

## 2 The configurations of the hearing modality

The tasks of the mammalian ear are accomplished by some astonishing and elegant mechanisms.  
*Geisler, 1998*

### 2.1 Introduction

This work will consider three major configurations of hearing: the gross anatomy of the modality, the more detailed morphology of the major parts of that modality, and the physiology of the modality.

While the morphology of hearing has been studied extensively in many species, the interconnection of the neural paths, both anatomically and physiologically, have seen only limited study. The available data is based primarily on what is usually called traffic analysis (determining where individual neural paths begin and end). These studies have, to a large part, ignored the functional role of the midbrain in hearing. This chapter will be brief as the anatomy of hearing is not a major focus of this work and the morphology, histology and neurological signaling paths will be developed in considerable detail in later chapters.

It is expected that readers are quite familiar with the morphology of the peripheral hearing system and the areas of the cerebral cortex involved in hearing. However, it is assumed that they are less familiar with the critical role of the midbrain, and the interconnections of the midbrain, in hearing. A series of citations will be presented for those desiring a review of the morphology of human hearing. It is also assumed that the reader is unaware of the relevant physical features of the cochlea that lead to its remarkable performance. These features are discussed in this work for the first time.

The morphology of many species has been studied in order to better understand human hearing. As noted in Chapter 1, the mechanical-to-neurological transduction mechanism of the mammals differs fundamentally from the non-mammals, particularly with regard to the shape of the cochlea. A second major difference, even between the other mammals and humans is the development of the diencephalon of the midbrain. These functional differences are so great that data and concepts relating to other species can only be introduced into the description of human hearing with caution.

It is important to note that the diencephalon of humans is much more developed than that of any other species (except the echolocating mammals). It is the development of the diencephalon that separates the enhanced aspects of hearing found in humans from the other mammalian (and probably even the primate) species. Attempting to analyze the operation of the hearing modality without considering the diencephalon as a critical component is unrealistic. The characteristics of hearing in the lepidosaurs, archosaurs, and even amphibians and monotremes differ so greatly from that of humans that the discussion of these characteristics is not particularly relevant to the discussion of human hearing.

Areas of focus in this chapter will be; the action of the middle ear as a "transformer," the coupling between the stapes and the cochlear partition (the critical mechanical portion of the Organ of Corti), the physical arrangement of the cochlear partition (with emphasis on the tectorial membrane), the physical, hydraulic and electrical isolation of the sensory neurons and the physical organization of the diencephalon.

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lurato<sup>1</sup> has provided useful graphics for understanding the range of sizes involved in the morphological structures of hearing. It is necessary to proceed from the level of gross anatomy to detailed morphology, histology, cytology and finally molecular biology in order to understand the hearing modality. Individual elements ranging in size from a few centimeters to less than 10 Angstrom play roles in hearing.

The critical role played by the curvature of the cochlear partition, within the cochlea itself, cannot be appreciated from its morphology. This feature is directly related to the physiology of the cochlear partition. Similarly, the critical importance of slowing the velocity of the acoustic energy can only be appreciated within the physiology of the cochlea. These two features are major subjects of Chapter 4.

Understanding the physiology of hearing is critically dependent on the electron microscope for understanding the molecular biology of the cell. With this tool, the difference between the neural elements and all other elements of a cell can be defined. Some of these elements, and their physical arrangement, are critically important to the creation of the key element of the neural system, the active electrolytic semiconductor device defined earlier as the Activa. The discussion of the morphology, and the electrophysiology of the neuron will be reserved for Chapter 3.

A particular problem in understanding the hearing system is the use of significantly different nomenclature for the same elements in the histological, physiological, and morphological communities. Past researchers have also employed unusual, usually irrelevant and sometimes fanciful, names to identify various neuron types at the histological level. Cajal originally called what he observed to be a dominant class of neurons in the CNS "pyramid or psychic neurons." Unfortunately, the name pyramid was accepted in the subsequent literature although it is difficult to find any common geometric features shared with a pyramid. These naming practices make it very difficult to harmonize the literature in this area. In some instances, this work will associate new and more precise definitions with some of these older names.

The variations among the auditory systems of species are as broad as it is in the visual systems. There are major differences between the major phyla as well as among *Chordata* alone. There are major differences in the morphology and performance related to all three major components of the peripheral parts of hearing, the outer, middle and inner ears. Many of the lower chordates have virtually no outer ear, with the tympanic membrane visible on the surface of the head. The more sophisticated chordates have highly maneuverable outer ears that contribute to the source location task. A major change related to the middle ear occurs in the development of the terrestrial mammals. The middle ear is transformed from a simple single-element rigid connecting "push-rod" between the tympanic membrane and the oval window leading to the inner ear to a three-bone hydro-mechanical ram system and not a simple lever system. This ram provides a much better impedance match between the external acoustic environment (air) and the fluid environment of the inner ear.

An equally major change occurs in the inner ear of mammals. Mammals have a far wider spectral (frequency) range than other families and species. This change is closely related to the spiral character of the cochlea. The spiral form not only allows a longer frequency selection mechanism to be included in a smaller space, it also contributes to a wider frequency spectrum than found in other families (such as the birds and monotremes).

Masterton, Heffner & Ravizza have provided an excellent statistical analysis of many of the features of human hearing in the context of evolution (particularly among the mammals)<sup>2</sup>. Their phylogenetic tree for selected species is particularly interesting. One of their most interesting findings is that human hearing is far from the best among the mammals based on several criteria. The limited high frequency capability of the human is now an anomaly among the mammals. Its source location capability is considerably compromised by its lack of ability to redirect the pointing of the outer ears.

### 2.2. A brief anatomical background

The entire auditory and vestibular sensory systems (except for the external ear) are located within the skull of mammals. However, major portions of these systems are not contained within the CNS. They operate as peripheral sensory systems just like all other major sensory systems. Because the PNS elements of these systems are nearly surrounded by the cerebral cortex in humans, it is difficult to portray the systems clearly. Galambos has provided a useful caricature of the overall human hearing system<sup>3</sup>. The most detailed cutaway view is presented in the 1940 book by Brodel and reproduced in Wever<sup>4</sup>. Moller has also reproduced a figure from Melloni (1957) showing a cutaway of the auditory system from the front<sup>5</sup>. Gulick et al. have provided another view from Melloni orienting the oval window and inner ear relative to the axes of the head<sup>6</sup>. Unfortunately, these are all partial descriptions of the hearing system.

The size and proportions of the elements of the brain associated with hearing varies immensely between humans

and other mammals because of the difference in optimizations associated with their habitat. While the cerebral cortex is relatively large in humans, the inferior colliculus and other elements associated with source location are relatively small. Some texts suggest the inferior colliculus is functionally insignificant and morphologically vestigial in humans. What is occasionally labeled the inferior colliculus frequently appears to represent the combination of the medial and perigeniculate nuclei.

Figure 2.2.1-1 presents a caricature of the human auditory system (with the cerebellum shown dotted and the occipital lobe of the cerebral cortex omitted) along with a perspective of those elements within the head. The main figure shows the thalamic reticular nucleus (TRN) enclosing the pulvinar lobes of the thalamus and forming the three major elements of each half of the mesencephalon, the medial geniculate nucleus, the perigeniculate nucleus and the inferior colliculus. Clearly, the medial geniculate nucleus is in no sense medial relative to the total brain or the other elements of the mesencephalon. The internal capsule (corpus pricipia) containing the commissure connecting the two halves of the pulvinar inside the thalamus is also shown. The major connections with three lobes of the cerebral cortex are shown. These connections are bilateral. There is a close working relationship between each medial geniculate nucleus and its associated temporal lobe. These units will be described functionally as the MGN/temporal lobe couple. There is a similar close relationship between each perigeniculate nucleus and its associated pulvinar resulting in the functionally defined PGN/pulvinar couple. The TRN acts as the principal switching, command and control element of the brain. In that role, it plays an important role in communications with the cognitive portion of the cortex through the parietal lobe of the cerebral cortex. These relationships are discussed in Chapter 8.

The cerebellum, while not highlighted in his discussion, plays a major role in the auditory system (PBV, 15.2.5).

### 2.2.1 Gross anatomy of the peripheral auditory system

The peripheral elements of the auditory system consist of both acousto-mechanical and neurological elements. The strictly acousto-mechanical elements of the outer ear, the pinna, are not of major interest here. Most of the dynamic features of the pinna have atrophied in humans. However, remnants of the associated musculatura and nerve paths remain. The remaining functions of the pinna are to provide some directional sensitivity, to insure good sensitivity across a wide acoustic frequency range, and to collaborate with the auditory canal in insuring an acceptable impedance is established at the interface with the tympanic membrane over this frequency range. Shaw has provided a detailed look at the nomenclature of the external ear<sup>7</sup>.

Care is required in defining the remainder of the auditory system outside the CNS in sufficient detail to understand its physiology as well as its morphology. Again a figure by Brodel, and reproduced in Flock, appears to be the best available overall graphic<sup>8</sup>. It stresses the presence of bone in critical areas. Bone plays a major role in channeling the sound to the middle ear, providing anchorage for the mechanical levers of the middle ear and providing the required rigidity to the motion sensitive elements of the labyrinth that includes the cochlea.

The middle ear (the region defined here as between the outer surface of the tympanic membrane and the fluid wetted surface of the oval window) plays a key role in terrestrial mammalian hearing. This definition stresses the role of the middle ear in delivering acoustic energy from a pneumatic environment to a fluid environment. The middle ear provides the critical impedance transformation between the low impedance character of sound in air and the higher impedance associated with sound transmission in fluids.

The labyrinth is a complex structure that is usually dismissed as irrelevant in the hearing literature. However, a review of this intricate structure shows it serves two distinct roles. It supports the vestibular system that provides orientation information to the subject. It also supports the auditory system by providing a home for the cochlea and spiral ganglia. The complexity of the labyrinth is largely due to its highly optimized packaging. It seeks to provide the highest possible rigidity to the elements of the body most susceptible to extraneous mechanical motion. The arrangement is more concerned with packaging economy (economical use of bone) than the sharing of functions. Girard has provided the most useful graphic showing how the paired labyrinths are arranged in close proximity to the brainstem<sup>9</sup>.

While not often discussed, the labyrinth contains a physical vestibule that is shared between the vestibular system and the auditory system. It is the fluid filled chamber where the acoustic energy from the middle ear is delivered. The energy is delivered to the vestibule as a longitudinal (pressure) wave traveling at a nominal 1500 meters/sec. It is the task of the caecum of the vestibule to convert this energy into a surface acoustic wave carrying the same information but traveling at a nominal six meters/sec. This is accomplished by a "launcher" mechanism within the

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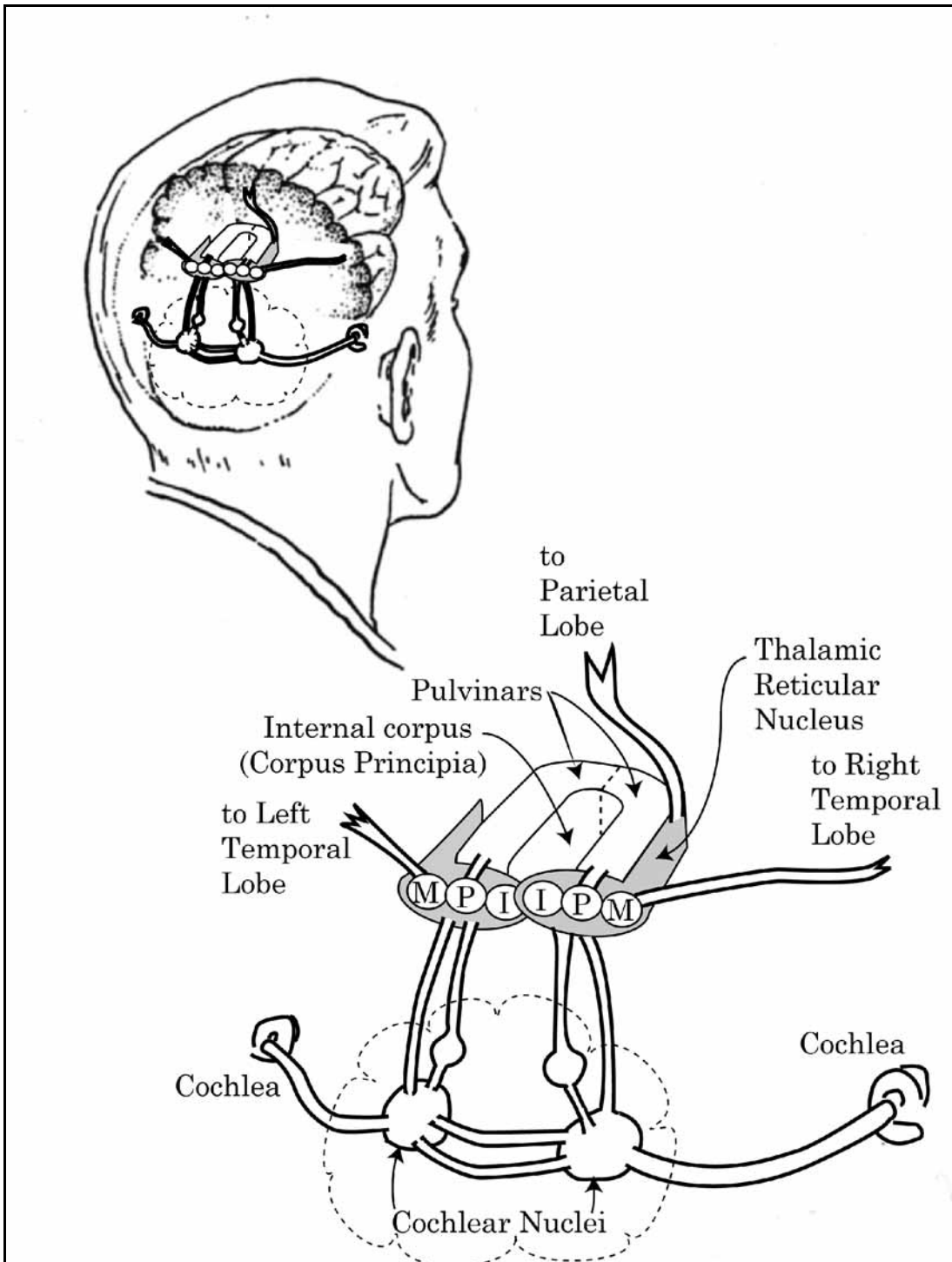


Figure 2.2.1-1 Caricature of the human auditory system (cerebellum shown dotted). The central portion of the figure corresponds to the mesencephalon and diencephalon of the cerebrum as seen from the rear with the cerebellum removed. M; medial geniculate nucleus. P; perigeniculate nucleus. I; inferior colliculus. In both views, the occipital lobe of the cerebral cortex has been cutaway.

as an extension of the gelatinous surface of the tectorial membrane. This surface faces the basilar membrane as it extends from the vestibule into the cochlear partition of the cochlea.

While not frequently discussed, the labyrinth contains at least five separate and distinct groups of mechanically excited sensory neurons. Flock<sup>10</sup> describes the location of these groups of neural circuitry. Their presence and similarity provide insight into the operation of the sensory neurons of hearing. In some of these groups, the cilia are subject to transverse forces. Others are excited by axial forces. In the case of hearing, it will be shown the cilia are primarily driven by axial forces.

It has become common in hearing to overlook the functional role of the labyrinth in the interests of a simplified pedagogy. As a result, the hearing literature does not provide significant information showing the anatomical and morphological arrangement of the cochlea within the labyrinth. A great many caricatures have been reproduced suggesting a direct connection between the stapes and oval window, and the "scala vestibuli" of the cochlea. Often, the vestibule has been omitted from the presentation completely. This is unfortunate. The best information is found in the surgical literature of otolaryngology, with Anson & Donaldson being a particularly strong source.

The surgical literature shows the vestibule and the scala vestibule are not directly connected from an acoustic perspective. They are only connected by small ducts for purposes of homeostasis. These ducts exhibit an acoustic impedance much too high to transfer energy efficiently to the scala vestibule. Richany et al<sup>11</sup>. and other medical texts confirm, the oval and round windows are not perpendicular to the long axis of the cochlear partition at its base, and they are not located in a common plane.

The work of Anson & Donaldson has the best imagery located to date<sup>12</sup>. Their frontplate to Part II is particularly clear in showing the stapes does not interface directly with the canals of the cochlea as frequently assumed. Figures III-98, III-96, III-87, III-80, III-29 are particularly relevant in showing that the stapes is a considerable distance from what most images suggest is the cochlea itself. Figure 49 in Vidic & O'Rahilly stresses this point<sup>13</sup>. There is no direct acoustic connection between the stapes and the cochlea. The stapes connects to the vestibule of the labyrinth (a morphological feature that is not related to the nearby but separate scala vestibuli). Harrison & Hunter-Duvar have also provided an electron micrograph that shows the location of the stapes as remote from the cochlea itself<sup>14</sup>.

Caution must even be exercised when reviewing Anson & Donaldson. In the first two editions of this work, they conformed to the common wisdom and showed a caricature of the oval window intimately associated with the scala vestibule of the cochlea. However, in the third edition of 1981, Anson & Donaldson make a very important observation regarding their caricature in figure III-54 (that they dropped from the 4<sup>th</sup> edition of 1992). "The windows are shown as if they lay on the same level; the oval window is pictured as if it opened into the vestibular scala, not into the vestibule." While their semantics is inverted, the assertion is clear. The oval window opens into the vestibule of the labyrinth and not into the scala vestibule! The plates they reference in the 4<sup>th</sup> edition do not show an intimate connection between the scala vestibuli and the vestibule. This observation will become important in Chapter 4.

