OHC. The limited electro-motility of the OHC, as a function of the axoplasm potential, plays no role in hearing under *in-vivo* conditions.
- No resonant elements (either mechanical or electrical) are found within the auditory biological system.
- No sinusoidal representation of any simple tone associated with the stimulus are found within the system at points beyond the pedicles of the sensory neurons (except for tones with very low frequencies). At these locations, the stimulus is represented by a signature, corresponding to the envelope of the applied energy at a specific frequency.
- The neural circuits orthodromic to the pedicles of the sensory neurons process the information describing the stimulus based on the amplitude of the signature, the start time of the signature, and its place of origin (when appropriate). The signature does not contain any other representation of the frequency of the stimulus.
- The neurological system is an electrolytically-based electrical system that propagates information via electrical currents to the exclusion of chemical neuro-transmitters. The system consists of a myriad of electrolytic conduits and active electrical circuits, each with the biological equivalent of a man-made transistor—an Activa—at its center. The Activa and consequently each neuron is a three-terminal electrolytic device, instead of the previously assumed two-terminal device. The roles of the previously defined neuro-transmitters are redefined within their true role related to providing electrical power to the neurological system. These materials are redefined in terms of their roles as neuro-facilitators and neuro-inhibitors.
- The signal sensing, low-level signal processing, and high-level signal manipulation within the auditory system are performed in the analog domain, to the virtual exclusion of pulse signal processing. On the other hand, signal projection over distances greater than 2 millimeters is invariably performed by the conversion of the analog signals to their pulse-type counterpart. A neural circuit processing pulse-type signals is often described as phasic in the medical literature. The individual pulses within these phasic signals are described individually as action potentials.
- The complex multi-zone architecture of the auditory system supports the extraction of many types of information from the initial stimulus. This information extraction from the neurological signals resulting from the acoustic stimulus occurs in multiple individual signal manipulation engines. These engines typically incorporate from one to four million active analog circuits within a surface area of about one millimeter (a density not yet achieved by man-made transistor circuits). Frequently, multiple engines are associated with an individual morphological named part of the neurological system.
- The architecture and circuitry of the CNS supporting hearing and vision are very similar and often shared. This suggests all sensory modalities employ a common neural architecture and circuitry with only the peripheral sensory neurons differing. Even the auditory nerve shares a common architecture with the optic nerve.
- The points where the auditory system of humans deviates from that of other species (including the higher primates) are becoming better defined. This will help evaluate future investigative work as well as theoretical discussions more precisely.
- A substantial technical description of all of the psychophysical output capabilities of the auditory system of humans has not yet been developed. The performances of other biological systems are in a similar state. This situation necessarily limits the discussion of the performance capabilities of the system based on this work. However, selected performance capabilities can be described. These capabilities provide an explanation regarding many previous speculations. It also helps document certain capabilities that have only been described conceptually before. This work approaches certain aspects of the concepts of "attention" and "consciousness" but is unable to proceed farther because of the lack of supporting information in the technical literature.
- This work makes a variety of suggestions regarding additional investigative work that is of utmost importance to

understanding the auditory modality in greater depth.

Demonstration of the validity of these observations forms the primary goal of this book and its associated—and extended—supporting material available at the author's previously described website.

1.1.7 A comprehensive performance requirement and technical description of hearing

A goal of this work is establishing a clear transition between previous work considered exploratory research in character and future work that can be considered applied research. To mark this transition, it is important to present a clear description of the performance requirements related to hearing.

1.1.7.1 The operational regimes, modes and stages of hearing

Careful investigation of the hearing modality shows that four distinct operating regimes are needed to describe its operating range. The normal regime of operation is the phonotopic regime. However, the mesotopic regime can be defined most easily. The mesotopic regime typically occupies the intensity level between 15 and 45 dB SPL. It is the regime in which the hearing system can be most appropriately described as operating linearly. The perceived signal amplitude is directly proportional to the intensity of the stimulus. Below the mesotopic regime is the kaumotopic regime (below 15 dB SPL). The hearing system operates linearly in this regime with respect to any external stimulus but the overall performance is largely limited by internal noise sources. There are indications the later stages of the system reduce their effective acoustic bandwidth in the kaumotopic regime. To extend the operating range of hearing, the hearing modality implements an internal feedback mechanism within the range of 45 to 90-100 dB SPL. The resulting regime is called the phonotopic regime. In this regime, the perceived loudness of a stimulus increases more slowly than the amplitude of the stimulus. This phenomenon is associated with the logarithmic compression provided at the output of the sensory neurons.

At stimulus levels above 90-100 dB SPL, the hearing modality operates in an overload mode called the hypertopic regime. The internal feedback associated with the phonotopic mode is no longer functional and significant nonlinear compression occurs within the signaling channels. The result is significant signal distortion within the system, and frequently damage to the hair cells.

The hearing modality attempts to perform its tasks continuously, whatever the regime associated with the collection of external stimuli. These tasks can be described using a framework of individual operating modes. Six largely independent operating modes are found within the hearing modality. These modes have been given functional names to aid understanding. They are;

1. The Alarm mode—a largely reflexive operating mode designed to protect the subject against external threats, even before its cognitive capabilities become aware of the threat.
2. The Awareness mode—a mode designed to support a general familiarity with the external environment surrounding the subject.
3. The Analytical mode—a mode designed to determine the unique characteristics of specific acoustic signals or events associated with the surrounding environment.
4. The Cognitive mode—the mode developed to consider the meaning of signals received from the Awareness and Analytical modes (and frequently after the fact from the Alarm mode).
5. The Volition mode—the high level mode used by the cognitive elements of the CNS to instruct the lower level element of the efferent neural system to take action.
6. The Command mode—the low level mode used to prepare and implement instructions (via the musculo-skeletal system) received from the cognitive elements of the CNS, and to carry out preprogrammed responses upon instruction from the Alarm mode circuitry.

Some of these modes are subdivided into sub-modes because of the significantly different tasks they support. These sub-modes will be defined as the need arises.

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To support the operating modes defined above, the hearing system is divided into a series of functionally different operating stages. The descriptive names of these stages are as follows:

0. The Physiological Stage prior to transduction,
 - A. The Outer Ear,
 - B. The Middle Ear,
 - C. The Inner Ear prior to transduction,
1. The Signal Generation Stage including transduction,
2. The Signal Processing Stage,
3. The Signal Propagation Stage,
4. The Signal Manipulation Stage,
5. The Signal Cognition Stage, and
6. The Response Stage associated with the musculo-skeletal system.