While the hearing literature typically caricatures the cochlea as a standalone object with an external surface reminiscent of the shell of a marine snail, this is grossly misleading. Surgical texts make it abundantly clear that the cochlea actually consists of a very complex fluid-filled cavity within a much larger piece of bone (the bulla or temporal bone) associated with the cranium itself. The shape of the cochlea can only be represented materialistically by making a lost-wax mold of this cavity (frontpiece of Anson & Donaldson, 3rd Edition). This process is aided by initially removing the only substantial part unique to the cochlea, the cochlear partition bisecting the chamber of the cochlea.

As also noted in the 3<sup>rd</sup> edition of Anson & Donaldson (footnote, page 178), the modiolus or axis of the spiral of the cochlea is typically in the horizontal plane in humans.

Within the context described above, the graphics provided in the four editions of Anson & Donaldson and provided by Harrison & Hunter-Duvar<sup>15</sup> writing in Jahn & Santo-Sacchi provide the best description of the anatomical structure of the cochlea available.

The morphological role of the cochlear nucleus is ambiguous. While this large neurological structure is physically located adjacent to or embedded in the wall of the brainstem (near the lower part of the fourth ventricle), its physiological role appears analogous to that of the neurological portion of the retina in vision. It generates a large number of uniquely definable and purposed signals that are grouped into nerves that appear to be diverging as they make their way along the remainder of the brainstem toward the midbrain and the cerebral cortex. Divergence is typically a characteristic of the peripheral nervous system. It appears useful to associate the cochlear nuclei with the peripheral nervous system.

## 2.2.2 Gross anatomy of the CNS related to hearing

As noted earlier, Gulick has described the CNS elements related to hearing as comprising about a dozen individual neural nuclei (consisting of one or more processing engines) before the system converges on the mesencephalon of the brainstem. These engines are arranged in a very complex three-dimensional structure along the brainstem before reaching the midbrain. The arrangement is difficult to portray graphically and equally difficult to access experimentally. The arrangement appears to provide the earliest possible extraction of information defining the external spatial location of the source of acoustic signals. As in vision, these early circuits locate within the lower brainstem are closely associated with the alarm mode of the hearing modality. An animal frequently reacts to a threatening stimulus before the higher neurological centers become aware of the threat.

Up to and including the mesencephalon, the nuclei generally appear in pairs. Beginning with the diencephalon, there are multiple structures that may or may not appear in pairs. The higher the level of processing, the more likely the structures, like the thalamic reticular nucleus and the parietal lobe, are not paired. All of these structures contain multiple processing engines that have not been explicitly identified.

Figure 2.2.2-1 provides a series of cutaway views based on the profile of the brain shown in the inset on the left. It highlights the location of most of the discrete nuclei. Added for purposes of discussion are the parietal lobe (that would be out-of-plane in frame 4), and the cerebellum. The parietal lobe is directly above the thalamus in the cerebral cortex of humans. The parietal lobe is believed to contain the saliency map, describing the current state of the environment surrounding the subject. As shown in the inset, the cerebellum is directly behind the brainstem and largely covered by the cerebral cortex in humans. The cerebellum provides critical memory functions associated with the precise location of external stimuli and the generation of precise commands to the muscle system. A major portion of it is dedicated to the hearing modality.

A more faithful rendition of the dedicated engines of the hearing modality would divide the "primary auditory cortex" into two discontinuous segments, the primary auditory cortex centered on area 41 and the associative auditory cortex located within areas 22 & 39. It would also subdivide the thalamus into distinct morphological areas associated with various functions.

The complex interconnection of the nuclei will be addressed at a high level in Section 2.4.

### 2.2.2.1 Terminology is in a state of flux

Terminology is a significant problem in morphology because it has been evolving from multiple earlier systems of notation. Few authors continue to refer to the cerebral hemispheres as the telencephalon. They are more often labeled part of the cerebrum. Nolte (1999) defines the thalamus as part of the cerebrum but Nolte & Angevine (2000) define the thalamus as distinct from the cerebrum (page 1). In many documents related to the lower animals, the thalamus is usually considered the terminal portion of the brainstem instead of part of the cerebrum. In this case, it is considered part of the midbrain (mesencephalon). Still others have settled on the designation "diencephalon (literally the in-between brain)" to describe an additional division between the cerebrum and the midbrain.

An alternate labeling makes the telencephalon (the cerebral hemispheres) the neo-cortex, and the diencephalon and mesencephalon the paleo-cortex. This leaves the cerebellum a separate entity. The cerebellum will play an increasingly important role in future hearing and vision research.

In this context, the term cortex is synonymous with the brain and the spinal cord is exterior to the cortex. While the spinal cord is generally considered a morphological element, as noted above, *there is actually a pair of spinal cords* encased in an armored articulated cable tray made up of vertebrae. The two chords support the bilateral organization of the human along with the appropriate reflex arcs between the two sides.

While the temporal lobes of the cerebral cortex have been most intensely studied, primarily because of their easy accessibility, they are not the primary elements of hearing in the higher mammals. The elements of the brainstem are arguably the most important elements of the CNS in hearing. From a functional perspective, the major morphological elements dedicated to hearing in humans consist of the mesencephalon, the diencephalon, the cerebellum and the temporal lobes of the cerebral cortex. The functional role of these elements will be developed in the following chapters.

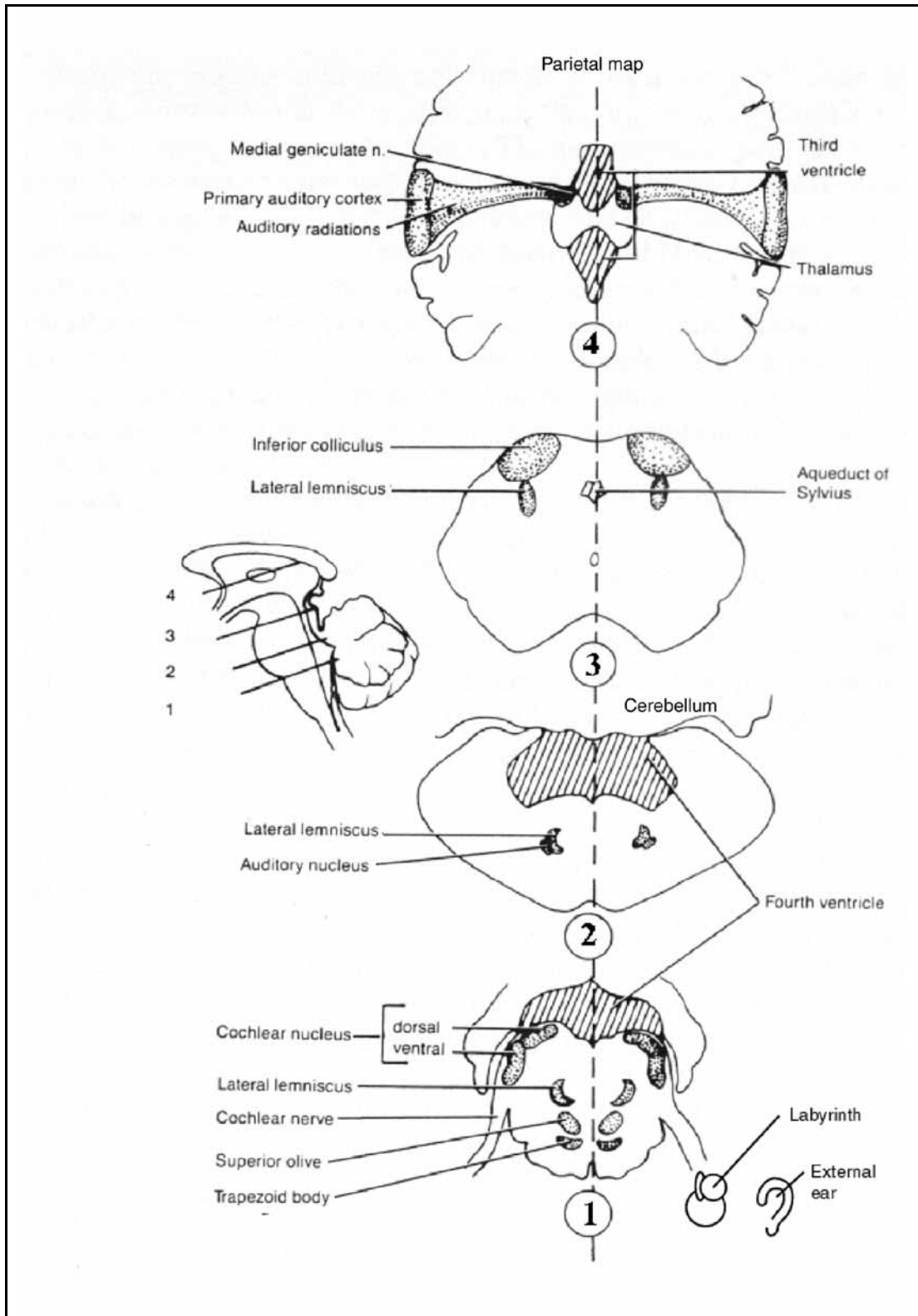


Figure 2.2.2-1 Four horizontal sections at the levels indicated in the insert. The dashed line represents the midline, and the top and bottom of each section represent the dorsal and ventral directions, respectively. Note the singular names for the paired bodies. From Gulick, et. al, 1989.

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Rather than reproduce material on the morphology of the elements of the brain orthodromic to the midbrain, the reader is directed to some excellent sources. Nolte provides several figures defining the topographic characteristics of the human brain at the introductory level<sup>16</sup>. At a more detailed level, Nolte & Angevine should be consulted<sup>17</sup>. Affi & Bergman have provided a recent text and atlas of the brain that provides many definitions of morphological terms<sup>18</sup>. It also provides a discussion of the morphogenesis and initial embryology of the brain. The morphogenesis of the human brain is well illustrated in figure 3-17 of Carpenter & Sutin<sup>19</sup>. Many of the better images in the literature originated in an excellent early text by Noback<sup>20</sup>. The use of the term functional in the above works does not refer to signaling, but only the topological arrangement of the morphological elements of the neural system based on neural traffic flow.

This work will focus on a specific part of the diencephalon that is morphologically and topologically distinct from the remainder of the thalamus. This thalamic reticular nucleus appears to play a key role in the control of both the supervision and the operation of the nervous system. The tissue of the TRN forms both the outer covering of the thalamus (within the diencephalon) and the folded structures of the mesencephalon.

### 2.2.2.2 The architectonics of the temporal lobes

The cerebral cortex directly supports hearing via two areas of the temporal lobe, a "primary" area and an association area. The primary auditory area is located in the fissure of Sylvius adjacent to the superior temporal gyrus. It is also as close as possible to the medial geniculate nucleus. This area spills over into areas numbered 41 and 42 by Brodmann. Affi & Bergman have provided the best illustration of this area by peeling the temporal lobe away from the frontal and parietal lobes<sup>21</sup>. The association area is not well defined. Different authors associate it with different parts of areas 22 and 39 of Brodmann. Wernicke showed that this area plays a major role in speech comprehension (percept integration, Section 8.2.5). Noback provides one of the clearest discussions of the nature and features of the auditory cortex (pp 159-161 & 231-244). Sonderquist has provided additional details related to these auditory areas<sup>22</sup>. These areas have been explored more fully in the monkey than in man.

The effects of artificial electrical stimulation of the auditory areas and the operation of the overall system following damage to these areas is controversial within the literature. The following paragraphs will present conflicting views in some areas, based on that literature.

Noback notes the tonotopic organization of the area within the sulcus (his figure 10-5). This discussion follows that of Noback with some changes in nomenclature. Low tones are localized laterally and high tones are localized medially. The medial area of the monkey may have a reverse tonotopic organization.

Stimulation of the areas 41, 42, and 22 elicit sensations of sound described as cricket chirping, bells, humming, buzzing and whistling. These labels represent more abstract signals than just pure tones. The sounds are perceived as coming from the opposite ear. During stimulation, conversation picked up by the ears cannot be perceived. At times, deafness may be subjectively sensed.

A patient with a lesion in area 22 on the dominant side is serious. While still able to hear, the subject has profound difficulty in the interpretation of sounds. The spoken language may be utterly meaningless or extremely difficult to comprehend. He is not deaf, but cannot perceive the content of the conversation. This condition is sometimes labeled "word deafness" or "auditory receptive aphasia." The patient can speak but he makes many mistakes without realizing it. Lesions of areas 41 and 42, on one side, result in the inability to locate the source of sound readily from auditory cues, but only a slight loss in communications capability.

### 2.2.3 Gross anatomy of the brainstem related to hearing

Exploring the physiology of hearing within the brain stem in the living human has been largely forbidden by moral (ethical) issues, except following traumatic injury. As a result, most of the electrophysiology associated with the morphology of hearing has been obtained from other species. Frequently, the species of choice has been the lower primates. The lower primates have proven invaluable in linking the morphology, the topography and the coarse topology of auditory modality. However, these primates are as a minimum much smaller than humans. At the more sophisticated levels, they are less advanced. It will become apparent that the larger and more advanced primates are not adequate analogs of the human when it comes to the information extraction capabilities of the human related to communications (and musical pleasure).

This work will show that specific elements of the diencephalon, some not previously identified in humans, are critically important to human hearing. It is the responsibility of the researcher to show the equivalent elements are present in the lower primates before attempting to draw parallels at the more sophisticated performance levels, such



as percept generation. The size and complexity of the pulvinar, and its interaction with the cerebellum, appear to be particularly critical to the performance of the human auditory system.

Figure 2.2.3-1 reproduces Noback's figure 1-8. It is one of the few graphics in the literature showing the physical organization of the diencephalon. While not shown explicitly, the bulk of the posterior thalamus is occupied by the pulvinar. Notice the two horizontal ranks of nuclei below the thalamus and generally labeled as parts of the mesencephalon. Not visible at this scale are the perigeniculate nuclei associated with each of the geniculate nuclei. The rankings of the nuclei and the location of the PGN can be identified more clearly in Mettler<sup>23</sup>. The pulvinar is in intimate communications with the LGNs and the MGNs, but most specifically with the PGNs (both visual and auditory).

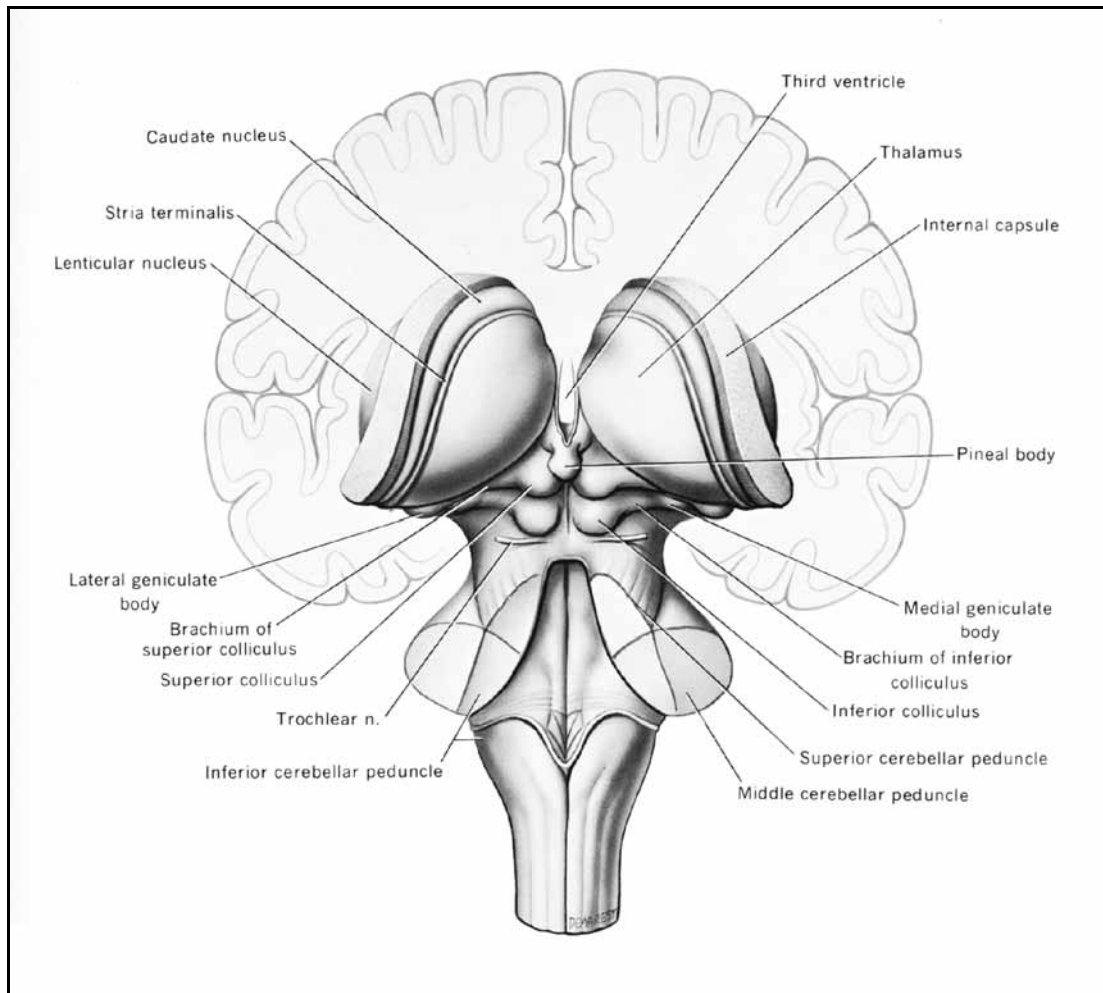


Figure 2.2.3-1 The posterior human diencephalon above the mesencephalon. Each lobe of the thalamus is shown above two ranks of mesencephalon structure. The lateral geniculate nuclei of the upper rank are closely associated with vision. The medial geniculate nuclei of the lower rank are closely associated with hearing. The inferior colliculus is closely associated with sound source location. The two Brachium of the inferior colliculus are alternate names for the perigeniculate nuclei of hearing. From Noback, 1967.