The definition of these stages greatly simplifies describing the hearing and neurological system. Their detailed definition will occur later. Until that point, the names will be used generically.

1.1.7.2 A brief conventional requirement for hearing

Gummer's preface²⁹ highlights the technical performance specifications he believed were generally accepted by the hearing community and to be applicable to the hearing system:

1. Sensitivity to Angstrom displacements of the basilar membrane.
2. Response time in microseconds.
3. Operation over an intensity range of 120 dB SPL (a million-fold in pressure).
4. Frequency range of 100 Hz to 20 kHz.
5. Detection of intensity changes of 1 dB and frequency changes of 0.1%.
6. Extraction of signals in noisy environments (signal-to-noise ratios of -20 dB).

While these specifications provide a suitable introductory specification, they include a variety of assumptions that have not been supported by a comprehensive model and theory of auditory operation. This work will provide a more formal specification based on a more defensible model and a comprehensive theory. It will be shown that most of the above specifications, particularly the first, third and sixth require more careful (and probably more extensive) wording.

1.1.7.3 Top level functional performance specifications of hearing

The global requirements listed by Gummer require considerable expansion before a comprehensive model of hearing can be developed. The process is necessarily interactive. As the detail level of the model improves, additional aspects of the requirements become important. Simultaneously, the requirements themselves become complicated functions of other variables, rather than simple numerics. Section 9.8.1 reviews the complete performance requirements of hearing. These requirements can be summarized here as a guide to the organization of the material to follow.

The top level requirement specification for any system is functional. This is also true in the biological sphere. The major functional requirements on hearing are similar to those applied to vision.

1. The first functional requirement is to protect the animal from danger, a function performed by the alarm mode of auditory system operation.
2. The second requirement is to provide a perspective on the ecological environment surrounding the animal, a function performed by the awareness mode of the system.
3. The third requirement is to provide, or contribute to, an analytical capability that can determine the value of recurrent sounds in the environment. This requirement supports many lower level requirements. These include determining the character of threats, determining the presence of food (particularly for predators), aiding in the location of both threats and food, and carrying on communications with other members of the same species.

These are the major performance requirements shared by nearly all animals equipped with the hearing modality.

A fourth performance requirement is found in those species using active acoustic ranging (sonar in the human vocabulary). That requirement is to process the received echoes generated by the sound generating modality to provide optimum position and ranging information to the animal for purposes of navigation, food acquisition, communications and rendezvous within a species.

A fifth performance requirement is found in the human only (as far as can be determined). A requirement exists to recognize and appreciate very fine differences in frequency (on the order of 0.3%) and rapid changes in frequency (20-40 octaves per second over intervals of less than 50 ms) within complex acoustic stimuli. While undoubtedly placed on the system to provide precise voice recognition in communications among the species, it also provided a unique capability with respect to music appreciation.

A global requirement is that the system provide its output signals in a totally abstract format compatible with the saliency map used to accept other sensory inputs and to describe the environment surrounding the animal.

A final global requirement is to make maximum use of the common signaling architecture and signaling circuitry used in the rest of the neural system.

Finally, one other performance level requirement exists. The system is expected to fail gracefully during the expected lifetime of the species and provide a minimal capability following a variety of traumatic and/or organic failures.

1.1.7.4 Second tier, technical, performance specifications of human hearing

Human hearing is designed, in conjunction with the visual system, to satisfy the above functional specifications while operating in air over a wide frequency range. This range extends from nominally 100 Hz (60 dB down from nominal performance near 1000 Hz) to 15,000 Hz (at 15 dB below the 1000 Hz performance). The system can perform marginally outside this range, particularly among the very young. However, it is not designed to perform outside this range. The system is designed to operate over an acoustic intensity range that is very large. However, it is not required to operate over all of this range simultaneously if it can adjust its sensitivity rapidly.

At the low intensity extreme, the system is designed to provide a threshold intensity level defined as 20 micropascals, a value typified by a very quiet wind-free sandy desert environment. This level is near the limit of Brownian motion associated with the tissue of the hearing system and is compatible with the "noise" generated by the blood flowing in and around the hearing apparatus (after special precautions have been taken to minimize this noise source). This level is defined as 0 dB SPL where SPL refers to a sound pressure level referenced to a specific pressure level of 20 micropascals.

The human hearing system is designed to accommodate very high intensity sounds for short intervals. The interval is compatible with the ability of the person to turn away from the sound source or physically cover his/her ears. Nominally, the system is required to accommodate a sound intensity of 120 dB above the threshold level for up to a few seconds without any damage. This is a sound intensity level one million times higher than the threshold value. While a requirement exists to accommodate this large dynamic range without damage, no requirement exists that it must accommodate this intensity operationally. The operational requirement will be shown to be an instantaneous dynamic range of approximately 46 dB and the ability to select such an instantaneous range out of the overall range as appropriate.

Within the above frequency, intensity and temporal envelope, the system is designed to meet a variety of other technical requirements.

The minimum sensitivity increment requirement within the instantaneous dynamic range is approximately 1 dB. The minimum temporal resolution requirement defined for the system is approximately 0.5 ms (500 μ sec).

The system is required to categorize sounds, and recognize by comparison with previously stored signatures of similar sounds, from among an uncountable number of separate sounds. These sound can consist of multiple individual components that vary in both frequency, intensity and changes in intensity with time throughout the above

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operating envelope. The individual components of each sound may have a duration of from a few milliseconds (sound of a gun shot) to many seconds.

When interpreted in terms of the communications requirement, it appears the system is required to categorize two distinct sets of sounds. The first consists of a minimal set of sounds compatible with verbal communications among members of the species. The second consists of a more sophisticated set of sounds compatible with recognizing the verbal communications of individuals within that species.

To satisfy the above performance requirement (and assuming the hearing system includes a dedicated memory capability), the system includes a performance requirement for updating that memory through learning (following a minimal genetically provided pre-load).