The structure labeled the internal capsule plays a major role in sensory perception. Although shown on the external surface of the thalamus, it is much larger in the region between these two features and plays an analogous role to the corpus callosum, the major commissure between the two cerebral lobes. Figure 1-6 of Noback shows its close relationship with the corona radiata leaving the thalamus for various destinations on the inner surface of the cerebral cortex. The stria terminalis and the caudate nucleus are shown conceptually in this figure. In the terminology of this work, they are closely associated with the physiologically defined thalamic reticular nucleus (TRN). The caudate

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nucleus is a major node of the diencephalon connecting to the parietal lobe of the cerebral cortex (Noback, chaps. 14 & 16) while the stria terminalis provides communications with the limbic system (Noback, chap. 15).

The thalamus is covered by a distinctly separate structure described in the above figure as the caudate nucleus but known here as the thalamic reticular nucleus (TRN). This structure covers more than 80% of the surface of the thalamus. It is the critical command and control center of the nervous system. It provides an overall supervisory function related to all of the sensory inputs and the transfer of abstract data to the saliency map of the parietal lobe. In this role, the supervisory function controls the switching of signals between a variety of different paths between major engines of the neural system.

Many of the structures designated as part of the mesencephalon, appear to be formed as an extension of the TRN. The lateral geniculate nucleus (LGN) of vision is known to consist of a rolled section of the TRN. The rolling has generated a structure of up to ten neural layers thick that allows the spatial correlation of the various chromatic and brightness signals of vision along with the merging of the information from the two eyes. The visual PGN is also formed as a specialization of the LGN.

The MGN and auditory PGN, by analogy with the LGN, are also believed to be formed by a rolled portion of the TRN.

Gacek gives a description of the morphology of the medial geniculate nuclei ca. 1972<sup>24</sup>. He notes the division of the MGN into two principal parts, the pars principalis and the pars magnocellularis. The pars principalis is composed of many closely packed small cells. He further notes that nearly all of the commissure associated with the pars principalis connect with the temporal lobe of the cortex (forming the MGN/temporal couple defined below).

"The pars magnocellularis is that region of the medial geniculate that is medioventral to the pars principalis and is composed of loosely arranged large cells. Much less is known about this division. Evidence for a cortical projection from this division is weak." It is proposed that the pars magnocellularis of Gacek is the perigeniculate nucleus, PGN, of this work. Its neural projections are primarily to the pulvinar which it adjoins.

Gacek notes "there are no commissural neurons at the medial-geniculate level." The equivalent of commissural neurons are found within the internal capsule of the diencephalon. Gacek also notes the position of the reticular formation but does not describe its role. The reticular formation is called the thalamic reticular nucleus (TRN) in this work.

The acoustic portion of the PGN is analogous to the visual portion of the PGN. It is a multi-dimensional associative correlator. The precise spatial arrangement of this correlator is not yet known. The large size of the neurons within the PGN is associated primarily with their long dendrites. The PGN is primarily responsible for recognizing patterns differing in frequency content and amplitude content at specific intervals of time. It may have a secondary role in comparing such patterns as a function of short term time differences. It is proposed that comparing and recognizing longer term temporal patterns is the responsibility of the temporal lobes of the cerebral cortex.

Both PGNs are intimately associated with the pulvinar immediately rostral to them. A leader in the study of the pulvinar is Chalupa<sup>25</sup>. As late as 1991, he includes a paragraph title: "What Does the Pulvinar Do?" without providing a substantive answer. He does provide a list of functional features associated with the pulvinar and a comprehensive bibliography. Chalupa addresses the fact that the size and differentiation of the pulvinar increase markedly as one ascends the evolutionary scale. He describes the pulvinar as the largest nucleus in the thalamus and recognizes its role in extrageniculo-striate visual communications.

A major problem has been the precision of the probing of this area designed to determine the fields in object space associated with different areas of the pulvinar and associated bodies. The probing has generally lacked geometric precision and little or no attempt at temporal differentiation has been made (particularly with a precision below three milliseconds in humans and a smaller number in smaller animals). Most of the available data comes from experiments involving vision.

Carpenter & Sutin have recently provided a highly illustrative view of the thalamus and its subdivisions<sup>26</sup>. However, Steraide et al. have provided a significantly different view based on more conceptual drawings<sup>27</sup>.

### 2.2.3.1 The cortex of lower mammals

Diamond has performed an extensive investigation into the central nervous system of a variety of lower mammals<sup>28</sup>. While they appear to be very similar topologically, they vary considerably morphologically. His comments on signaling paths will be addressed in Section 8.1.5. Ruch & Fulton (no relation) have presented a side view of the

monkey brain that can be compared to the above figures for human brains<sup>29</sup>.

A larger proportion of the engines of the auditory system are located on the surface of the cortex in the cat. Gulick has provided an annotated side view of the cortex of cat and discussed the tonotopicity of the signals at that location<sup>30</sup>. Wever has provided several alternate representations of the cat neocortex that differ from that of Gulick<sup>31</sup>. Merzenich has provided multiple views of the aural areas of the cat and monkey cortices based on our evolving knowledge of them<sup>32</sup>.

As in the case of vision, an early investigator adopted the term primary auditory cortex for an area of the cerebral cortex that is clearly not primary within the context of the complete system. Many investigators have asserted that humans and other mammals can hear adequately and perform normally in the absence of either or both temporal lobes of their cortex<sup>33</sup>. It is the midbrain, consisting of the thalamus, inferior colliculus and the pons that are the critical elements of the auditory neural system. Diamond has asserted (page 2), "For example, Sperry showed that cutting the corticocortical pathways from sensory areas to motor areas of the monkey failed to produce any loss of learned habits, any loss of object recognition, or indeed any obvious deficits whatsoever." The reason is simple, his direct paths between these areas are secondary. The primary paths, as in vision, pass through the thalamus reticular nucleus (TRN) and the associated internal commissure between halves of the thalamus.

## 2.3 The morphology of the PNS of human hearing

It is critically important that the most substantial evidence available be reviewed when making decisions applicable to the detailed morphology of the modality. While simple cross-sections are adequate for describing the external ear, more sophisticated techniques are needed to study the labyrinth, and specifically the cochlea. In the absence of personal dissection, the best available evidence is in two forms, photography of the actual tissue after appropriate dissection and the generation of models based on the Born Method. The Born Method appears to be a variant of the widely used lost-wax method. It generates faithful multi-dimensional reproductions of the in-situ structures without dissection. The critical importance of this technique will become obvious in the following sections.

The elements of hearing in the PNS have traditionally been divided into the outer ear, the middle ear, the inner ear and the spiral ganglia of the inner ear. Because of its functional role, this work chooses to consider the cochlear nucleus part of the PNS. This work makes a more precise division between the outer and middle ear and the middle and inner ear. The division follows the physiology of hearing. The outer ear includes all of the external structure and the auditory canal but terminates at the external surface of the tympanic membrane. The tympanic membrane can be considered a fixed "hard" wall as far as the pneumatic environment is concerned.

This work has identified a crucial functional element of the ear generally ignored in the past. The presence of this element requires modifying the definition of either the middle ear or the inner ear to support this function.

Figure 2.3.1-1 shows the elements of the middle and inner ear in caricature in conjunction with the remainder of the labyrinth.

This view shows the eustachian tube equalizing the pressure across the tympanic membrane at zero frequency. It also emphasizes the fact that the conventionally defined middle ear interfaces with the vestibule of the labyrinth rather than the scala vestibuli as generally assumed in the pedagogical and academic literature of hearing. Finally, it emphasizes the physical prominence of the extension of the cochlear partition (the caecum of the vestibule) within the vestibule and its location relative to the oval window. This prominence is crucial in the transfer of acoustic energy from the oval window to the tectorial membrane of the cochlear partition (Section 2.3.3).

### 2.3.1 Morphogenesis of the auditory system

Information on the morphogenesis and initial operating capacity of the human auditory system is not easily located in the academic research literature. However, excellent information is available in the surgical portion of the medical literature. This information addresses both morphogenesis and fully developed elements of the peripheral neural system dedicated to hearing.

Brownell has discussed the evolution of the labyrinth<sup>34</sup>. He suggests that the vestibular part of the labyrinth evolved about 400 million years ago. The cochlea evolved about 200 million years ago. The earliest cochlea possessed only minimal change in curvature along the cochlear partition and only functioned over a limited frequency range (like present birds<sup>35</sup>). Cotanche & Corwin show the basilar papilla of the bird cochlea curving from 45 to 60 degrees<sup>36</sup>. The owls went further than most birds by evolving a cochlear partition of about ½ turn (180 degrees) and a wider frequency range<sup>37</sup>. With the advent of the mammals, the change in curvature of the cochlea became significant, with

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a total length frequently reaching 2-4 complete turns. The frequency range of their hearing is directly related to their degree of cochlear partition curvature. As in the case of the owl, the mammals that have developed an active echo-location system have further optimized the curvature of their cochlear partitions at locations associated with specific frequencies. Interestingly, the straight cochlear partition so commonly discussed in hearing research offers no frequency discrimination capability (Section 4.5).

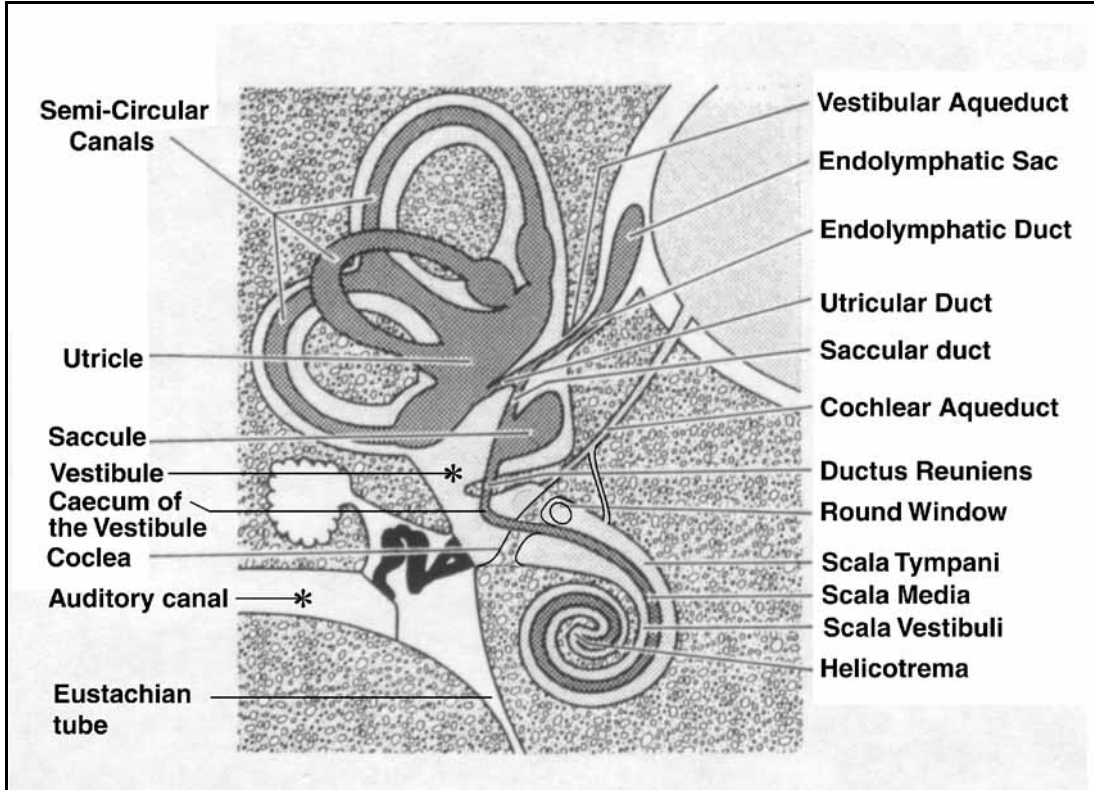


Figure 2.3.1-1 A caricature of the labyrinth with the cochlea acoustically isolated from the vestibule by bone, except for the access via the vestibular caecum (a.k.a. cul-de-sac of the cochlear partition). The cochlear partition is labeled the scala media in this image. The interpretation portrayed here agrees with the surgical record but not the conventional wisdom within the hearing community. Modified from an earlier caricature in Jahn & Santos-Sacchi, 1988.

The first two chapters in Edelman et al. give a very thorough discussion of the morphogenesis of the avian cochlea<sup>38</sup>. An interesting conclusion is that the process is quite similar to that forming the eyes. The cochlea is formed of ectodermal tissue. The “hair cells” of hearing, like the photoreceptor cells of vision are derived from a common cell type that also produces conventional hairs on the external surfaces of the body.

Doan et al. have provided some useful information for those studying hearing in neonate animals<sup>39</sup>. They note, “Rats younger than 10 days of age had a poorly defined middle ear as well as a closed ear canal. By 10 days after birth the tympanic membrane and the ossicles beneath were clearly defined, but the ear canal was still closed.” Continuing, “Fluid could be seen within the middle-ear space when viewed through the tympanic membrane, . . .” “The ear canal was completely open and the bulla was clear of fluid by 12 days after birth.” Investigators using different species should consider these findings in relation to their subjects.

The human auditory system is known to achieve some level of prenatal operation. Harrison provides a table showing the human may be able to perceive sounds 120 days before birth<sup>40</sup>. However, this capability is achieved before the clearing of the auditory canal and the middle ear space.

Anson & Donaldson describe the membranous labyrinth as the fundamental part of the ear<sup>41</sup>. They also describe its formation. “It is the first to form; even before any other part of the internal ear develops, the peripheral processes of the acoustic nerve reach its membranous wall.” They note that the cochlear portion of the membranous labyrinth, the cochlear duct or scala media, is initially almost straight. By the seventh week, it consists of one turn. The complete multi-turn configuration is achieved by the eleventh week. The neurons interface with the structures within

the membranous labyrinth during the eleventh week of the fetus. Ossification of the otic capsule is complete by the twentieth week. The internal ear is unique in that it reaches maturation (adult size) during the twentieth week of incubation. At that time it has a base diameter of 9 mm and an axial height of 5 mm (page 164). They note that the cochlea is essentially fully developed and full size at the time of birth in humans. Some question arises concerning the low frequency performance of the infant hearing system because it has not been documented that the complete gel surface of the tectorial membrane has been formed.

As noted by Bredberg, the cochlear duct is the first feature of the cochlea formed during human morphogenesis<sup>42</sup>. Up to the age of eight weeks, it is the only part of the auditory system present in the human fetus. It originates as an outgrowth of the saccular portion of the otocyst. Bredberg provides comprehensive data on the prenatal and post natal human hearing modality. He notes the presence of a kinocilium in each of the sensory neurons, both IHCs & OHCs, in the four-month-old human fetus (page 54). This feature apparently atrophies early in life. They are not reported in the literature of human adults. This would suggest the kinocilia play a role in aligning the structures of the Organ of Corti. Such kinocilia are found commonly among small (generally young) mammals used in hearing research.

### 2.3.2 The outer ear

The morphology of the outer human ear is well documented elsewhere. It will not be discussed here except to note four main features. It forms an efficient horn capable of collecting energy over a wide frequency band arriving from a variety of directions. The horn bends the wavefronts associated with the collected energy so all of the wavefronts are nominally traveling within the auditory canal perpendicular to, and with a curvature matching the curvature of, the tympanic membrane of the middle ear. The impedance of air within the auditory canal, and associated with the energy delivered to the middle ear, is different from the impedance of the external acoustic field. The impedance of the tissue forming the auditory canal is sufficiently high that it does not absorb significant energy from the air within it.

Goodhill (page 23) gives the diameter of the tympanic membrane (pars tensa) as 9 mm with a radius of curvature of 4–5 mm. Others have said the membrane is conical, rather than spherical in shape. Both of these shapes are designed to prevent the membrane from vibrating like a drumhead. The membrane is mounted in a resilient ring rather than a hard ring. While this element is frequently called the ear drum (eliciting the vision of the vibrating modes of a drum), Geisler portrays it as a piston and Bekesy shows clearly that it moves more as a rigid body than a vibrating body<sup>43</sup>.

Rosowski has provided the most extensive mathematical model of the external ear and the conventional middle ear<sup>44</sup>. The model terminates by treating the cochlea as a single port network with all of the applied energy flowing through both the oval and round windows. Rosowski notes that "this assumption is very common in the literature, but has only been loosely tested." This work does not support his two-port concept since most of the energy extracted by the sensory neurons is dissipated within the piezoelectric mechanism of those neurons.

### 2.3.3 An expanded definition of the middle ear

Previous conceptual definitions of the middle ear and inner ear have left a significant function and morphological feature unidentified. The region between the oval window and the beginning of the Organ of Corti contains a physiologically critical functional element. It is used to transform the longitudinal (pressure) wave propagating rapidly within the vestibule into a surface acoustic wave propagating slowly along the gel surface of the tectorial membrane. The significance of this function and feature leads to a redefinition of either the middle ear or the inner ear (the cochlea and its contents). The situation and its description are more easily understood if illustrated functionally as in Figure 2.3.3-1.

The regions labeled  $B_1$  and  $B_2$  represent the definition of the inner ear presented earlier. Stage  $B_1$  represents the region between the external surface of the tympanic membrane and the pivot point of the lever formed by the ossicle bones. The tympanic membrane is shown operating as a differential motion sensor. At zero frequency, the pressure on each side of the membrane is equalized via the eustachian tube. Thus, the transfer function of stage  $B_1$  always exhibits a zero at zero frequency.