1.1.7.5 Third tier, implementation specifications for human hearing

To satisfy the above functional and technical performance requirements, the hearing system must implement three major functional capabilities and support those capabilities with a variety of supporting capabilities. First, the system must establish a means of acquiring the relevant acoustic signals and delivering them to a transducing mechanism of adequate capability in sufficiently undistorted form. Second, a frequency selective mechanism must be provided that is adequate for recognizing the difference between two closely spaced individual frequencies. Third, the transduction mechanism must perform the initial processing of the acquired acoustic signals so that the subsequent signal processing and signal manipulation circuitry can perform the feature extraction function adequate to categorize the sounds as described above.

The first task is performed using easily recognized acoustic horns, an impedance transforming mechanism (involving the tympanic membrane, the bones of the middle ear and the oval window of the labyrinth) and a compression to surface-acoustic-wave transformer within the labyrinth (Section 4.4.2).

The second task is performed by a unique mechanism only discovered during the 1960's, the non-attenuating spatially-dispersive curved wave guide. This mechanism is formed by Hensen's stripe, a feature of the gelatinous (liquid-crystalline) surface of the tectorial membrane. The energy propagating along Hensen's stripe is spatially dispersed (across the surface of the liquid-crystalline structure) as a function of the curvature of the structure and the frequency of the individual energy component.

The third task is performed by sensory neurons containing a piezoelectric structure that can be excited by a stiff structural element called a cilium. The cilia are assembled into two different arrangements to form rigid structures. The cilia are driven axially by the above two-dimensional filter. Two separate sets of sensory neurons are used. One set accepts broad frequency band energy but with different degrees of delay, and an ever decreasing bandwidth between members of the set. Members of the other set collect energy over only a limited frequency range. The members of the set collect energy of different center frequency as they occur along the length of part of the above filter.

Following transduction, the resulting signals must be processed within the nominal signaling environment used by all other sensory modalities. This system is a "constant amplitude" system. Therefore, a primary implementation requirement is that the sensory neurons include an adaptation mechanism to normalize the output of the initial conversion process whatever the intensity of the stimulus.

An additional implementation requirement is that all signals to be transmitted between signal processing engines of the system must be processed within a maximum bandwidth of less than a few hundred Hertz per signaling channel. In certain cases related to source location circuits, this limit may be raised to less than 1000 Hertz per channel.

No requirement was placed on the system requiring it to process all of the information in serial steps. On the contrary, the system design was allowed to employ many parallel feature extraction mechanisms and be connected by the necessary general purpose signal transmission mechanisms. The resulting feature extraction signal paths are known to include the following as a minimum:

1. A set of signaling channels extracting energy from the stimulus on a narrow frequency selective basis, usually

associated with what are called the outer hair cells of the cochlea.

2. A set of signaling channels extracting energy from the stimulus on a broadband but decreasing maximum frequency basis, usually associated with what are called the inner hair cells of the cochlea.

3. Two distinctly different signaling paths extracting source location information. One path relies upon the broadband channel sensory neurons, the inner hair cells, to compute location based on the time of arrival of the leading edge of the acoustic signal energy. The second path relies upon the narrowband channel sensory neurons, the outer hair cells, to compute location based on the phase difference between individual frequency components in longer duration acoustic signals.

Each of the above paths is implemented using a series of feature extraction engines tailored to the particular requirements of that path. As these paths proceed toward the higher neural engines of the central nervous system, there is a transition from a parallel path structure to what is generally described as a "star network" signaling structure. In a star network, signals are passed between a multitude of individual feature extraction engines on a point-to-point basis rather than along potentially circuitous linear paths.

The use of parallel signal processing provides significant protection against single-point failure of the auditory system. The use of parallel signal processing also supports a sophisticated top level interspecies requirement. This is the requirement to expand a given fundamental capability to satisfy a specific ecological environmental need. By implementing the system using parallel processing, individual feature extraction engines can be expanded in performance or be overlaid by an additional feature extraction mechanism.

The use of a star network configuration at the higher neural centers provides even greater protection against single-point failures. Within the ability of the engines to be reprogrammed, any single-point failure can be circumvented completely through retraining.

1.1.8 The evolution of Biological Hearing

As noted earlier, the scope of this work is focused on human hearing. Its development can be seen in an annotated phylogenic tree. Such a tree shows the close affiliation of human hearing with that of other amniotic species (reptiles, birds and mammals) within the terrestrial environment. Such a tree also highlights the differences between human hearing and that of other species.

Manley has noted the abundance of widely scattered data related to the evolution of hearing among different species³⁰. He focused on accumulating this data for the reptiles and birds. His data shows many aspects of evolution that differ between man and these species. Manley & Koppl provided a phylogenic tree as a function of geological age that is very useful³¹. Their figure has been replotted using a logarithmic ordinate and expanded as Figure 1.1.8-1. The modified version estimates the time when the so-called tympanic ear (or a middle ear) appears. The introduction of this impedance transforming element was crucial to the development of efficient hearing in air rather than water. It also clearly defines the introduction of the highly coiled cochlea as a feature that separates the mammals from the earlier monotremes. While calling for a revision in recent taxonomy based on this critical difference in auditory performance, this revision will not be pursued here. The monotremes and birds exhibit a limited auditory frequency range because of the limited curvature of their cochlea (or equivalent). Extensive data is available showing monotreme hearing is of mammalian form, but the frequency range capability is constrained because their cochleas are not coiled to the extent found in the mammals³².

The evolution of the perigeniculate nuclei is shown as proposed in this work. Whether the chimpanzee (the other member of hominoidae) has developed comparable nuclei is open to further study. The reader is referred to the original paper for the many details related to this tree. The description of so many mechanisms evolving separately but repeatedly in the same time regimes suggests the tree may be subject to further refinement.

The figure has also been modified to show the development of echolocation and the atrophication of the middle ear in the marine mammals (primarily *Cetacea*). The atrophication of the tympanic ear occurred because its impedance matching function was no longer required.

This work will not address the hearing in amphibians, and does not consider their hearing apparatus as homologous

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to that in the amniotes. While considerable research has been reported on hearing in the bullfrog, the physiology of this species differs markedly from that of humans and the other amniotes.