The tympanic membrane and the oval window can be considered rigid bodies in this simplified discussion. It is important to note the following. The performance of this configuration is not determined by the ratio of the length of the lever arms. This configuration is known currently as a hydraulic ram. Helmholtz first described it in 1877 as a pneumatic lever. The energy at the tympanic membrane is calculated as the applied energy density times the area of the piston. The energy density at the oval window is calculated as the energy density created in the fluid times

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the area of that piston. The performance of the ram is calculated from the ratio of these two energy densities. In simpler terms, the total force applied to the membrane times the lever arm distance,  $L_1$ , defines the moment transferred from the tympanic membrane. Similarly, the lever distance,  $L_2$ , divided into that moment defines the force applied to the fluid of the vestibule.  $L_1$  and  $L_2$  describe the perpendicular distance between the forces involved and the pivot point.

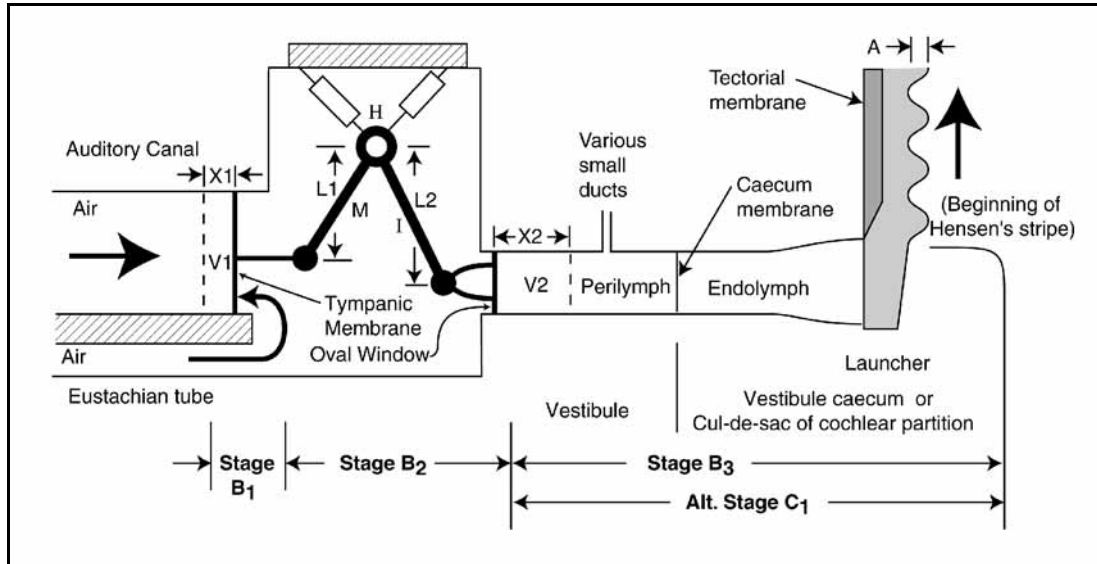


Figure 2.3.3-1 Expanded definition of the middle ear in terrestrial animals. The middle ear performs a major impedance transformation between the external pneumatic environment and the liquid-crystalline environment of the tectorial membrane. It also converts the longitudinal (pressure) wave within the vestibule into a surface acoustic wave that is transferred into the inner ear. M; malleus. I; incus. H; head of the malleus. The two bones forming the crank around the pivot point are firmly but not rigidly attached to each other. See text.

The portion of the cochlear partition within the vestibule is labeled the vestibule caecum or the cul-de-sac of the cochlear partition in the surgical literature. A new functional feature, labeled the launcher is found inside this caecum of the vestibule. This functional portion of the middle ear has not been identified previously in the research literature. The role of this launcher will be defined in detail in Sections 4.2 & 4.4.

The force applied at the oval window induces a longitudinal (pressure) wave propagating across the vestibule fluid (perilymph) at a high speed. This wave passes through the membrane of the caecum and encounters the initial gelatinous surface of the tectorial membrane as it appears in the caecum. The sloping surface at the beginning of the gel surface is described as the launcher. The launcher accepts the energy in the incident longitudinal wave and launches a new surface acoustic wave traveling on the surface of the gel. The mechanism is analogous to the action of the sail on a sailboat. The closer the angle between the longitudinal wave and the surface acoustic wave are to 90 degrees, the slower the acoustic wave travels. Beyond a certain angle, the process becomes inefficient. In hearing, the ratio between the two speeds is about 250:1. This functional arrangement is labeled section  $B_3$  of the middle ear. Alternately, this arrangement could be considered section  $C_1$  of a redefined mechanical portion of the inner ear.

Based on the above definition of the middle ear, the inner ear contains the traditional elements of the cochlea and extends from the bony wall of the vestibule to the extreme end of the cochlea. The energy entering this inner ear is in the form of a modified Rayleigh wave as defined more completely in Section 4.1.5.

The robust interface between the vestibule of the labyrinth and the cochlear duct is shown on page 267 of Anson & Donaldson, 4<sup>th</sup> Ed. They describe this picture as part of the Wisconsin Collection, series 121, X50. This figure also appears in Anson, Harper & Winch<sup>45</sup>. A similar figure (page 384) from the same series shows a slightly broader cul-de-sac with a width approximating 1.0 mm.

The size of the structures in the preceding figures can be put into perspective. The size of the stapes and incus are shown in comparison to a dime in Geisler (page 41). The stapes, "the smallest bone in the human body" according

to Goodhill (page 25), is no larger than the letter B in the word liberty inscribed on the dime.

Mathematically, the goal of the middle ear is to transfer the energy of the acoustic signal, in the form of a small displacement ( $X_1$ ) of a very large tympanic membrane to a relatively large displacement ( $A$ ) of a small highly specialized surface. The intermediate fluid displacement ( $X_2$ ) is only of academic interest.

### 2.3.4 The morphology of the inner ear—the cochlea

Figure 2.3.4-1 provides an annotated morphological cutaway of the human cochlea within its petrous temporal bone cocoon<sup>46</sup>. Notice the location of the air-filled tympanic cavity at the upper left. Not shown are the locations of the oval window connecting the ossicle bones within the tympanic cavity to the vestibule of the labyrinth and the round window connecting the scala tympani to the air-filled tympanic cavity of the middle ear. Notice also the helicotrema, the narrow canal connecting the two scala. No scale was provided by the originators of the figure. However, the diameter of the helicotrema is between 0.5 and 0.8 mm in diameter in humans (Bekesy, page 408). Based on this dimension, the cochlea, absent its bony case has major dimensions on the order of 6-8 mm ( a total volume considerably less than one cubic centimeter). The diameter of the overall cochlear duct is about 2 mm in diameter over most of its length. However, the only active area of the cochlear duct is the scala media, the smaller triangular area between Reissner's membrane and the basilar membrane. Each leg of this triangle is approximately 0.5 mm long. The tectorial membrane and the mechanically active portions of the sensory neurons are contained within the endolymph filled scala media.

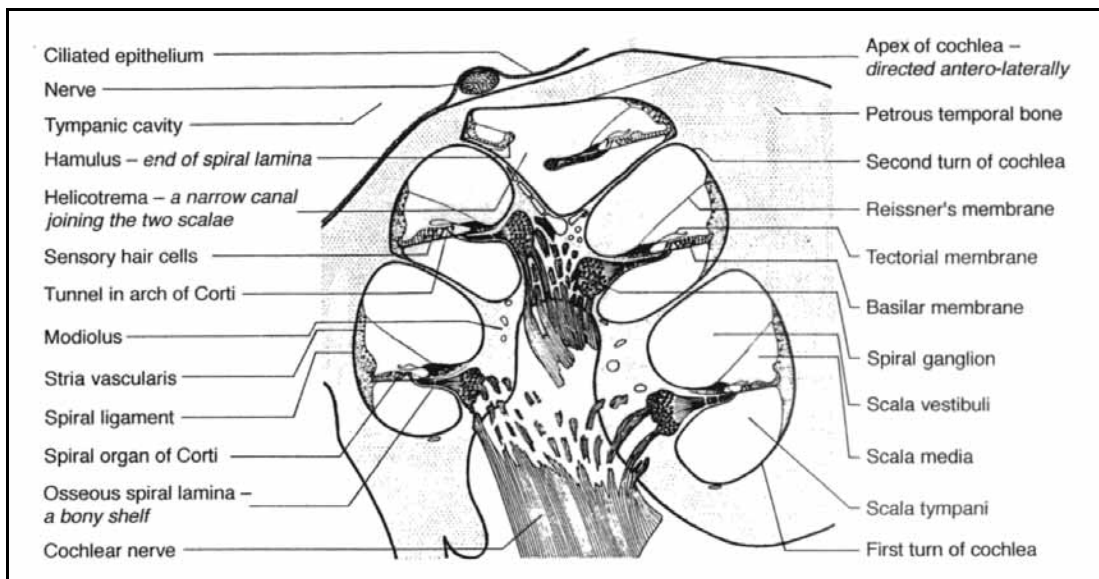


Figure 2.3.4-1 Annotated cross-sectional view of the cochlea. Note the absence of any external bony structure having the form of a snail shell. The cochlea consists of a cochlear partition separating two fluid chambers enclosed within the petrous temporal bone. The cochlea is coiled so as to pass through the plane of the paper multiple times beginning at the lower right. From Freeman & Bracegirdle, 1976.

Tiedemann has collected considerable precise data on the dimensions of the cochlea of the water buffalo, *Anoa bubalis*<sup>47</sup>. He has compared this to the less voluminous data for the human cochlea. Van De Water has provided a detailed discussion of the development of the inner ear of mammals<sup>48</sup>.

#### 2.3.4.1 Gross morphology of the cochlea

The spiral cochlea of mammals is a unique geometric structure. The spiral is a key feature of the mammalian cochlea. Its curvature accounts for the wider audio frequency range found in mammals compared to non-mammals<sup>49</sup>. It deserves even closer study because its detailed geometry illuminates the specific frequency performance achievable in specific species and individuals within a species.

Because of the small size, the isolation within a bony capsule, and the delicacy of the tissues involved, it is extremely difficult to locate a truly precise and descriptive image of the cochlea. The literature generally presents a variety of

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caricatures based on the investigator's point of reference. Useful caricatures are found in Goodhill<sup>50</sup>, Shambaugh & Glasscock<sup>51</sup>, Geisler<sup>52</sup>, Anson & Donaldson, and Jahn & Santos-Sacchi. The frontplate of Anson & Donaldson, showing the entire wispy PNS portion of the human auditory-vestibular system sitting on a dime, provides the best perspective of the cochlea<sup>53</sup>. For an unknown reason, the same caricature appears in left-hand and right-hand versions in different publications. Harada has provided a wide selection of electron micrographs showing details of the cochlea.

The caricature by Anson, Harper & Winch is particularly useful in understanding the overall operation of the cochlea<sup>54</sup>. It shows clearly the division of the interior of the cochlea into three distinct chambers extending over the length of the coiled cochlea. The two outer chambers are known to be filled with a fluid called the perilymph. The triangular inner chamber is labeled the scala media. It is formed by Reissner's membrane, the basilar membrane and the stria vascularis, and is filled with a different fluid labeled the endolymph. The endolymph is chemically tailored to protect the unique materials forming the gelatinous (liquid-crystalline) surface of the tectorial membrane from the perilymph.

All of the specialized materials and neurological circuits critical to the signal generation portion of the hearing modality are found within the scala media. These materials and neurological circuits are extremely sensitive to extraneous vibration and must be protected. The technique used to protect them is conventional. The tectorial membrane (excluding the liquid-crystalline surface facing the basilar membrane) and the basilar membrane represent two inertial masses. These masses acoustically isolate the active elements between them. This isolation is enhanced by the fluids in the two outer chambers surrounding these membranes acting as hydraulic dampers. The bony mass surrounding these two outer chambers is provided primarily as protection against physical trauma.

It is the primary role of the two inertial masses, the two outer fluid chambers, the scala vestibuli and the scala tympani, and the bony shell surrounding them to isolate the cochlear partition within the scala media from vibration and trauma. They play no other functional role.

The earlier assertion that the acoustic connection between the vestibule and the cochlear duct is confirmed by two representations of the complete labyrinth obtained by the Born method and the accompanying text in Anson & Donaldson. They have also provided several pictures and drawings based on sectioning (pages 265 & 277) that show the intimate relationship between the oval window, the vestibule and the cochlear duct in a new born human. While the figures must be studied with the aid of the text, they are quite informative. *Notice that the scala vestibuli and the scala tympani are not present in these views.* By comparing these figures, it can be estimated that the distance between the center of the oval window and the center of the "collection area" of the cochlear duct is 2-3 mm.

It is important to note there is no volume within the cochlea that is not filled with liquid, liquid-crystalline or solid material. Many earlier theories required the presence of a gaseous/liquid interface within the cochlea to support a surface wave traveling the length of the cochlea. Such a condition does not occur within a healthy cochlea.

### 2.3.4.2 Gross morphology of the scala media

Anson & Donaldson describe the scala media (cochlear duct) in some detail in their text (4<sup>th</sup> Ed, page 159) using the same words as in their 2<sup>nd</sup> edition.

Figure 2.3.4-2 shows a model of the cochlear duct (scala media) obtained using the Born method. The cul-de-sac of the cochlear duct is clearly displayed. The cul-de-sac appears compatible with the earlier cutaway view showing the cul-de-sac up against, and in acoustic communication with, the vestibule. The dimensions of the flattened end are about 1.0 by 1.0 mm. This area can be compared with the area of the oval window estimated at 2.0 square mm by Shambaugh & Glasscock. Anson, Harper & Winch show a similar image illustrating the same relationships<sup>55</sup>.

While it has been common to speak of the cochlea as a simple spiral in the vernacular (sometimes described as a logarithmic spiral, an equiangular spiral or a *spira mirabilis*), a more precise description is needed.

While difficult to see in this figure, the scala media performs two and one-half turns around a central axis that ends near the word media in the figure. It then continues in a particularly long and apparently convoluted section of the scala media between the cul-de-sac and the beginning of the spiral. In fact, there is a single mathematical function that describes the shape of the functional element (Hensen's stripe) within the scala media over its entire length. This form is known as a Hankel function.

It is important to note that the cochlear partition does not spiral down to a point. It is a truncated-Hankel function. Furthermore, the helix of the cochlea has an extended portion at its base that does not follow the simple form of the



function. The overall form of Hensen's stripe can be completely described as a modified, and truncated, Hankel function (Section 4.5).

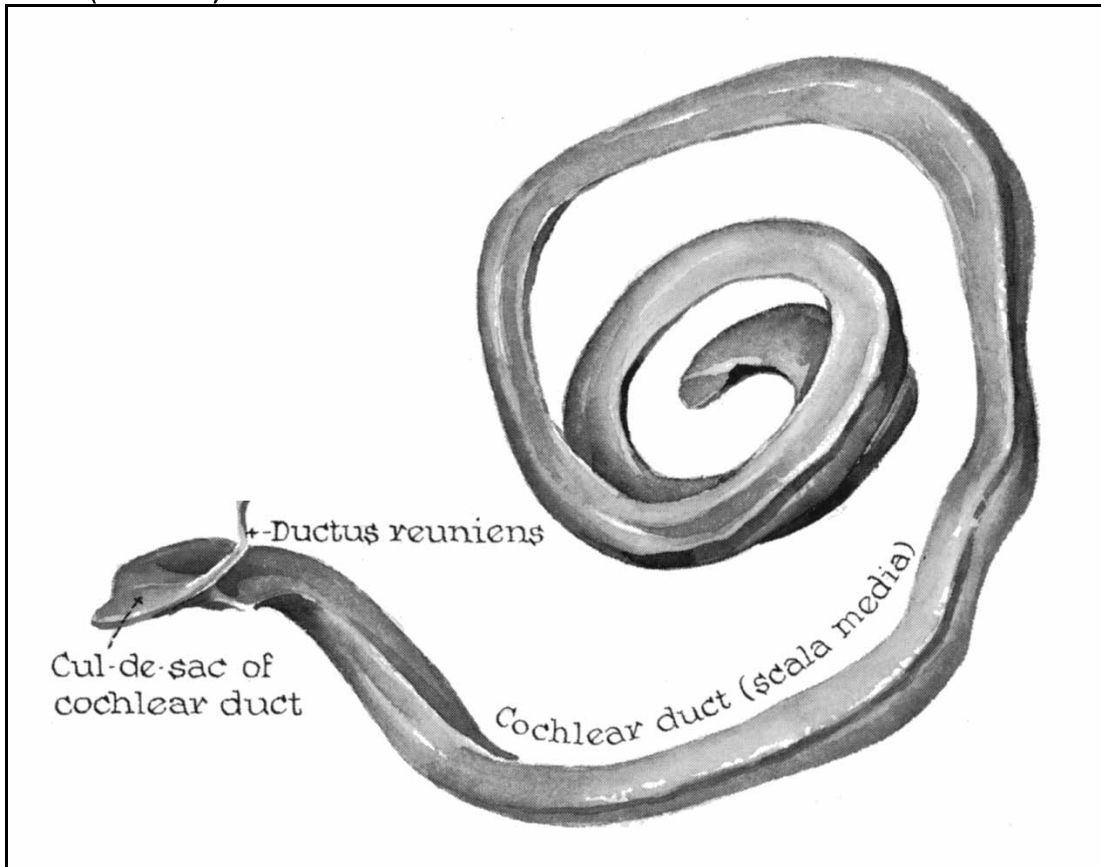


Figure 2.3.4-2 A model of the cochlear duct molded from a human cochlea using the Born method. The paddle-shape of the cul-de-sac is clearly displayed. Obtained from a 6 months old infant. From Anson & Donaldson, 4<sup>th</sup> Ed, 1992.