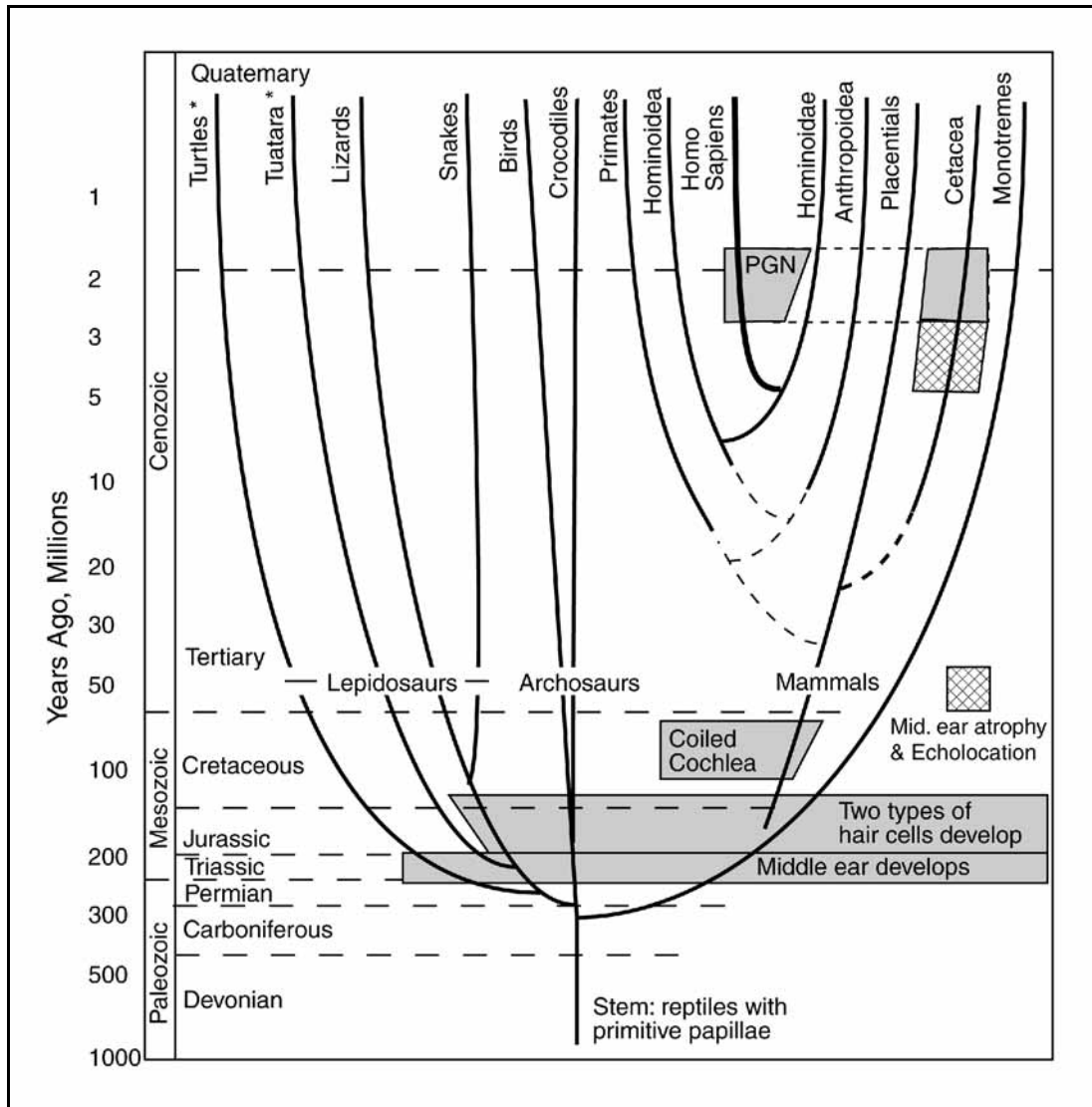


Figure 1.1.8-1 A phylogenetic tree of the animal kingdom plotted versus geological time. The development of the middle ear and the differentiation into two types of sensory hair cells are said to have occurred multiple times. The evolution of the perigeniculate nucleus has apparently occurred only once. See text. Reformatted and expanded from Manley & Koppl, 1998.

1.2 Important tools and ground rules in Hearing Research

Hearing has been studied from an exploratory research perspective for a very long time. Only recently, the state of human knowledge has reached the point where a more important mode, applied research has become possible in hearing. This work has provided many new insights that can now be researched more effectively. In performing this

research, achieving a higher degree of scientific sophistication is important. This section will briefly consider this subject.

1.2.1 Modeling of Neurological Systems

Modeling of neurological systems fall into two distinct classes, those mathematical models based only on intellectual activity supported by exploratory research, and those mathematical models based on realizable physical mechanisms. The latter provide a stronger model that is physically defensible and more compatible with continuing applied research. For one not versed in the design of physiological and psychophysical experiments, Green & Swets has provided a remarkable primer³³. They provide a very readable framework and a set of definitions for designing and interpreting experiments.

In Network Theory, the subject of realizability of a circuit topology is a major field. While a theoretician is free to visualize any circuit configuration, showing that it is realizable is necessary before it can be considered a potential solution to a physical world problem. The realizability rules prevent at least two anachronisms. They prevent the achievement of such things as a power increase (gain) without an active mechanism or device in the circuit. They also prevent the receipt of a signal before its generation at another point in the circuit.

With the arrival of the Electrolytic Theory of the Neuron, it can be shown that a neurological system is not capable of calculations involving transcendental functions. No example of a transcendental calculation within any neural system has been documented. To achieve similar results, the neurological system makes broad use of computational anatomy and lookup tables. Computational anatomy describes the rearrangement of a set of spatially, and/or temporally, related neural signals in order to achieve a result equivalent to that based on a complex calculation. The calculations within the auditory system employ correlations based primarily on algebraic sums and differences. The outcomes of such correlations are frequently used as indices (pointers) to locations in a lookup table. The value at that location in the lookup table is taken as the solution of the relevant process. On the other hand, the neural system can form the natural logarithm of a quantity by employing a diode-resistor network. This feature allows the neural processes of summing and differencing to be used to perform multiplications and divisions.

1.2.1.1 Ramifications of linear versus nonlinear systems

Moore raised a subject that has long simmered in the background of hearing research³⁴. Is the hearing system linear or nonlinear?