### 2.3.4.3 The cross-sectional morphology of the cochlea

It is difficult to find caricatures of the cross sections of the cochlea in the literature that agree with each other. A useful caricature of the cochlea is that in Kessel which dates from an earlier version in Kessel & Kardon<sup>56</sup>. It is closely followed by that of Allen<sup>57</sup>. Their view of where the basilar membrane terminates varies significantly in the area of the Cells of Claudius. In 1988, Santi provided several electron micrographs that clear up much of the variation among the caricatures of the Organ of Corti<sup>58</sup>. It clearly shows the Organ is not centered on the basilar membrane and the hinge points found in the structural models of Allen, and suggested much earlier, are not aligned perpendicular to the basilar membrane. Although these and other investigators discuss the basilar membrane as a compliant structure, they both show significant structure more suggestive of a highly rigidized beam.

Figure 2.3.4-3 shows the local arrangement at the tectorial/basilar interface that will be used here. This view is modified from Harada<sup>59</sup> who updated an earlier view of the second turn of a guinea pig cochlea by Davis (1953). The modifications show the gel-surface of the tectorial membrane and the capillaries within the stria vascularis and spiral ligament. The difference between the gel surface and the remainder of the tectorial membrane is shown clearly in figure 11 of Edge et al<sup>60</sup>. That figure also differentiates clearly between Hensen's stripe and the remainder of the gel surface.

Reissner's membrane is shown to consist of a single layer membrane of mono-cellular thickness plus occasionally other cells of unknown purpose. It does not offer any significant physical strength but does form a barrier between the perilymph and endolymph.

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The cochlear partition is shown as consisting of the tectorial membrane, the inner and outer hair cells and a variety of structural support cells mounted on the basilar membrane. The arrangement of the sensory neurons and the structural cells mounted on the basilar membrane has been labeled the Organ of Corti.

The stria vascularis plays an important role in the homeostasis of the Organ of Corti. The capillaries have been shown explicitly because these morphological structures are interconnected and form an electrical pathway that is significant in the electrophysiology of the sensory neurons.

The structural parameters of the materials forming the interior of the cochlea are not well tabulated. Most of the available analyses still assign ballpark estimates to more than one parameter. Note the rigidizing properties of the triangular inner tunnel of Corti and of the cells of Claudius. They would suppress any flexure of the basilar membrane related to the lateral direction. Note also the significant variety of longitudinal structures attached to the lower surface of the basilar membrane. These long structures would significantly restrict any flexure of the membrane in the longitudinal direction. These properties suggest that high frequency resonance phenomena play a minor role in the operation of the basilar membrane. On the contrary, the basilar membrane and its associated structures appear to represent a rigid inertial mass at the frequencies used in hearing.

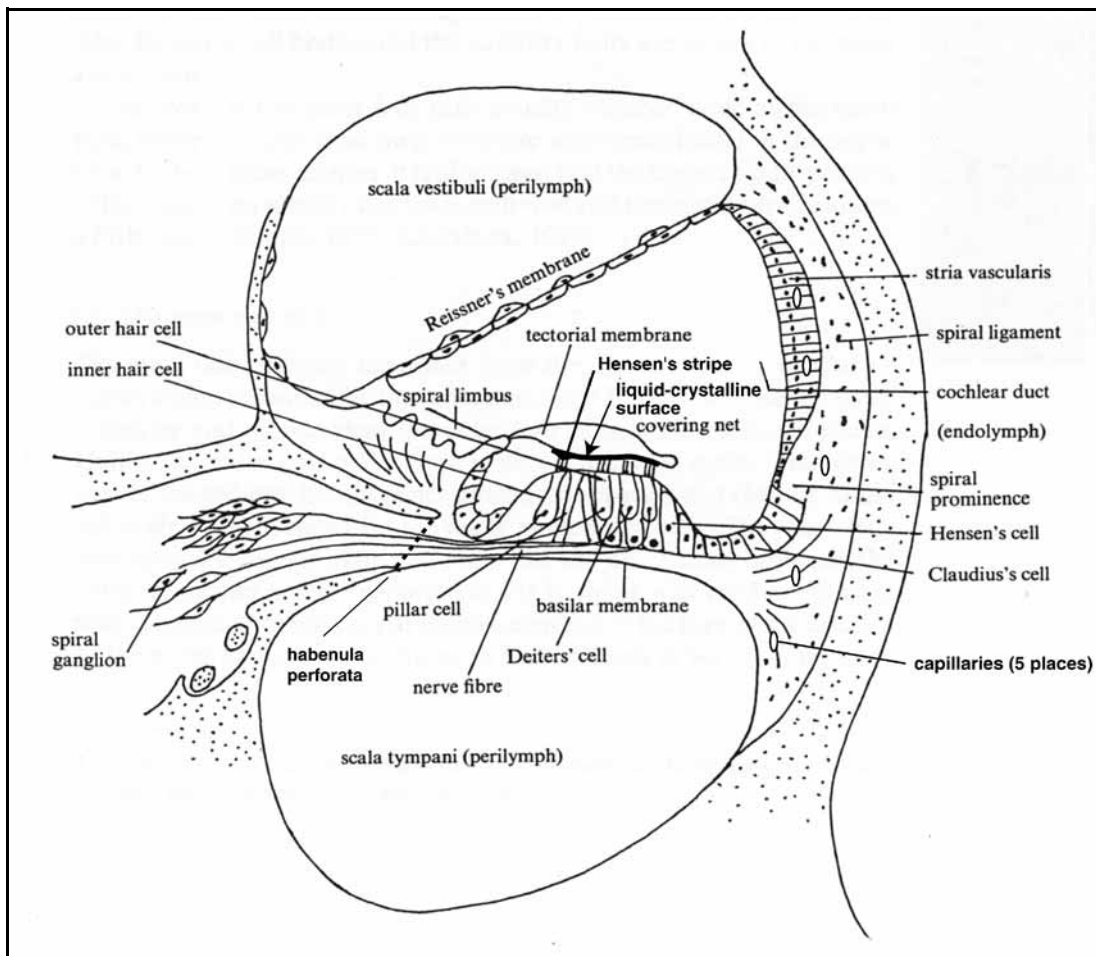


Figure 2.3.4-3 Cross-section of the cochlea showing the cochlear partition. The cochlear partition includes the basilar membrane, Reissner's membrane, the stria vascularis and all of the structures enclosed by them. These structures are bathed in endolymph. Traditionally, the Organ of Corti has been defined as the structures between the limbus and the cells of Claudius mounted on the basilar membrane. Some authors include the tectorial membrane in the Organ of Corti. The call-out to the tectorial membrane has been modified and the gel surface and the capillaries have been added to the figure originally from Davis 1953.

Jaffer et al. have described the role of the phalangeal processes (the pillar cells forming the tunnel of Corti) in rigidizing the structure formed by, and between, the basilar membrane and the reticular membrane enclosing the

sensory neurons<sup>61</sup>. This rigidizing further restricts the ability of either of these two membranes to vibrate at high frequency. They note, “suggestions can be made as to the function of the phalangeal processes and their curious cross-linked structure.” They then note, “The benefit of this adaptation is that large variations in CP displacement cannot occur along any two neighboring points.” “Therefore, we suggest that in order to involve active mechanics in the sensory mechanical process the cross-linked structure of the phalangeal processes has been evolved to maintain epithelial contiguity under sharp resonant conditions.” They did not quantify the level of elasticity and stiffness required of the basilar membrane to support hearing at high frequencies. This work goes further and suggests, the phalangeal structure works to prevent the oscillatory motion of the basilar and reticular membranes at frequencies of interest in hearing.

Naftalin et al. reported on the liquid-crystalline character of the tectorial membrane as early as 1964<sup>62</sup>. It is important to recall the critical nature of the crystalline axes of the liquid-crystalline material forming the tectorial membrane (and the nearby and underlying substrate) when attempting to illustrate the features of the cochlea. This relationship will be discussed in Chapter 4.

#### 2.3.4.4 The morphology of the cochlear duct–scala media

The cochlear duct, within the cochlea, plays a critical role in hearing. Quoting Engstrom & Angelborg, “The cochlear duct is surrounded by three, from a structural point of view completely different walls, all with their own specific functions.” It contains all of the elements of the Organ of Corti and one wall provides both endocrine support to, and electrical optimization for, the Organ of Corti.

Engstrom & Angelborg have provided a detailed description of the cochlear duct<sup>63</sup>. The fact that the endolymph within the cochlear duct exhibits an unusually high concentration of potassium while the perilymph, outside of the duct, exhibits a high concentration of sodium is physiologically important. Reissner’s membrane forming the barrier between the endolymph and perilymph has an unusual structure. It consists of one ectodermal layer facing the endolymph and one mesothelial layer turned toward the perilymph. The two layers differ considerably in structure. Santi has provided a micrograph of this structure<sup>64</sup>. Iurato has also provided an annotated electron micrograph<sup>65</sup>. The total thickness of the membrane averages 1– 3 microns except in the area of the soma of cells where it can reach 10 microns.

#### 2.3.4.5 The morphology of the Organ of Corti

Several good representations of the Organ of Corti are available. However, none of them properly represent the tectorial membrane without modification. The best available imagery of the cochlear partition were provided by Bredberg, Ades & Engstrom in 1972 using an early scanning electron microscope<sup>66</sup>. They also note the difficulty of preserving the tissue long enough for it to be imaged properly. The figures in Markin & Hudspeth and in Kessel & Kardon<sup>67</sup> provide well-annotated caricatures. Allen has reproduced a very good but less detailed cross-section caricature of the Organ of Corti credited to Rasmussen<sup>68</sup>. It shows the extremely limited access of the cardiovascular system to the neurons of the Organ of Corti. However, the variant in Lim will be used as a foundation in this discussion.

Figure 2.3.4-4 provides a schematic of the Organ of Corti that can be compared with that of Sally<sup>69</sup>. Sally described the gelatinous surface of the tectorial membrane facing the Organ of Corti as Kimura’s membrane. This structure is not a membrane. It is an amorphous, cell-free liquid-crystalline coating overlaying a specialized cellular surface of the tectorial membrane. The gelatinous layer has been cut away to allow viewing the row of IHC. Hensen’s stripe is shown on the surface of the gelatinous layer directly above the IHC. The continuous region of the gelatinous surface, extending from the IHC to the OHC, is the key to the operation of the tectorial membrane as a frequency discriminating SAW filter. The limbal region of the tectorial membrane should be shown connecting to the limbus of the cochlear partition. The internal spiral tunnel below the limbal region on the lower left is not labeled in this figure. Note the freestanding character of the individual OHC. This isolation prevents unwanted crosstalk between signaling channels.

Note the callout to the reticular lamina. This lamina forms a hermetic seal with the tops of the sensory neurons (both OHC and IHC). The cuticular plate and the cilia of each neuron are in contact with the endolymph while the cylindrical part and the foot of each neuron, interfacing with Deiters’ cells, are in contact with the perilymph within Nuel’s space. The reticular lamina, in conjunction with the basilar membrane, may also play a role in maintaining the vertical alignment of the sensory neurons.

Note again the complex structure of the basilar membrane. This complexity suggests this structure is incapable of supporting transverse resonances. This is particularly true of transverse resonances that vary in frequency

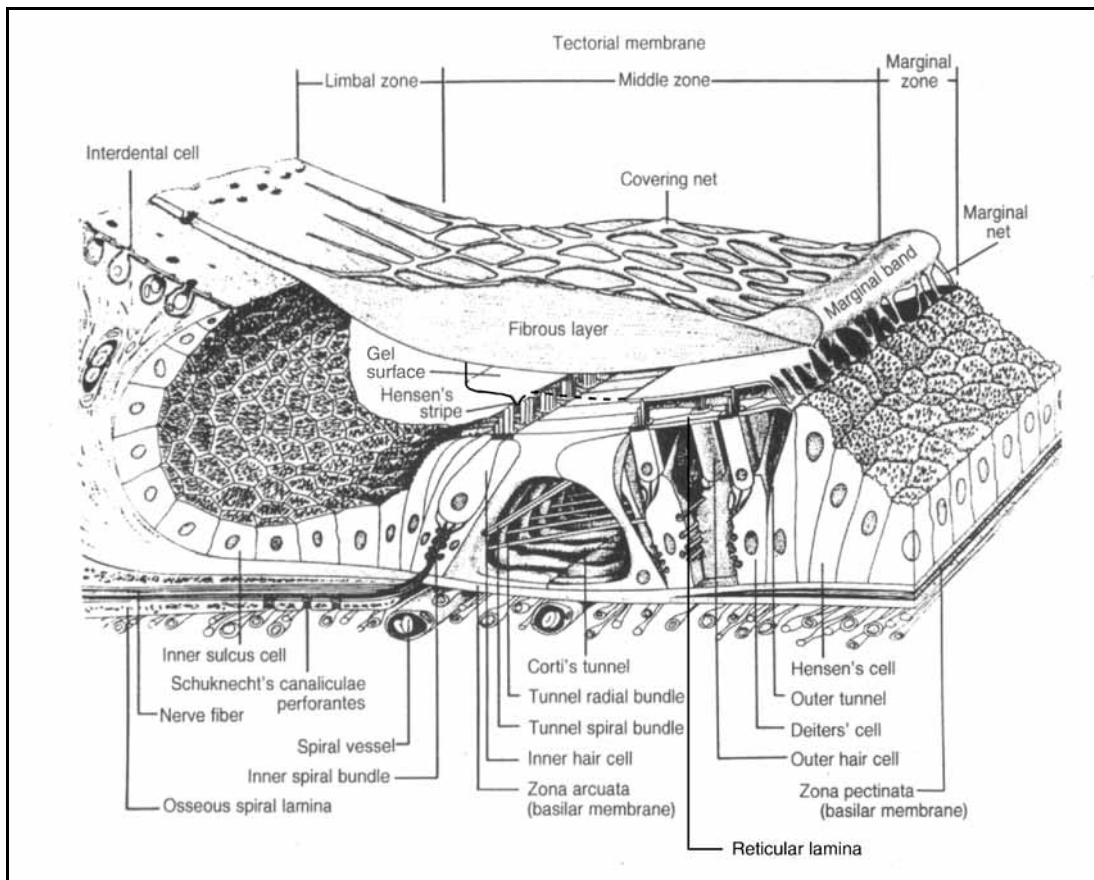


Figure 2.3.4-4 Detail of the cochlear partition at the Organ of Corti. The gel (liquid-crystalline) coating on the underside of the fibrous layer of the tectorial membrane has been cut away to show the inner hair cells. The callout's obscure the total cross sectional area of the spiral tunnel on the left. Note the complex structure of the basilar membrane, making it incompatible with any resonance phenomenon. Compare to Sally drawing in Allen, 1992.

incrementally along the longitudinal cochlea and must be highly independent of each other. Harrison & Hunter-Duvar have provided a photomicrograph of a human Organ of Corti showing the features discussed above in detail. Edge et al. have provided micrographs showing this relationship even more clearly in the gerbil<sup>70</sup>. Spoendlin has provided a better image obtained with a phase contrast microscope<sup>71</sup>. Spoendlin also provided a caricature of his figure in Zwicker & Terhardt that provides additional data concerning the habenula perforata<sup>72</sup>. The caption of that figure needs some reinterpretation. According to this work, the areas Spoendlin described as synapses between efferent and afferent neurons are common areas of electrostenolysis (Section 3.5). All synapses in the caricature are with the sensory neurons. An equally good image appears in Santi<sup>73</sup>. It provides more detail regarding the structure of the tectorial membrane.

Spoendlin has also provided a larger scale morphology of the sensory neuron/spiral ganglion nerve interface within the Organ of Corti. It shows clearly that the generator potentials received from the stage 1 sensory neurons are converted into action potentials within the stage 3 neurons of the spiral ganglion at a Node of Ranvier. The unique feature is that these Nodes of Ranvier occur before the soma associated with that neuron. Before reaching this Node, the dendritic fibers are unmyelinated but larger in diameter than the orthodromic myelinated axons.

A simpler but more extensive schematic is shown in Figure 2.3.4-5. It confirms the topology described by Spoendlin and is similar to one provided by Warr et al.<sup>4</sup>. The two efferent signal paths are shown at the upper left converging on the Organ of Corti from the superior olivary complex. The axons of these paths are typically myelinated and interrupted by Nodes of Ranvier (not shown). It will be shown in Section 5.3 that these low bandwidth efferent signal paths are used as part of the adaptation (gain control) system.

The two afferent signal paths are shown proceeding to the lower left and the cochlear nucleus. The initial portions (the dendrites) of these neurons are not myelinated but myelination typically begins after the first Node of Ranvier. In the case of the afferent neuron from the IHC, this occurs quite close to the IHC. In the case of the afferent neurons associated with the OHC, myelination also begins after the first Node of Ranvier. However, this node does not occur until a summation of signals from several individual OHCs has occurred within the dendritic structure. Nodes of Ranvier are shown at intervals along both of the afferent pathways. The shapes of the two ganglion cells are shown artistically and do not reflect a physiological difference between the broadband (type B) and narrowband (type N) channels. The Organ of Corti is shown in partial view. The tectorial membrane and Reissner's membrane are critical elements of the Organ of Corti.

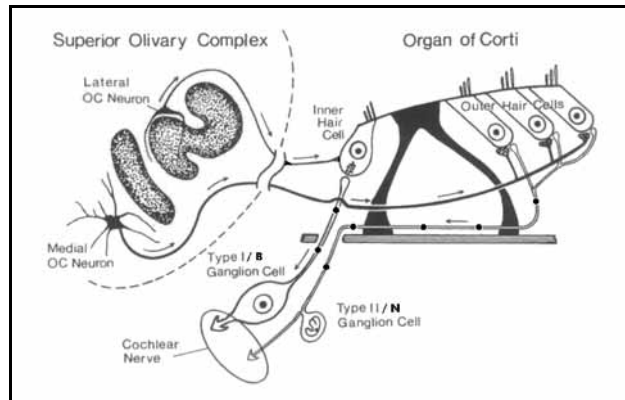


Figure 2.3.4-5 Schematic diagram showing innervation of the Organ of Corti. The two afferent and two efferent paths are shown. The afferent paths have been modified to show the Nodes of Ranvier. The neural path to the inner hair cell has been modified to eliminate synapse with the afferent path. See text. Modified from Warr, et. al., 1986.

### 2.3.4.6 The fluids of the cochlea

The operation of the cochlea depends fundamentally on the composition and electrical potential of two fluids occupying three spaces. The endolymph is known to be electrically and chemically isolated from the perilymph. The fluid in Nuel's space is electrically and chemically equivalent to the perilymph<sup>65</sup>. Nuel's space forms the environment surrounding all but the cuticular plate of the sensory neurons. This exception is critical to the operation of the sensory neurons. The endolymph fills the cochlear duct (scala media) between the reticular lamina and Reissner's membrane. It is known to be uniquely different from the chemical composition of the perilymph surrounding these structures. Its composition appears tailored to protect the liquid-crystalline surface of the tectorial membrane. Zenner, in Altschuler et al, (page 14) has noted that Bekesy first reported its anoxia. The endolymph is also at a different electrical potential than the perilymph. See Section 5.2.3.

Most of the studies related to these fluids have been based on the chemical neuron assumption and therefore frequently focused on the ions of the alkaline metals. Of greater importance to the operation of the neural system is the material presented by Godfrey et al, on the material now known to support the electrostenolytic processes that provide electrical power to the neurons<sup>66</sup>. Their Table 1 describes the constituents of these fluids critical to the glycolysis of glycogen to glutamate and their Table 3 describes the concentrations of glutamate and GABA within the Organ of Corti, essentially Nuel's space, as they compare to the endolymph. Table 1 describes the concentration of a group of metabolites and enzymes crucial to the operation of a neuron. Some metabolites support the metabolic health of both the neural and non-neural portions of the cell. Others are only concerned with the electrolytic health of the neural portion of the cell. Glycolysis, with particular emphasis on the glutamate shunt is presented in Section 3.5.3.

The major metabolites found within the fluids of the Organ of Corti are glutamate and aspartate, the primary and backup neuro-facilitators of the neural system, and GABA and glycine, the primary and backup neuro-inhibitors of the neural system. The latter are described as inhibitors because they are waste products of the electrostenolytic process. The metabolite portion of Table 3 is reproduced below. The portion related to a group of enzymes is of less importance. In the original title to the table, Salt & Konishi hedged their bets by listing the materials shown as "possibly related to neurotransmission." They are not related to neurotransmission from a signaling sense. They are neuro-facilitators and neuro-inhibitors involved in the process of providing electrical power to the neurons.

TABLE 2.3.2-1  
Distribution in the Guinea Pig Cochlea of the Substances Supporting Electrostenolysis

Substance	Organ of Corti		Stria vascularis	Reissner's membrane	OC SV	Average brain
	inner	Outer				
<b>METABOLITES; mmol/kg dry wt</b>						
Aspartate	19.1	22.1	2.5	2.2	5.9	10-15
Glutamate	59	74	25	9.6	2.8	36-54
GABA	2.2	1.7	1.9	2.1	0.95	8.4-9.2
Glycine	35	37	33	39	1.1	4.4-6.8

The references and footnotes applicable to these values are given in Salt & Konishi, 1986.

The significant difference in concentration between glutamate and GABA within the Organ of Corti is critically important to the operation of the neural portion of the neuron cell. Salt & Konishi noted the particularly high level of glutamate relative to the average for the brain and the non-neural tissue of the cochlea. Their observations relative to GABA complement this work. "GABA levels in the organ of Corti are much lower than the average level in brain and no higher than in non-neural structures of the cochlea (Table 3). Thus, although there have been provocative results favoring GABA or a GABA-like substance as a transmitter released from hair cells, the quantitative histochemical results stand with other evidence and oppose involvement of GABA itself." Later they discuss the role of glutamate and aspartate. "These measurements thus can provide no support for a neurotransmitter role of glutamate or aspartate in hair cells, unlike the results for the auditory nerve synapse in the cochlear nucleus." They conclude, "Glutamate and aspartate have much higher concentration in cochlear endolymph than in perilymph, while all other amino acids have the opposite distribution. Thus, although a transmitter role may be in doubt, some unique role of glutamate and aspartate in the organ of Corti may be identified by further studies."

Edge et al. have provided a set of artificial cochlear fluids that they used in their research<sup>77</sup>.

### 2.3.5 The morphology and physical properties of elements of the cochlear partition

This section will discuss the elements of the cochlear partition important to the understanding of hearing, except for the sensory neurons. The discussion of the sensory neurons will be delayed until the in depth theoretical discussions of Chapter 3 have been presented.

#### 2.3.5.1 The physical properties of the *static* tectorial membrane

The liquid-crystalline surface (facing the sensory neurons) of the tectorial membrane is entirely different from the surface facing Reissner's membrane covered by a net matrix. The liquid-crystalline face of the tectorial membrane exhibits unique dynamic properties that are critically important to the physiological operation of hearing. However, these characteristics are presented in Chapter 4. Only the static properties of the tectorial membrane will be addressed here.

The tectorial membrane is an element of complex shape and interior construction. It cannot be considered homogeneous for the purposes of hearing theory. The surface facing the scala media is frequently described as having a net like covering. Below this net is a relatively thick material that is heterogeneous at the molecular level and shows a poorly organized structure at larger scales. The protein material in this volume is coiled and cross-linked. The surface of the material facing the reticular lamina consists of a highly organized array of parallel protein molecules that are not coiled or cross-linked. This surface appears to consist of only one layer of molecules. This surface is in turn covered with a liquid-crystalline material that can support a surface acoustic wave.

Iurato has provided some early data on the tectorial membrane and a bibliography<sup>78</sup>. He begins, "The opinions on the structure of the tectorial membrane are manifold and contradictory." Except for values for the bulk physical parameters, and the electron microscope imagery in Iurato, most of the writings prior to 1978 can be disregarded. The relevant work begins with the description of the physical structure of the tectorial membrane of Kronester-Frei<sup>79,80</sup>. Pack & Slepecky have reported on the molecular differences between the forms of tubulin found within the microtubules of sensory neurons<sup>81</sup>. This same material is found in the fine structure of the tectorial membrane. They have stressed that "to understand how sound is processed in the cochlea, an understanding of the cellular differences along its length is crucial, and studying differential protein expression is vital to that understanding." Both

Harrison & Hunter-Duvar<sup>82</sup> and Santi have also provided excellent imagery of the tectorial membrane<sup>83</sup>. The Harrison & Hunter-Duvar image of Hensen's Stripe in context is particularly valuable.

Kronester-Frei has provided excellent electron micrographs showing that the molecular structure underneath the liquid-crystalline surface of the tectorial membrane varies considerably over its area. The surface of this substrate is remarkably uniform and consists of a structured array of protofibrils with a periodicity of 70 Angstrom and diameters of 110 Angstrom. The axis of the fibrils are arranged at a specific angle of about 71 degrees relative to the unconstrained edge of the TM and point toward the apex of the cochlea. This is a very important characteristic of the substrate. As noted by Novoselova, the curvature of the individual protofibrils is negligible from a structural perspective<sup>84</sup>. The most comprehensive electron micrographs of the "underside" of the tectorial membrane appear to be in Harrison (page 17). However, the precise method of preparation is not described and it is not clear whether the liquid-crystalline coating remained on the specimen. Some of the ribs shown may be the structure underlying the coating.

Along with the very low surface tension noted for the active surface of the tectorial membrane, it can be considered a flat, long, anisotropic plate. The indentations in the uniform area due to the OHCs can be seen by the discerning eye. The character of the surface changes abruptly at Hensen's stripe and shows ridges parallel to the edge in the region between Hensen's stripe and the attachment point of the TM at the limbus. The protofibrils in this area are described as type B, consisting of coiled and branched glycoproteins with diameters of 150-200 Angstrom. A similar change occurs in the region Kronester-Frei labels the marginal zone beyond the point of contact of the dendrites of the OHCs. Her figure 5c shows the transition from the protofibrils of the middle zone to the protofibrils of the marginal zone.

Kronester-Frei noted the significant changes (swelling by a factor of two) in the morphology of the TM when the fluids surrounding the element were changed, as has usually occurred during *in-vitro* experiments. The swelling is frequently noted in the literature. The swelling is due to the perilymph attacking the liquid-crystalline surface of the tectorial membrane. This phenomenon probably accounts for much of the inconsistency in the literature concerning the precise dimensions of the TM.

Maskaki et al. have recently provided stress-strain data orally related to the tectorial membrane in a set of knockout mice<sup>85</sup>. Their data suggests the presence of two different materials in the composition of the tectorial membrane. Although they did not claim the tectorial membrane consisted of two separate layers, they did suggest it was heterogenous based on their data. They noted the data suggested that one of the materials had a stiffness approaching zero (the characteristic of a perfect liquid-crystalline gel). The presence of two materials is further supported by the comments in Cotancke & Corwin. They suggest two separate cellular sources for the protein material and the gel material<sup>86</sup>. The surface tension of the liquid-crystalline coating is extremely low and is known to exhibit unusual features. Radiman et al. have reported on these features in a similar man-made material<sup>87</sup>. They described their material as a clear highly viscous bilayer exhibiting liquid-crystalline structure with a well-defined periodicity. They reported "ringing" that was within the human audible range. Referring to their gels, "(i. e. they ring like a bell when tapped gently) a feature which seems to be associated with the presence of underdamped transverse phonon modes in these systems." The material was highly sensitive to temperature and tended to become resonant at temperatures near 20 Celsius depending on the level of hydration. At lower levels of hydration, they observed relatively uniform properties over an acoustic frequency range spanning three decades. The investigators exhibited surprise that the material did not show a real elastic modulus at zero frequency. This lack of a modulus at this frequency confirms the liquid-crystalline nature of their material.

They noted the change in character with hydration is associated with the transition from a liquid-crystalline to a solid-crystalline behavior. Their conclusion was "Linear rheology confirms that dissipation at high (audible) frequencies is very low and is consistent with the phenomenon of 'ringing' in which shear modes in the gel couple to sound via the gel surface."

### 2.3.5.2 Details of the morphology of the reticular lamina

Page 25 of Harrison, shows a micrograph of the reticular lamina of the cochlear partition in plan view. It shows the cilia of both the IHC and OHC penetrating the lamina, along with other features. The reticular lamina forms a hermetic seal around the cuticular plate of the neurons. The distance between the IHC and the first row of OHC is about 20 microns. Additional information on the arrangement of the OHC and IHC in chinchilla is given by Santi et al<sup>88</sup>. They show the spacing as larger than in Harrison, ranging up to 30-40 microns between the IHC and the third row of OHC.

### 2.3.6 The morphology of the spiral ganglia and the auditory nerve

It is difficult to find images of the nerves of the PNS. Kiang has provided one of the best for the cat<sup>89</sup>. While no scale was provided, the short length of the nerve is evident. Its total length approximates the maximum diameter of the cochlea. The location and size of the spiral ganglia and other features, including the cochlear nucleus, are clearly shown. The diameters of the individual axons are given as between two and six microns and are represented by a unimodal distribution. He also notes the presence of a small number of efferent fibers within the auditory nerve.

The reader is cautioned that Kiang's use of the description of the auditory nerves as "primary" lacks a strong foundation. The stage 1 sensory neurons must be considered the primary neurons. The neurons of the spiral ganglia support stage 2 signal processing and it is only the afferent axons associated with stage 3 signal projection that are found in the auditory nerve.

Kiang used the term primary unit for the purpose of annotating which neurons were of interest according to his criteria (page 13-16). Based on this work, his discussion on page 15 can be reformulated. He found that when probing the fibers within the auditory nerve, some of them were impacted drastically by the presence of the probe, to the point that they stopped producing action potentials upon probe penetration. These fibers were clearly neurites (dendrites or podites). The slightest change in the potential within the conduits of these elements can change the pattern of action potential generation. Alternately, Kiang found that insertion of the probe into other fibers had little effect on their temporal performance or the amplitude of their positive going action potentials. This is typical of an axon. As long as the potential of the axon remains negative with respect to the neurites, the operation of the neuron as an action potential generator is largely unaffected. It was Kiang's intent to describe the axons as of primary interest in his experiments, compared to the neurites, and not to suggest these axons were primary elements in the overall operation of the auditory system. Thus, his primary unit was the axon of a stage 3 neuron.

On page 16, Kiang reviewed another physiological criterion for primary units based on latency. Using this criterion, he described the signals of shortest latency as primary. He dismissed it as not compatible with his results. The shortest latency is merely associated with axons related to the sensory neurons located nearest the cochlear base and with the highest CF.

Not explored by Kiang was the division of the signals within the auditory nerve into a group with minimal spontaneous rates of action potential generation (associated with the intensity channel) and a group with nominal spontaneous rates that are associated with the frequency channels.

### 2.3.7 The morphology of the cochlear nucleus

As noted earlier, the assignment of the cochlear nucleus to its proper anatomical position depends on a variety of considerations related primarily to its physiological role. Because of the similarity of its physiology to that of the retina, the fact it generates signals that are highly divergent, and its location adjacent to the wall of the brainstem, it has been associated with the PNS.

The morphology of the cochlear nucleus is very complex. It consists of more than a dozen identifiable nuclei (or engines) of significant size.

Oertel & Young have recently presented a review of the cochlear nucleus that is generic to all mammals<sup>90</sup>. While addressed from the morphological perspective, and using a variety of fanciful names, it contains considerable data on the interconnection of the neurons of the cochlear nucleus.

## 2.4 The physiology of the auditory system

Section 1.1.7 defined a series of very high level operating modalities within the neurological system that are shared among the sensory modalities. Section 1.3.1 presented two block diagrams describing the operation of hearing. However, neither of these presentations provides an adequate framework for describing the functionality of hearing. This is partly due to the use of the same types of neural circuits to accomplish different objectives. More significantly, it is due to the use of a special group of neural circuits to achieve efficient signal propagation over distances greater than two millimeters. These special circuits are used widely both between major neural elements and within neural elements of significant size.

This section will define a set of stages of hearing combining various detailed functions and circuits into groups that provide a clearer understanding of how hearing is accomplished. These stages will then be used to annotate both



high level and low-level circuit schematics of hearing as well as provide an alternate form of block diagrams wherein one stage (stage 3) appears ubiquitously but not explicitly.

A short subsection will conclude this section describing the largely unappreciated fact that most of the neurons of the hearing modality, and of the neural system in general, operate in the analog domain. Recognition of this fact contributes to understanding the great difficulty encountered creating “neural networks” and similar emulations using pulse and digital circuit techniques.

### 2.4.1 Functional stages in hearing

The above figure includes a series of labels related to the stages of hearing. These labels were previously defined in the equivalent figure for the visual system. They greatly aid in characterizing major portions of the auditory system and in localizing the discussions that follow. The system is divided into a series of neurological modules, stages 1 through 6, and a series of acoustic (non-neural) modules described as stage 0. Stage 0 contains a series of functional elements that can be further subdivided into stages A through C, and a metabolic module (not shown), stage Z. These stages are defined as follows.

Stage A consists of all functions associated with the outer ear. In humans, this is a largely passive morphological structure with specific acoustic properties. These properties vary considerably among individuals. In many mammals, stage A includes the six muscles, operating in pairs, that control the pointing of the outer ear. Stage A ends with the presentation of the acoustic signal to the location occupied by the tympanic membrane (the membrane itself is a functional part of stage B).

Stage B consists of the middle ear. The middle ear includes the tympanic membrane, a group of small bones, muscles and ligaments, the oval window at the entrance to the vestibule and caecum of the vestibule. Associating the oval window with the middle ear, instead of the inner ear, groups all of the dynamic mechanical aspects of hearing into one stage. This grouping also allows the launcher described in Section 2.3.3 to be considered part of the middle ear.

Stage C consists of the acousto-mechanical portion of the inner ear. It consists of all non-neural elements of the morphological cochlea beginning where the scala media is differentiated from the caecum of the vestibule. Stage C is responsible for concentrating the initial surface acoustic wave on the liquid-crystalline surface, generated by the launcher, into a more concentrated form propagating along Hensen’s Stripe. It is also responsible for subsequently dispersing this concentrated energy, based on frequency content, into the physical area where the outer hair cells are located.

Stage 1 (analog) encompasses the signal detection process. It involves the establishment of the intensity signal channel by the inner hair cells, IHC, and the frequency specific signal channels by the outer hair cells, OHC. The signals in these channels originate in the energy distribution found within Hensen’s Stripe (the intensity channel) and the energy dispersed perpendicular to Hensen’s Stripe (the frequency channel). Both channels contain large numbers of individual neurons generating signals that are passed to the next stage in parallel. This stage ends with the presentation of the signals at the pedicels of the phonoreceptor cells.

Stage 2 (analog) consists of the signal processing carried out between the pedicels of the sensory neurons and the encoding process carried out by the first Activa of the stage 3 ganglion cells. Being a functional element in the signal processing stage, the synapses associated with the pedicels will be considered part of Stage 2. Similarly, the neurites of the ganglion cells prior to encoding are also key players in the signal processing of Stage 2.