A linear system is clearly defined. "For a system to be linear two conditions must be satisfied. First, the output of the system in response to a number of independent inputs presented simultaneously should be equal to the sum of the outputs that would have been obtained if each input were presented alone. Secondly, if the input to the system is changed in magnitude by a factor of k , then the output should also change in magnitude by a factor k , but be otherwise unaltered. These two conditions are known as superposition and homogeneity, respectively." Moore continued with a corollary. "Further, the output of a linear system never contains frequency components that were not present in the input signal."

Moore goes on to observe, . . . "some parts of the auditory system behave as though they were approximately linear, while others behave in a grossly non-linear way." This statement raises two issues. First is the question whether one is discussing a specific internal component of the system, or a transfer ratio between different nodes of the system. Other than the capacitances (and inductances) found within the neural system, virtually every other component in the system is nonlinear. This will be shown most clearly in Chapters 3 and 5. A fact of greater importance is that hearing and all other sensory modalities of the neural system employ sampled data techniques. These techniques are used primarily for signal propagation over long distances (typically more than a few millimeters) within the system.

In a fundamentally nonlinear system, analysis of the system can be carried out in a variety of domains. The sampled data portion of the system is best analyzed in the Z-domain of servomechanism theory. This method of analysis will not be used in this work, although it is critical to the complete understanding of the signal propagation mechanism. Of more utility is the distinction between large signal conditions versus small signal conditions within a nonlinear circuit. The transfer function between the input and output of a nonlinear system is by definition nonlinear. However, over a limited operating range, the transfer function may be approximated by a linear function. Under this condition,

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called *the small signal condition*, the system may be considered linear. For larger ranges, *the large signal condition* applies and the system must necessarily be treated as nonlinear.

The exponent of one-third between the perceived response and the stimulus for stimuli within the phonotopic regime documented by Stevens is clear evidence of the nonlinearity of the auditory system over its primary operating regime³⁶.

1.2.1.2 Adopting the Laws of Maxwell instead of Kelvin

The biological community has attempted to investigate the neural system using the least demanding mathematical tools possible. The result has been the very slow development of hearing theory and understanding during the last half of the 20th Century.

Understanding the General Wave Equations (GWE) of James Clerk Maxwell (a.k.a. Maxwell's Equations) are absolutely necessary to the understanding of the hearing modality. These equations have been presented in many mathematical forms. However, their understanding requires a familiarity with second order differential equations.

It will be shown that Maxwell's GWE provides the straightforward answer to two major questions of hearing. The first is how is frequency selection accomplished within the cochlear partition without the presence of any resonant circuits, either mechanical or electrical? The answer is developed in Section 4.4. The second is how are the action potentials propagated along the axons of the impulsive neurons? The biological community adopted a misconception proposed by Hermann, in the 1860's based on the work of Lord Kelvin, and have not deviated from that conception until now. The failure of Hermann's concept was already known at the time of its publication by other members of his institute, namely Maxwell. Maxwell's alternate concept based on his GWE went on to underpin and explain the electronic revolution of the 20th Century.

1.2.2 Maintaining consistent units in neurological research

Considerable flexibility is found in the terminology used in hearing research. The community lacks its own standardizing body. This situation frequently leads to less than clear terminology in the literature.

The description of conventional acoustic energy flow is particularly difficult because of its intrinsic three-dimensional propagation. The task in this work is even more difficult because of the importance of unconventional Rayleigh wave energy flow. Most analyses of conventional acoustic energy flow attempt to restrict this flow to two dimensions, or even one dimension, to simplify the mathematics. A further complication is that acoustic energy propagates by a reciprocating wave motion, as opposed to a steady movement. As a result, the majority of the quantities used in acoustics are "effective values" based on root-mean-square (RMS) calculations.

Section 4.1.5 will address the unique aspects of both conventional longitudinal (pressure) acoustic waves in bulk materials and surface acoustic waves traveling along an interface between two materials.

The MKS system of units has historically been awkward to apply to acoustics because of the size of these units. The CGS system, or a mixed system, has frequently been used in the literature for this reason. A brief Google search will illustrate the confusion the above situations have caused. A broader application of dimensional analysis would avoid a great number of the inconsistencies found in the literature. Because of this problem, a glossary has been prepared as Appendix A of this work.

1.2.2.1 The definition of acoustic power and intensity levels—dimensional analysis

Assertions such as "the acoustic power is equal to the product of pressure times particle displacement" are frequently encountered in the literature. However, a simple dimensional analysis would show this statement is incomplete. This product defines the power per particle per movement! The power in a realistic situation is the above value multiplied by the number of particles involved (in a unit area) times the number of movements per second (the frequency).

The dimensional units of work and power do not change among technologies. When expressed in the Mass-Length-Time domain, they are:

$$\text{Work} = \text{M} \cdot \text{L}^2 \cdot \text{T}^{-2}$$

$$\text{Power} = \text{M} \cdot \text{L}^2 \cdot \text{T}^{-3}$$

The units of pressure are $\text{M} \cdot \text{L}^{-1} \cdot \text{T}^{-2}$. The units of volumetric flow are $\text{L}^3 \cdot \text{T}^{-1}$. The units of one-dimensional flow are $\text{L} \cdot \text{T}^{-1}$. The units of cross-sectional area are L^2 .

By associating the pressure with the voltage and the volumetric flow with the current in an electrical circuit, a relationship of the form impedance = Pressure/volumetric flow can be formed with the units $\text{M} \cdot \text{L}^{-4} \cdot \text{T}^{-1}$. Alternately, a relationship of the form impedance times cross-sectional area = Pressure/linear flow can be formed where the impedance has the units $\text{M} \cdot \text{L}^{-2} \cdot \text{T}^{-1}$. In this formulation, the impedance alone is expressed as the density of the fluid (with units of $\text{M} \cdot \text{L}^{-3}$) times the linear velocity of the fluid. Power can now be defined as a product of the square of the pressure times the cross-sectional area divided by this impedance term (density times the linear velocity.).

Power can be described as;

- the product of the pressure and the volumetric flow or by
- the product of the pressure and the one-dimensional flow and the cross-sectional area.
- the product of the square of the pressure times the cross-sectional area divided by the product of the density times the sound velocity in the bulk medium.