Stage 3 (phasic) encompasses the signal projection circuits of the auditory system. The signal projection function is highly developed and easily characterized in *Chordata*. It is used wherever it is necessary to transmit neural signals over significant distances (typically a millimeter or more in myelinated neurons and tens of microns or more in unmyelinated neurons). This includes both the efferent and afferent signal paths of the peripheral nervous system (PNS) and the paths within the brain, or central nervous system, (CNS).

Within the auditory system, the stage 3 projection function is used routinely. It is used to transmit signals over the auditory nerve to both the cochlear nucleus and beyond to the other elements leading to the cortex. In this usage, groups of stage 3 neurons are called nerves. Within the cortex, stage 3 projection neurons are used to interconnect the different feature extraction engines, the logic units of the forebrain and the initial motor system command generation centers. In that role, stage 3 circuits are called commissure.

Stage 4 (analog) consists of all of the higher level signal manipulation neurons that are found subsequent to the

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arrival of signals at the brain from stage 3. It may be useful to subdivide this stage to clarify the fundamental difference in the signal manipulation occurring in different regions of the cortex. This is typically done by subdividing regions of the cortex consisting of one million or more neurons into individual feature extraction engines. One million neurons typically occupy only a very few square millimeters of the surface of the cortex.

Stage 5 (analog in the cortex) consists of cognition of the abstract afferent signals received from stage 4, volition (initial efferent) signal generation within the cortex and supervisory signals generated to control the midbrain acting as gatekeeper. As in stage 4 above, it is difficult to make clear distinctions at this level between the portions of the stage that involve analog signal processing and pulse signal projection within and between areas of the cortex.

Stage 6 (analog) consists of the efferent command signal manipulation and generation performed within the midbrain. The efferent system will not be addressed extensively in this work.

A stage Z can be defined if desired to encompass the metabolic functions associated with the auditory system. These can be divided into two major components, those associated with morphogenesis and those associated with the electrical supply to the neurons. The latter are primarily concerned with the supply of glutamic acid to the electrostenolytic process associated with each neuron and the removal of the reaction product GABA.

Most of the earlier laboratory investigations into the nervous system have concentrated on the PNS, and particularly the stage 3 projection neurons, for two reasons. They are easily accessible, and controlled levels of stimulation, and even trauma, are easily induced. Except as a result of trauma, the study of CNS neurons is much more difficult. In the case of the human auditory system, the accessibility of the stage 3 neurons is difficult. However, access to the other neurons is even more difficult. Because of this situation, no report of in-vivo stage 1 signal recording has been found in the literature.

### 2.4.2 The gross signaling paths of the auditory system

Because of the extreme focus on the neurons generating Stage 3 action potentials by the experimental community, nearly all of the available data on the signaling paths of the auditory system describe traffic paths. These traffic paths have been identified primarily by observing the impact of lesions on normal operation. Brugge has provided valuable information on the major traffic routes of the CNS with a few comments concerning monaural and binaural operation in some nuclei of the system<sup>81</sup>. He did not discuss the encoding of the signals generating this traffic or the electrophysiology of the circuits carrying this traffic.

Iurato has provided a general discussion of the signaling paths associated with the auditory PNS<sup>82</sup>. The major traffic paths between the PNS and CNS are the VIIth and VIIIth cranial nerves. The ascending signals from the IHC and OHC pass through the spiral ganglia for processing before being passed along the VIIIth cranial nerve (vestibulocochlear) to the cochlear nucleus and the rest of the CNS<sup>83</sup>. It appears that some of the descending signals to the outer, middle and even the inner ear are passed down the VIIth cranial nerve (facial).

#### 2.4.2.1 The top level schematic of the ascending paths

Describing the topology of the auditory CNS based on the morphological literature alone is difficult. Investigators tend to concentrate on the PNS or the CNS of the system with little continuity between these extremes. Furthermore, the configurations of different species, based on morphology alone, vary considerably. An understanding of the operation of the system is necessary to create a meaningful overall schematic.

With the operating modes defined in Section 1.1.7 clearly in mind, the topology of the ascending paths of the auditory system within the CNS can be described using Figure 2.4.2-1. The figure has been expanded considerably beyond similar figures in the literature. First, it adds additional definition about the higher cognitive functions within the central nervous system (CNS). This is particularly apparent for the diencephalon where several elements of the thalamus are shown explicitly. These elements play a crucial role in both the health of the individual and the quality of his/her sensory experiences. It is also apparent concerning the parietal lobe of the cerebral cortex where a saliency map has been defined. While this map cannot be morphologically defined because of its holonomic (and therefore dispersed) nature, the locus of this map appears to be within the parietal lobe. The figure shows signals being passed back and forth between the thalamus and the temporal lobes but no direct connection between the temporal lobes and the parietal or frontal lobes of the cerebral cortex. Second, the figure shows multiple ascending paths between the cochlear nucleus and the CNS. The path labeled MOC originates in the medial superior olivary complex and carries many individual neural channels containing tonal (narrowband) information. The path labeled LOC originates in the lateral superior olivary complex and carries many individual neural channels containing

primarily wideband information related to the leading edge of stimuli. The precise character of the signals in these paths remains controversial.

The figure combines the proposals of many earlier workers. The figure shows a familial resemblance to two early figures of House et al<sup>94</sup>. The lower portion follows Lorente de No<sup>95</sup> with additional features introduced from Kiang<sup>98</sup>.

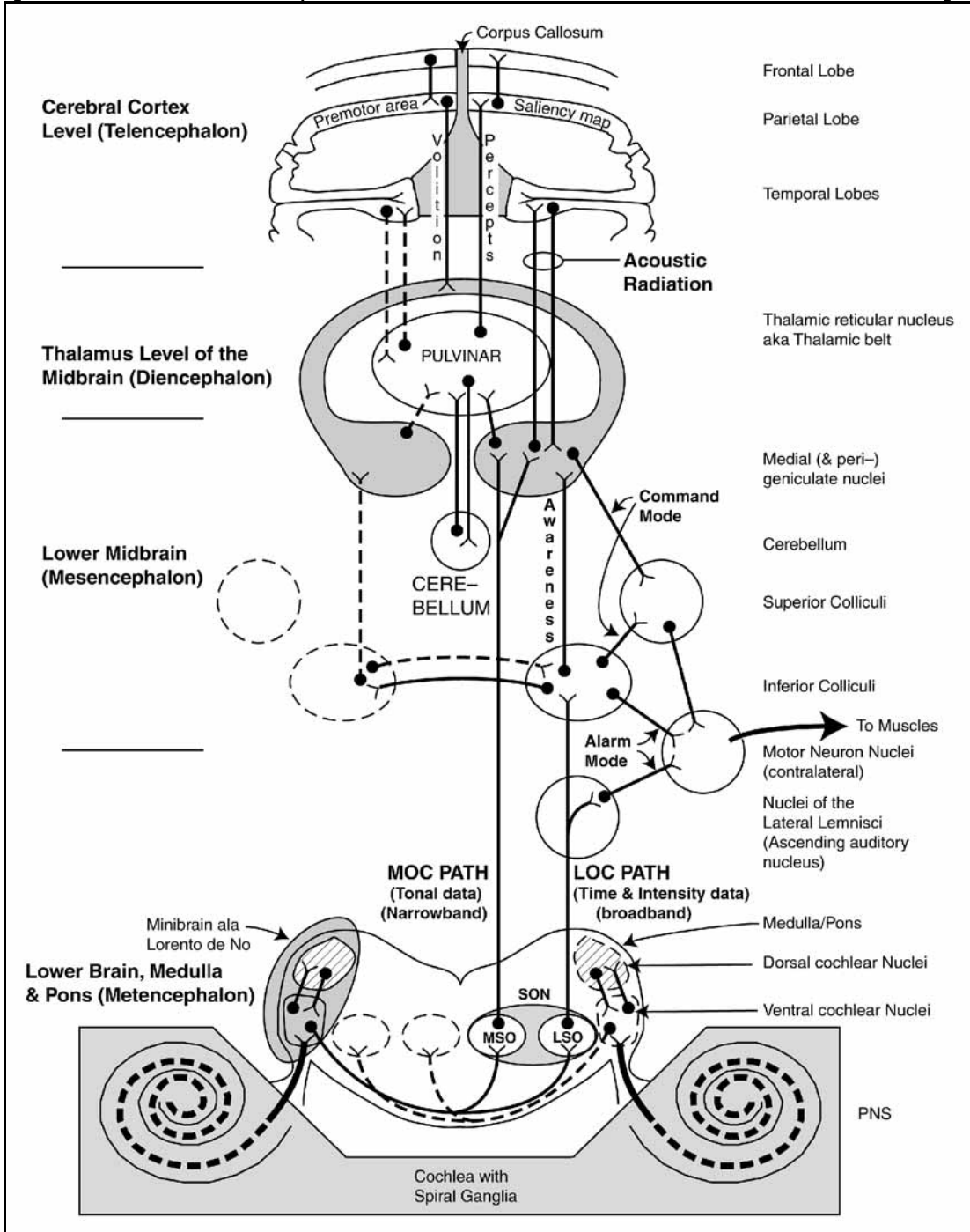


Figure 2.4.2-1 Top level schematic of the circuits of the auditory system within the CNS of the human. Figure represents a “reduced mesh” of the complete schematic. MSO & LSO; medial and lateral superior olivocochlear complex. MOC & LOC; channels associated with the medial and lateral olivocochlear complexes. Note the bifurcation of the MOC near the thalamus. See text for extensive discussion.

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Morest<sup>97</sup> and Harrison<sup>98</sup> have also contributed features to the figure. Liberman provided both a schematic of the auditory system within the medulla (pons in the context of this work) and a very important report on a negative experiment<sup>99</sup>. His information on the paths that are crossed versus not crossed is important. Gulick et al. provide both a schematic and pictorial description of the ascending auditory tracts. Their schematic shows two major ascending paths similar to those shown here<sup>100</sup>. Yost has recently provided a set of caricatures describing the ascending and descending neural paths along with a figure describing the bilateral nature of many of these paths<sup>101</sup>. Roederer has also provided a simple block diagram equivalent to the figure<sup>102</sup>. He annotates the reflex action associated with signals generated at the level of the inferior colliculus. These actions are analogous to the alarm mode actions diagramed here. The nomenclature used by these investigators is far from consistent. Gacek provides a more artistic but less detailed rendition of the figure<sup>103</sup>. He labels the thalamic reticular nucleus (TRN) the reticular formation. The material in the figure related to the midbrain and the cerebral cortex is by this author. The medial (MSO) and lateral (LSO) portions of the superior olive are shown separately. This separation and many other features of the figure are consistent with that of Ganong<sup>104</sup>.

The schematic continues to present only the major signaling paths. These paths will be expanded further when specific functions associated with hearing are explored. The full complexity of the interconnections cannot be shown in a simple two-dimensional drawing. Finally, the figure adds considerable notation characterizing the major signal paths. The LOC and MOC paths shown are concerned primarily with the information content (the "what") of the stimuli. The signal paths shown diverging to the right at the nuclei of the lateral lemniscus and at the inferior colliculi, are primarily concerned with the location (the "where") of the stimuli.

As in the case of the auditory nerve, the relative size of the LSO and MSO tells something about the auditory capabilities of a specific species. Animals that depend on source location and echo location tend to have large LSOs, possibly to the exclusion of the MSO structure. Bats, dolphins and blind mice (*Spalax*) fall in this category. Animals more adapted for communications rather than direction finding, tend to have larger MSO structures (with small or vestigial LSOs). Humans, chimpanzee and gibbons fall in the latter category according to Harrison & Howe<sup>105</sup>.

Young et al. have provided a figure similar to the bottom center portion of this figure<sup>106</sup>. They describe two distinct vertical paths, the intermediate acoustic stria (IAS) and the dorsal acoustic stria (DAS). From the art, it appears the IAS originates in the PVCN and is equivalent to the MOC. The DAS originates in the DCN and is equivalent to the LOC. However, many question marks appear in the art.

The extremely limited amount of data available makes detailed description of the signals carried by the LOC and MOC paths quite difficult. They must remain tentative for this reason (Section 6.5.1). It is quite possible that these two physiological paths share a common morphological space over portions of their travel. Eggemont<sup>107</sup>, referencing a 1987 paper<sup>108</sup>, has recently described the path via the lemniscal nucleus as containing narrowly tuned neurons.

Imig & Morel have provided a figure roughly equivalent to the top portion of the above figure. The feature of their block diagram is it distinguishes between tonotopic and non-tonotopic paths. However, the thalamus is not subdivided into its significant physiological parts. The best descriptions of the subdivisions of the thalamus are apparently found in the field of vision research (PBV, 15.6.1).

The figure begins with the two cochleas of the peripheral nervous system and their associated spiral ganglia. These ganglia are strung out along a nerve as indicated by the heavy dashed lines. This nerve is almost impossible for researchers to explore in-vivo because of the bony structure surrounding the cochlea and the intricate arrangement. Probing the analog (tonic) signals between the sensory neurons and the spiral ganglia is even more difficult. The heavy line, describing the auditory nerve, is shown terminating in the ventral cochlear nuclei (VCN) as an artist's privilege. The neuron actually contacts both the ventral and dorsal cochlear nuclei (DCN) and may send individual neurons on to the medial geniculate nuclei (MGN), or inferior colliculus (IC). Most of the neurons of the auditory nerve are ascending. The cross section of the auditory nerve is spatially organized and separates the neurons that exhibit "spontaneous rates" (SR) of action potential generation from those with a nominal SR of zero. These two classes can be related to the OHC sensory neurons and the IHC related neurons, respectively.

As in most neural sensing subsystems, the signals from the left cochlea, DCN and VCN cross over to the contralateral side of the brainstem where they interface with the medial and lateral superior olivocochlear nuclei (MSO & LSO). This division separates the signaling paths of the spectrally related data and the temporally related intensity data. The temporally related data proceeds up the LOC path while the tonal data proceeds up the MOC path. Note that the data has already been transformed into signatures representing the intensity of the data related to a specific place along the cochlear partition.

The figure shows the first point where binaural signal processing occurs is at the level of the MSO and LSO. The signals have encountered the minimum possible amount of signal delay and distortion at this point. Suggestions also appear in the literature that some of the IHC from the basal region of the cochlear partition, and their neural connections to these bodies may operate at wider bandwidths than typical sensory neurons. There are reports of pulse rates as high as 1000 pps among these circuits. Such circuit modifications would be supportive of the excellent differential time delay measurements reported for the system when tested binaurally.

The MOC path is shown as projecting directly to the medial geniculate nucleus (MGN) while the LOC data is shown also supporting the operation of the inferior colliculus. This is an oversimplification for purposes of illustration. The lower portions of both the MOC and LOC paths are found within the lateral lemniscus. The operation of the IC appears to be centered on control of the external ears in most species. Appropriate cross links are shown between the two ICs to support this activity. However, signals are also passed to the superior colliculus (SC) to activate other muscles as appropriate. Signals from the IC are also forwarded to the MGN containing both the processed acoustic signals as well as information on the commands sent to the ears and other elements of the skeletal-muscle system. Lorente de No has commented on the indistinct separation between the posterior portions of the SC and IC (page 64).

The nuclei of the lateral lemniscus play an important role in the literature of auditory morphology. However, their functional role has not yet been defined to this author's satisfaction.

The thalamic reticular nucleus (TRN) is a little known but critically important part of the neural system. It is also known as the reticular formation or the reticular belt. It, along with the thalamus itself, are deeply hidden (and protected) at the very center of the brain. The TRN forms a coat surrounding a majority of the thalamus and its major element, the pulvinar (The outer edge of the shaded thalamus). The thalamic reticular nucleus is the primary supervisor and controller of all neural activity. Nearly all neural signals passing to or from the pulvinar, and other elements of the thalamus are monitored by, if not intercepted by the TRN. In response to its supervisory role, it can exercise its control role and reroute many messages. The TRN includes several critically important sub-elements including the geniculate nuclei located along the posterior surface of the pulvinar. These include the lateral geniculate nuclei (LGN) of vision and the medial geniculate nuclei (MGN) of hearing. Although frequently spoken of in the singular, they are both paired bodies. Each body of the LGN and MGN can be subdivided into sectors. One of these sectors is labeled the perigeniculate nuclei, PGN, later in this work. Harrison has noted the reciprocal pathways between the temporal lobes and the MGN of the thalamus<sup>108</sup>. While speaking of the temporal lobe, Eggermont has confirmed this obscure but critical fact (page 110). "More specifically, the projection from the auditory cortex back to the medial geniculate body contains ten times more fibers than projected to the auditory cortex initially."

The temporal lobes provide a variety of correlation activities including comparing sequences of interps in order to create higher level interps. These interps are returned to the TRN where they are combined with other sensory information into a consolidated interp (or percept). The resulting signal is then passed to the saliency map within the parietal lobe of the cerebral cortex. The saliency map is accessible by the higher cognitive engines of the frontal lobe.

The pulvinar, cerebellum and the parietal and frontal lobes of the cerebral cortex operate largely in the abstract domain. They show few signatures that can be associated with object space. These signatures are largely found in the temporal and posterior lobes of the cerebral cortex and the geniculate bodies. The signatures found in the colliculi can be related to the auditory system tonotopically but only with difficulty. Their receptive fields are usually measured, not the radiation with respect to the environment or cochlea. The signatures in these bodies are shared with too many other signatures unrelated to hearing.

After manipulating the information it receives from the parietal lobe, the frontal lobe prepares instruction based on its own volition. These high level commands are passed down the volition mode channels to the TRN for further distribution to the skeletal-muscle and glandular systems. For simple instructions, the TRN can forward the signals directly to the superior (and inferior) colliculi for implementation. However, to insure smooth and precise response, the signals are usually passed to the cerebellum and back. It is the responsibility of the cerebellum to expand the high level commands into detailed operating commands that can be implemented *in toto* by the colliculi and the motor neuron nuclei.

#### 2.4.2.2 Top level block diagram of the ascending neural paths

Figure 2.4.2-2 shows an annotated top level block diagram corresponding to the schematic diagram. The block diagram summarizes much of the material developed in the following chapters. It more clearly documents the

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functional differences between major parts of the system in a graphical format. The major differences involve the detailing of the Signal Detection, Stage 1 and the more complete description of the engines of the cortex. Stages 0 & 1 and most of stage 2 can be considered dedicated to the hearing modality. Most of the elements labeled within the cortex are shared between hearing and other modalities. The organization shown within the cortex is similar to that of the visual modality as shown in Section 1.3.1.

The elements shown in the top row involve frequency band limiting elements. The character of these limits is suggested by the first-order transfer functions shown below the boxes. The outer ear acts primarily as a wideband transformer, although it shows a number of local peaks and valleys in its transfer function. The middle ear acts as a bandpass filter, with a low frequency limit ( $\omega_{ML}$ ) introduced by the eustachian tube and a high frequency limit ( $\omega_{MH}$ ) based on the limited stiffness of the ossicle bones. Stage 1 begins with a space within the labyrinth known as the vestibule. The energy from the oval window is transferred to the launcher of the cochlear partition through this space. The acoustic frequency response of this space has not been reported. However, it probably does not limit the first order performance of the system. It is shown as a low pass filter with cutoff frequency of ( $\omega_{VH}$ ). The launch mechanism (or launcher) plays a critical role in hearing, it is a fixed morphological structure that transforms the longitudinal compression wave associated with the acoustic energy of the outer and middle ear into a surface acoustic wave traveling along Hensen's stripe within the cochlear partition. This surface acoustic wave travels at a nominal velocity of six meters/sec compared to the nominal 1500 meters/sec of the longitudinal wave. This reduction in velocity by a ratio of 250:1 is a key parameter in the hearing modality. The typical surface acoustic wave, combined with its substrate, are known to have an upper frequency limit above one million Hertz. It is not a limiting factor in the acoustic bandwidth of hearing.

The curvature of Hensen's stripe, as it travels along the gel surface of the tectorial membrane, is the key to the frequency discrimination capability of hearing. The acoustic energy is dispersed as a function of both frequency and curvature, thereby giving rise to the "place-frequency relationship" within the hearing modality (Section 4.4). This dispersal results in the formation of two distinct types of neural signaling channels, a set of narrowband channels associated with the outer hair cells (labeled F for frequency) and a set of wideband channels associated with the inner hair cells (labeled I for intensity). The transfer functions of these two sets of channels are shown symbolically by the single function,  $F(\omega, x)$  where  $x$  relates to the distance traveled from the functional "base" of the cochlear partition.

The sets of I and F signals are intercepted by the sensory neurons according to their geometric positions relative to Hensen's stripe. All of the sensory neurons of hearing are functionally identical. Only minor differences are seen in their mounting arrangements and in the grouping of their stereocilia. The stereocilia are piezoelectric transducers that generate an electrical current within the dendritic space (D) of the neuron. This signal is amplified and "standardized" by the electrolytic amplifiers within each neuron before it is converted to a voltage at the pedicle of the neuron. Once the acoustic signal is transduced to an electrical signal, it is no longer represented by an intensity at a specific frequency in the acoustic domain. It is represented by an amplitude and a frequency in the electrical domain. Besides transduction, the sensory neuron performs as an integrating amplifier and a voltage translation device. The integration amplifier has an integration frequency of 600 Hertz in humans. At excitation frequencies substantially below this frequency, the circuit acts as a linear amplifier. At excitation frequencies substantially above this frequency, it acts as a perfect charge integrator. At these frequencies, the signal output at the pedicle of the neuron is the height of the DC pedestal and not the amplitude of any AC component present. This mode of operation has caused great confusion in the literature and led to the sensory neurons being described imprecisely as rectifiers. Because of the sampling characteristics of the subsequent neural circuits, the output voltage at the pedicle averaged over a 30-millisecond interval constitutes the *signature* projected up the signaling chain. The neurological system relates this signature to its place of origin along the cochlear partition. It does not relate it to any stimulus frequency.

Each sensory neuron, or small group of neurons, synapse with an initial signal processing neuron within the spiral ganglia. This neuron performs as an analog voltage to action potential (pulse) encoding circuit (defined here as a stage 3 neural circuit). The resulting signals are passed to the stage 2 signal processing neurons before being again encoded by stage 3 circuits for passing to the cochlear nucleus via the auditory nerve. In the remainder of this figure, all of the projections of neural signals between major engines of the CNS involve pulse format signaling (performed by stage 3 circuits and shown by hatched paths). The signal processing and signal manipulation within an engine are performed using analog signals. The single hatched paths are generally one-way while the crosshatched paths are two-way.

The first occurrence of bilateral (binaural) signal processing occurs within the superior olivary complex. Binaural processing will not be treated in this work.

All of the stage 4 and stage 5 neural processing occurs within the Cortex as indicated by the gray surround of the engines in this area. The key feature to note is the supervisory role of the thalamic reticular nucleus (TRN). This

functionally identified engine is found as a thin layer covering a majority of the diencephalon (thalamus). It also exhibits folded extensions forming the engines of the mesencephalon. Nearly all of the sensory signals delivered to the CNS pass through and are controlled by the TRN. Functionally, the TRN is able to inhibit and reroute many of the signals delivered to it. The importance of this supervisory and control function cannot be over stressed. Only a small part of its activity is controlled by the conscious portion of the brain.

The TRN is partially reticulated and partially smooth neural tissue, indicative of its multiple functions. The smooth portion is generally associated with its supervisory functions while its reticulated portion is generally associated with its correlation and switching processes. The reticulated portions form the MGN, PGN and IC of hearing.

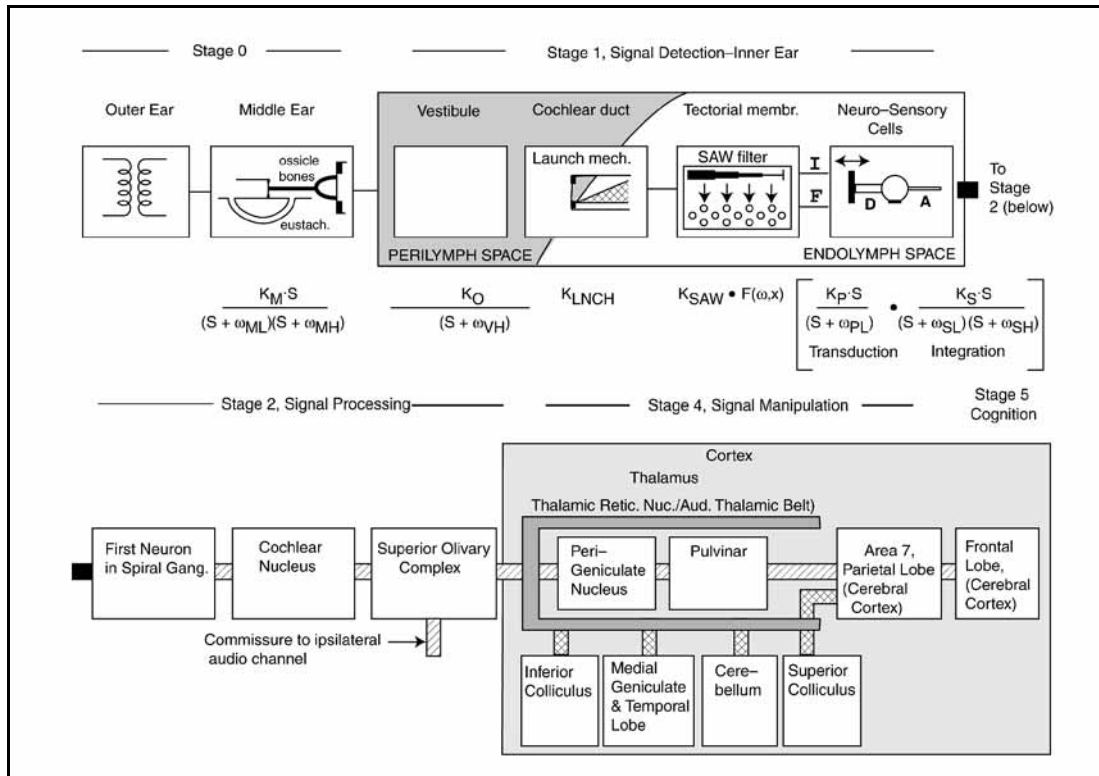


Figure 2.4.2-2 Annotated ascending portion of the Top Level Block Diagram of the auditory system showing the flow of information from the outer ear to the cognitive portions of the brain. Solid connections carry analog information. Hatched connections are stage 3 commissure. Cross-hatched connections are two-way stage 3 commissure. The transition of the signal energy from a high velocity compression acoustic wave in the perilymph space to a low velocity surface acoustic wave in the endolymph space within the inner ear is indicated by the curved border. The commissure to the other audio channel supports the earliest possible derivation of angle information related to any acoustic source. The crucial role of the thalamic reticular nucleus in its supervisory and switching roles is apparent. See text.

Based on analogy with the visual system, the morphologically defined colliculus bodies can be divided into two types. The inferior colliculus is primarily involved in coordinate extraction, associated with identifying acoustic sources in object space.

The superior colliculus is more closely associated with the conversion of "high level" instructions received from the cerebral cortex (volition mode activity) into multiple and precise "low level" commands (command mode activity) required by the muscular system to provide smooth and coordinated motions. However, to develop the necessary

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lookup tables, it must learn from the signals received by the sensory modalities. This function is discussed in Section 8.8.6.

Gulick et al., made a global assertion that requires species specific qualification (page 192). "Regardless of the site of origin within the lower acoustic nuclei, the vast majority of ascending neurons terminate in the inferior colliculus." Humans are known to make less use of object-space spatial information than many other species. As a result, the role of the inferior colliculus is relatively small. Some authors have asserted it is rudimentary in humans. A majority of the ascending neurons can be expected to extend to other signal manipulation centers in humans, particularly the morphologically adjacent PGN.

The TRN plays a major role in routing the ascending neural signals to their appropriate functional areas. Those signals dealing with communications appear to be routed to the PGN/pulvinar couple (shown within the TRN). Those dealing with the spatial location of external sources are routed to the IC. Those signals dealing with general awareness appear to be routed to the MGN/temporal lobe couple.

The output of the signal manipulation performed within the PGN/pulvinar, MGN/temporal lobe and the IC result in signals called percepts. These percepts are returned to the TRN for assembly into a saliency map describing the current state of the environment surrounding the subject. This saliency map is believed to be stored within the parietal lobe of the cerebral cortex, Top level 7. This area can be readily accessed by the stage 5 cognitive neurons of the frontal lobe. The stored information has lost all traceable characteristics related to the original sensory signals. The information is stored in the abstract code of the neural system.

As noted more and more frequently in the literature, the cerebellum, superior colliculus and portions of the pulvinar are not bilaterally symmetrical. These portions are performing high-level, and abstract, signal processing that is not easily related to the bilateral morphology of the animal body.

### 2.4.2.3 The descending neural paths of the peripheral hearing system

As noted in Section 2.3.4, there are efferent neurons synapsing with the sensory neurons of the cochlear partition. Understanding the role of these neurons has been very difficult, even after more than fifty years of investigation. In 1981, Ross titled a serious discussion concerning the efferent neurons, "Centrally originating efferent terminals on hair cells: fact or fancy<sup>110</sup>?" He stressed that the point of origin of the neurons known to terminate at the sensory neurons remained largely unknown. The situation has not changed significantly since. Ross described the efferent neurons as part of the VIIIth cranial nerve and reviewed the research accomplished up to that date. Summarizing, he said, "They suggest, moreover, that the parasympathetic neurons, including those to the inner ear, are phylogenetically very old and functionally related to basic, homeostatic matters." These positions suggest that the efferent neurons play no role in the signaling related to hearing.

More recent authors have proposed a role for the descending neural paths in sharpening the effective bandwidths of the sensory neurons. These proposals have been introduced to bridge the gap between the calculated bandwidth of vibrations of the basilar membrane and the measured bandwidth of individual Stage 3 signaling paths within the auditory nerve. Some of these proposals involve a local neural loop between the IHC and OHC. They generally require a wideband efferent neural circuit with capabilities far beyond those of the adjacent afferent neurons. These proposals are not supported in this work.

Harrison has provided a top level diagram of the efferent auditory neural paths at a very cursory level<sup>111</sup>. Chapter 5 will define the role of the efferent neurons not associated with homeostasis as elements in a very low bandwidth gain control mechanism.

### 2.4.3 Neural signal processing and manipulation are performed in the analog domain

While not obvious from the introductory texts on hearing, the mammalian neural system operates primarily in the analog signal processing domain. Only the projection of signals over distances greater than two millimeters requires the use of pulse signaling techniques. Unfortunately, it is far easier to record stage 3 pulse signals than it is to record and analyze signals from the other stages of neural processing.

#### 2.4.3.1 The dominance of analog neurons within the neurological system

It is important to realize two facts. Berthold & Rydmark estimate 99.9% of the neurons in mammals are found in the central nervous system with the remaining 0.1% in the peripheral nervous system<sup>112</sup>. From a different perspective, 95% of all neurons are electrotonic, they do not generate action potentials. Less than 5% of all neurons,



only the stage 3 projection neurons, generate action potentials.

Even within the 0.1% of the neurons assigned to roles in stage 3 signal transmission (projection), the number of actual neurons can be quite large and their diversity in morphological form at the detailed level is great. Usually this diversity appears to be due more to the available topography than to functional differences.

As noted earlier, it is now known that less than 5% of the neurons in the typical chordate, consist of projection neurons operating in the all-or-nothing mode. The vast majority of neurons operate in the linear, i. e., electrotonic mode. The "all-or-nothing" concept plays no part in the operation of these neurons (that constitute 95% of the neurons in any chordate species).

#### 2.4.3.2 Limiting the "all-or-nothing" concept of neural activity to stage 3

Piccolino has described the evolution of the "all or nothing" hypothesis of the "English school" of the late 1800's<sup>113</sup>. Their work involved the muscles and the (stage 3, projection) nerves leading to those muscles. The concept was first presented on a global basis, the muscle only reacted at full force above a sharp threshold of stimulation. Piccolino illustrates the coarse response obtained by Lucas in 1909. This figure actually showed an incremental increase in the mechanical response of the muscle that led to the dissection of the muscle and nerve tissue into more fundamental units. The resulting theory was then restated to reflect the operation of these fundamental units. However, this was insufficient. It is now known that the muscles respond as integrators and receive a series of discrete pulses from the associated projection neuron. In this operating mode, each action potential associated with the projection neuron can be considered an "all-or-nothing" phenomenon. However, the reaction of the muscle over any finite interval during which more than one action potential is received, is linearly related to the number of pulses received. While each action potential is based on an "all or nothing" monostable oscillator, the train of pulses typically generated by such an oscillator actually encodes an analog signal that is not all-or-nothing.

### 2.5 The complexity of the human CNS based on parts count

An important feature to note is the density of neurons within the human cortex. Although, the local density varies greatly, two situations are of great importance; the very densely packed three-dimensional organization of the pulvinar of the thalamus and the more common thin laminar sheet of the majority of the brain. Although not generally recognized, the majority of the cortical tissue is a very thin laminate of neural material consisting of typically six discernable layers (frequently subdivided into sublayers depending on the amount of detail defined within each layer). The cortical tissue is one-sided in the sense that all input and output commissure connect through only one surface of the laminate. Different layers are frequently characterized by neurons of different geometry and size. It is convenient to treat each of these types of brain separately and calculate a nominal number of standard size neurons within a unit volume for each type of brain. For discussion, take the standard size of a neuron as a 10-micron diameter sphere on 10-micron centers (with no limitation on the number or length of neurites or axons extending from this volume).

For the pulvinar of the diencephalon, a highly folded and nominally bulk structure, a 2 x 2 x 2 mm mass would contain approximately eight million neurons. Assuming two neurons to a circuit element equivalent to a two-state flip-flop, this is approximately the memory capacity equivalent to about four megabits of RAM in a PC. There is a problem of terminology here. The computer industry speaks of RAM in terms of an 8-bit word as one byte. Thus, four megabits of RAM is equivalent to 0.5 megabytes of RAM. If this circuit capacity were devoted to computation instead of memory, it would be roughly equivalent to the computing power of a modern PENTIUM IV microcircuit.

For a thinner structure, such as the cerebellum or the cerebral hemispheres, such equivalent neural volumes would require greater surface area. In the case of the cerebral hemispheres, with a thickness of 0.5 mm, a surface area of about 4 x 4 mm would be required to provide eight million neurons. This is also the approximate computing power of a PENTIUM IV microcomputer chip. The cerebellum is generally thicker than the cerebral hemispheres but less than two mm thick. It would require an area of intermediate value compared to the earlier values to achieve the same capacity.

Based on these crude estimates, and without considering whether the individual synapses of a cortical neuron could constitute a complete memory element each cubic centimeter of the pulvinar is equivalent to about 625 PENTIUM IV computer chips and each square centimeter of the planar portions of the brain (including the area within the sulci) is equivalent to about six PENTIUM IV computer chips. If a memory unit is formed by a single synapse between two neurons (instead of a pair of neurons), the above estimates of the number of equivalent computer chips are low by a factor of about 1000.

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