The last form provides the framework for defining the relative sound level as:

$$\text{relative level in dB} = 10\text{Log}(\text{power}/\text{power}_{\text{REF}}) = 20\text{Log}(\text{pressure}/\text{pressure}_{\text{REF}})$$

A problem occurs frequently in the literature when authors use the term intensity to refer to either the power density (power per unit area) of the stimulus or the pressure of the stimulus. When used to describe power density, an increase by a factor of 10 in the intensity equals 10 dB. If the term is used to describe the pressure, the same increase by a factor of 10 equals 20 dB. Intensity will be used to describe power density in this work.

A second area of concern involves the definition of the reference power or the reference pressure in the AC (or reciprocating) environment. The expression for power includes a component related to the effective linear velocity. This effective linear velocity can be defined in terms of a shorter velocity moved multiple times within a given interval. Stated differently, the power is proportional to the square of the pressure times an incremental velocity times frequency. The higher the frequency of the stimulus, the less pressure difference needed to achieve the same power level.

In any definition of a reference pressure level (such as 20 micropascals, 20 μPa), it is advisable to define the applicable frequency. Otherwise, the related power level cannot be determined. Normally, the frequency is taken as 1000 Hertz but it is unspecified.

1.2.2.2 Formalizing the concept of impedance

Students, graduate students and practitioners in hearing are frequently not well versed in the concept of impedance. When used in the acoustic environment, it takes on a considerably different meaning than that found in simple low frequency electrical circuits. The simple concept is adequate as long as the physical dimensions of the electrical circuit elements, or their mechanical analogs, are sufficiently small. Under this condition, the currents can be considered constant throughout the circuit at any given instant. When this condition is not satisfied, it must be recognized that any disturbance will be propagated as a wave. The impedance associated with a wave normally has a complex value that can be described by a similar wave. It is described using complex notation.

The term impedance as used in hearing research is unusual. As Beranek notes in the "Bibles of Acoustics," it occurs in four different mathematical forms (and a variety of specialized forms)^{36,37}. These basic forms are fundamentally different, although the first three result from different placement of parameters when solving the basic differential equations of sound propagation.

The principal definitions used by Beranek are:

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The acoustic impedance, Z_a :	$Z_a = p/Su = p/U$ in dyne-sec/cm ⁵
The specific acoustic impedance, Z_s :	$Z_s = p/u$ in dyne-sec/cm ³
The mechanical impedance, Z_m :	$Z_m = pS/u$ in dyne-sec/cm

where p is the sound pressure in dynes per square centimeter, u is the linear velocity in centimeters per second and S is the area for which the impedance is being defined, in square centimeters. $U = S \cdot u =$ volume velocity, in cubic centimeters per second. Notice the difference in units for these three forms. The electrical impedance is defined entirely separately and differently from each of the above definitions. Acoustic calculations have historically been made in the CGS system rather than the MKS system, but with the power expressed in watts.

The acoustic impedance is most commonly used in applied acoustics where it is also called the ASA impedance, having been standardized by the American Standards Association. The specific acoustic impedance is most often used in theoretical acoustics. The mechanical impedance is frequently used when the interface between mechanical and acoustic systems is of primary interest. The type of impedance selected by the user must be explicitly named.

The acoustic ohm is not equal to the conventional electrical ohm or the mechanical ohm. Conversions between these nomenclatures can be difficult and frequently depend on the form of the acoustic enclosure, if any. In the case of a small enclosure compared to the acoustic wavelength, the acoustic impedance may be expressed in terms of the mechanical impedance. It is equal to the mechanical impedance (in mechanical ohms) divided by the square of an area, the cross-sectional area of the medium. The acoustic impedance of a sound traveling through a medium is given, at a given plane by a complex expression.

Investigators must explicitly define their choice of impedance units (the electrical ohm, the acoustic ohm, the mechanical ohm, etc.) and insure that they maintain consistent units throughout their calculations.

In hearing, several elements of the system are frequently described as transformers. An ideal transformer is an ideal impedance transforming device. However, a real transformer includes its own energy consuming (lossy) characteristics. As a result, the transformer usually introduces an impedance discontinuity. As a result, some energy is usually reflected at the input to a transformer. This energy is frequently measured in acoustic experiments related to hearing.

The impedance of a transformer is different at its input and output. The common factor in the operation of a transformer is its transfer of energy. The power level remains the same at the input and output of a transformer (except for internal losses).

When discussing the performance of either the outer or the middle ears, it is imperative that the impedance representing the transformer leading to the next element be accounted for. The impedance represented by the tympanic membrane for the outer ear and the oval window for the middle ear must be included in any calculations. Much of the confusion in the literature concerning the amplification factor associated with the middle ear can be resolved by including the input impedance of the inner ear in the mechanical model of the middle ear (Section 2.3.3 & 4.2.2).

It must also be recognized that the term impedance is frequently used in the vernacular to describe a single resistance, capacitance, inductance, diode, etc. where the complex angle associated with each component is unstated but understood.

Based on the above units, the acoustic ohm is related to a volume propagation velocity in the medium. It is expressed in units of cm³/sec. Alternately, the mechanical ohm is related to a linear propagation velocity in the medium with units of cm/sec. It will be shown that the mechanical ohm is most appropriate in hearing research once the mode of operation of the tympanic membrane and the oval window are established. These elements both operate as pistons moving axially. The ASA/acoustic ohm is most useful when describing the external acoustic field and the auditory canal.

1.2.2.3 Describing hydraulic situations precisely

When discussing the pressures in the auditory canal and the cochlea, it is extremely important that the concepts related to power and impedance discussed above be adhered to. The transfer of energy through a series of transformers is bound by the laws of the transformer, whether electrical, mechanical or hydraulic.

When discussing a hydraulic system, a description of the total power or energy at a plane perpendicular to the flow of that energy is generally necessary. If only the pressure of the wave is to be discussed, defining the impedance of the medium at that point (or somehow providing information concerning the displacement associated with that pressure intensity) is absolutely necessary. If only the displacement is discussed, the area of that displacement and the pressure causing that displacement must be indicated. A discussion of the pressure or displacement alone has little meaning.

As a prime example, the pressure wave at the tympanic membrane (or at the oval window) is frequently expressed in absolute amplitude. At 0 dB SPL, this amplitude is extremely small. Several authors have compared this amplitude with the diameter of a hydrogen atom, etc. The problem is that acoustic energy is not defined by a one-dimensional amplitude. Speaking only of the amplitude of the pressure has led to very awkward assertions concerning amplitudes much smaller than the diameter of the hydrogen atom.

As will be shown in this work, the energy presented to the oval window generates a relatively low amplitude displacement spread over a large area (compared with Hensen's stripe). Within the cochlear duct, this energy is transferred to Hensen's stripe as a surface acoustic wave of much smaller extent but much higher amplitude. This larger amplitude is used to affect the sensory neurons. This amplitude is orders of magnitude larger than the diameter of a hydrogen atom. It is typically in the range between 0.01 microns and a few microns (Section 4.6.3).

1.3 The baseline models of the auditory system

The scope of the analyses in the following chapters is broad. Within the limitations of space, these analyses will be drawn together in Chapter 9 using a series of summary figures describing the performance of the hearing system. To aid the reader, the remainder of this chapter will preview some top level schematic, block, and circuit diagrams that will be developed later in detail. It is hoped the reader will be able to interpret the information in later chapters more easily based on this framework.

1.3.1 The top level block diagram

Figure 1.3.1-1 shows a top level block diagram of hearing as found in the human but applicable to most lower mammals. In human, the ability to move the external ears (the pinna) has generally atrophied during evolution. However, the capability is still found in some individuals.

The ability to move the ears is quite important in other species. In those cases, the outer ears are controlled by a set of six muscles (just like the eyes) under the control of the precision acoustic servomechanism (PAS). The figure highlights several features of the system that are seldom emphasized. First, the outer ear acts as a "transformer." They can change the intensity of the incident acoustic energy (power) without changing the total power present (e. g., it does not act as an "amplifier"). Second, the eustachian tube, connecting the inner ear cavity to the throat, plays a significant role in the normal and abnormal operation of the hearing modality. Technically, it provides a return path for air under pressure that insures a zero in the transfer function of the middle ear. Homoeostatically, it prevents a buildup of pressure that could otherwise be quite painful and decrease the performance of the hearing modality significantly.

The system is divided into a series of stages in this figure. These are the divisions that will be used in the following chapters to isolate large functional elements of hearing for orderly investigation. To be consistent with other works, the sensory neurons will be associated with stage 1 and the initial signal processing neurons will be associated with stage 2. The acousto-mechanical elements of the system will be associated with stage zero. Stage 2, Signal Processing, is defined as occurring in the peripheral nervous system (PNS) while Stage 4, Signal Manipulation is defined as occurring within the CNS. Stage 5 contains the neurons of the cerebral cortex associated with cognition. Stage 6 consists of the Command implementation subsystem associated with the musculo-skeletal system (the lower pathways in the figure). The label "Stage 3" is missing. Stage 3 consists of the Signal Projection elements of the

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system that provide the communications channels between the other stages labeled 1 through 6.

The acousto-mechanical elements of the hearing system will be assigned to stage 0. These elements include the outer and middle ears as well as the portions of the inner ear prior to the interface with the cilia of the cochlear partition within the cochlea.

Licklider was one of the first hearing investigators who attempted to subdivide the hearing modality into a series of independent stages³⁸. Although not as uniquely defined as the stages used here, his definitions closely parallel those of the stages 1, 4 & 5 of this work. With hindsight, Licklider's paper seems to hint at much of the theory presented here (except for his focus on an autocorrelation mechanism).

As a point of reference, Huxley & Hodgkin explored only the axon portion of a specialized signal processing neuron found in Stage 6 (command implementation) of a member of *Mollusca*. The squid giant axon was one of a pair used in a delay line designed to synchronize multiple muscles sequentially. Such an axon would not be expected to generate true action potentials and it did not. Furthermore, the signal propagated along this axon *in-vivo* at an atypical speed tailored to the size of the animal. This axon was physically disturbed by cannulation and removal of the axoplasm prior to data gathering in an early version of voltage-clamping. Great care must be employed in equating the results of Huxley & Hodgkin to specific *in-vivo* neurons found in other stages of the neural system of animals found in other phyla.

Describing the hierarchal location of the cochlear nucleus is somewhat ambiguous at this time. Four major factors contribute to the difficulty. Morphologically, it is usually described as part of the "lower brain" and therefore part of the CNS. However, like the neural portion of the retina in vision, it is located near the brain but operates much like other peripheral parts of the neural system. Its complexity is similar to many other engines of the CNS. Like the retina, it is mostly, if not completely, involved in the integration of signals, not feature extraction. It integrates signals from the hearing, vestibular and proprioception modalities. Although internal exceptions are found, its overall task appears to involve signal convergence rather than signal divergence. Thus, it is shown as an element of stage 2, part of the peripheral nervous system. If the cochlear nucleus was performing mostly feature extraction, it would logically be an element of Stage 4. This designation will be explored more fully in Chapters 6 & 8.

This diagram does not show the distinct roles of the inner hair cells and outer hair cells of the cochlear partition. In later diagrams, these roles will be defined in much greater depth than in any previous work.

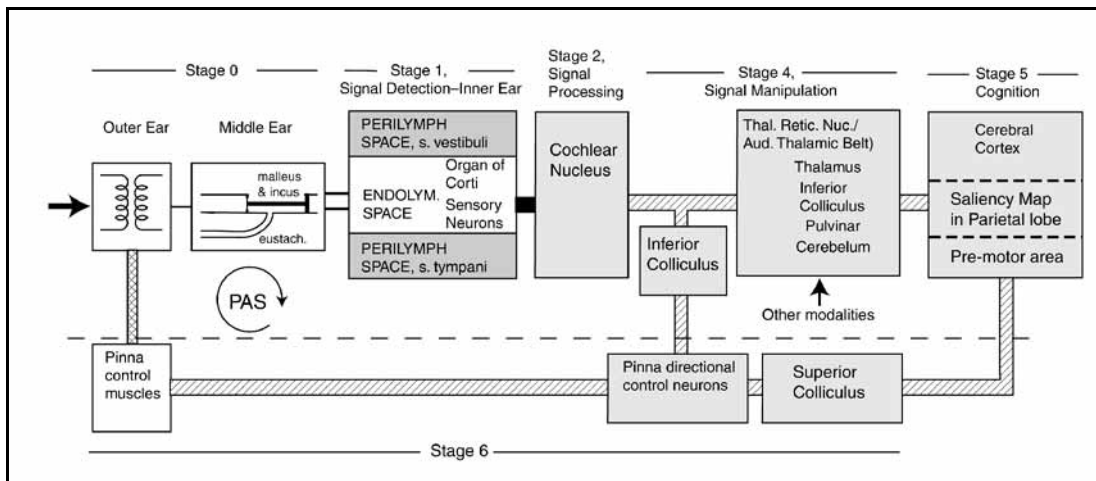


Figure 1.3.1-1 Top level block diagram of hearing in humans. The eustachian tube is shown because it introduces a zero into the transfer function of the middle ear. The perilymph filled space of the cochlea plays no direct role in hearing. The cochlear nucleus is shown in stage 2 because it is involved in signal combining rather than feature extraction, as in stage 4. The inferior colliculus is shown bridging the main neural signal path rather than interrupting it.

1.3.1.1 A comparison of the physiological model of vision and hearing

The author has recently published a companion volume on the operation of the biological vision and a more extensive manuscript on the internet as noted above (Section 1.1.6). This manuscript, *Processes in Biological Vision* [PBV, 8 & 9] provides a complete description of the discovery of the Activa and the development of the Electrolytic Theory of the Neuron. The recent preparation of these works provides a rare opportunity to compare the operation of the visual and auditory systems from a functional perspective based on materials created during the same period. Figure 1.3.1-2 shows the close parallel between these two systems in chordates. The upper half, representing vision, and the lower half, representing hearing, are virtually identical even when using the conventional morphological names. Only the physiological energy collecting mechanism, the transduction mechanism associated with the sensory neurons, and the software used in information extraction are changed.

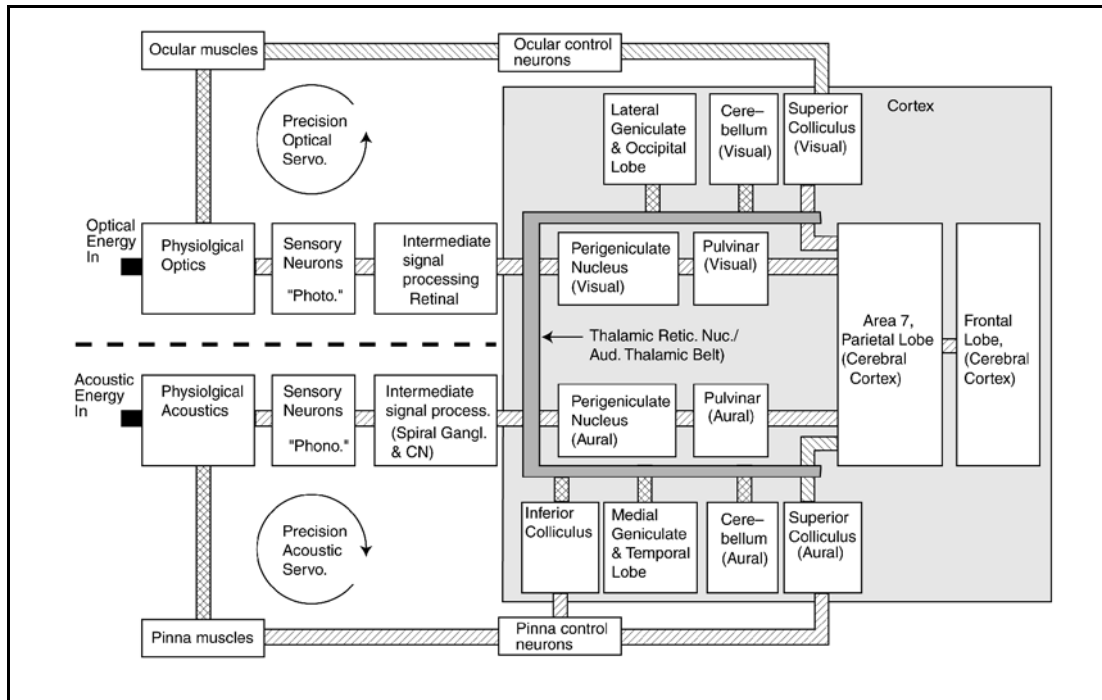


Figure 1.3.1-2 A comparison of the visual and auditory system block diagrams based on the Electrolytic Theory of the Neuron. The figure is generic to many families of the phylum, *Chordata*, but even more specifically to the amniotes. While the ability to move the ears has largely atrophied in humans, it remains a major capability among other members of the family.

The figure is generic to all chordates. Members of the families *Mollusca* and *Arthropoda* do not employ hearing in the same sense that chordates do.

The term chordate is used above to resolve a common problem in taxonomy. Division of the animal kingdom into vertebrates and invertebrates does not provide a consistent criterion nor an adequate range of categories. There are three major phyla of animals, *Chordata*, *Mollusca* and *Arthropoda*. By simple logic, a shark is an invertebrate since it lacks calcified vertebrae. However, it and many other species are clearly chordates; they exhibit a notochord running along the dorsal extreme of the vertical centerline of the body. It is the position of the notochord that is the primary criterion separating the family *Chordata* from the family *Mollusca* and *Arthropoda*. Whether the vertebrae are calcified is not a realistic criterion for defining animal families.

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In the human, the capability of moving the ears, as suggested at the lower left, has atrophied during evolution. However, this capability remains very important in other chordate species. It is suggested this loss of capability in humans was a tradeoff with the increased capability of the human to rotate his eyeballs through a much wider angle than other species.

The critical role played by the thalamic reticular nucleus (TRN), occasionally described as the auditory thalamic belt, is shown by the fact that nearly all neural paths pass through it. During this passage, the signals are both monitored and switched. Further details regarding this figure will be developed in Section 8.1.1. Considerably more detailed block diagrams and circuit diagrams will be presented in Chapters 8 & 9 after the necessary background has been established.

1.3.2 The top level schematic diagram

Figure 2.2.2-5 in the next chapter provides a top level physiological schematic of the hearing modality in a morphological context that will be familiar to most readers. The major morphological entities are labeled on the left. The descriptions of many smaller elements are shown on the right. The figure follows the conventional practice of only illustrating one side of the bilaterally symmetrical signaling paths between the cochlear nucleus and the elements of the CNS beginning with the diencephalon.

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