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HISTORY OF MEDICINE

An Abbreviated History of the Ear: From Renaissance to Present

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In this article we discuss important discoveries in relation to the anatomy and physiology of the ear from Renaissance to present. Before the Renaissance, there was a paucity of knowledge of the anatomy of the ear, because of the relative inaccessibility of the temporal bone and the general perception that human dissections should not be conducted. It was not until the sixteenth century that the middle ear was described with detail. Further progress would be made between the sixteenth and eighteenth century in describing the inner ear. In the nineteenth century, technological advancement permitted a description of the cells and structures that constitute the cochlea. Von Helmholtz made further progress in hearing physiology when he postulated his resonance theory and later von Békésy when he observed a traveling wave in human cadavers within the cochlea. Brownell later made a major advance when he discovered that the ear has a mechanism for sound amplification, via outer hair cell electromotility.

> *"Remember and Venerate the Masters and Their Art."*
> — *Richard Wagner,* Die Meistersinger

THE RENAISSANCE

The study of the anatomy and physiology of the organ of hearing was hampered by the relative inaccessibility of the temporal bone. Before the Renaissance information regarding the anatomy of the organ of Corti was scarce. Even Leonardo da Vinci showed little interest in the structure of the organ of hearing [1].

It was not until the sixteenth century that the anatomy of the organ of hearing began to be described. Vesalius is rightfully regarded as the founder of the new anatomy school. However, it was not this anatomist who substantially expanded our knowledge of the organ of hearing. In otology, one has to recognize that Fallopio's achievements surpassed the ones of Andreas Vesalius. However, Vesalius' work is of importance to otology and should not be underestimated [2]. One of the major contributions of Vesalius was his suggestion that the organ of hearing should be removed from the skull for investigation. This observation is still valid today and has proved fundamental for increasing our knowledge of the anatomy and physiology of the organ of hearing. Vesalius also performed anatomical dissections of the organ of hearing in animals

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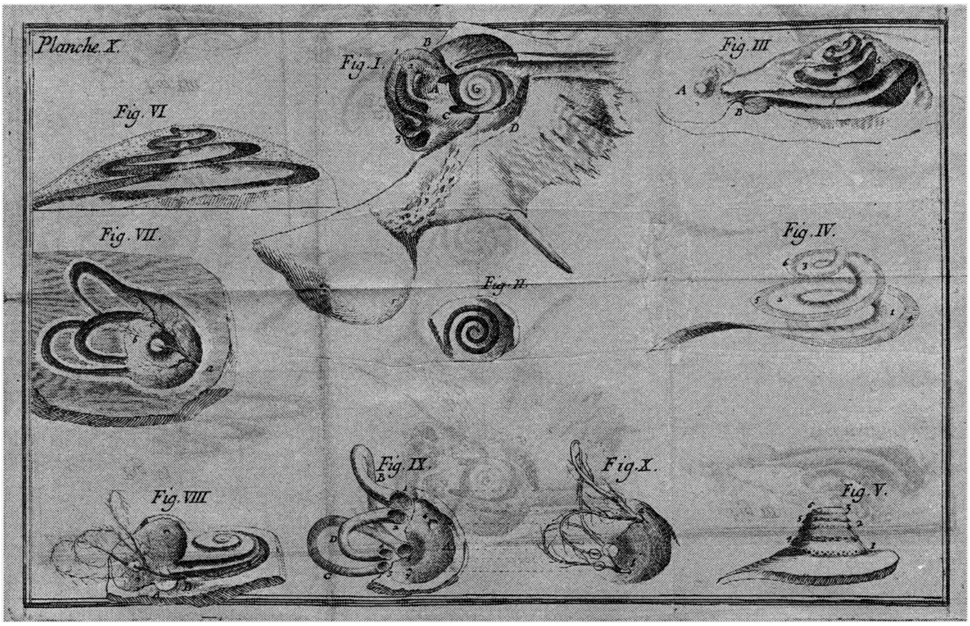

Figure 1. **"Traite de l'organe de l'ouïe: contenant la structure les usages & les maladies de toutes les parties de l'oreille," by M. Du Verney. Paris: Estienne Michallet, 1683. Reproduced with permission from the Houston Academy of Medicine, Texas Medical Center Library, Houston, Texas.**

since he believed that this approach would increase our knowledge of the human hearing organ. Even though Vesalius advanced the anatomical knowledge of the organ of hearing he did not pursue this field intensively. This is exemplified in his failure to identify and describe the stapes. Gabrielle Fallopio di Modena would make further progress in otology. "Fallopio of Modena is outstanding among the Renaissance anatomists because he combines extensive knowledge with rare nobility of character," Adam Politzer writes in his extensive treatise on the History of Otology [1]. His principal contributions include a detailed description of the tympanic membrane, the auditory ossicles, the two windows, the promontory, the chorda tympani, the labyrinth, the semicircular canals, the cochlea and the auditory nerve. He was the first anatomist to describe the auricular muscles with certain detail [1]. He also provided a description of the "*Canalis Falloppiae*," which is better known as the facial canal and contains the facial nerve. While studying the cochlea Fallopio was the first to describe the spiral lamina.

Another important anatomist of this period is Bartolomeo Eustachio. The most important Treatise of Eustachio in relation to otology is the "Opuscula anatomica, Venet, 1563," it contains the section "Epistula De auditus organis." In his epistle Eustachio writes that he discovered the stapes before Ingrassia, another Italian sixteenth century anatomist. Eustachio provided an unequivocal description of the tensor tympani and established that the chorda tympani is a nerve branch from the facial nerve. But Eustachio's most known contribution is his description of the structure that holds his name: "The tube of Eustachio." Eustachio also contributed to the study of the semicircular canals and the cochlea, described the spiral lamina and the modiolus.

Eustachio postulated that the auditory ossicles and the tensor tympani were involved in the mechanism of sound transduction. Eustachio also believed that the tensor tympani is a muscle under voluntary control.

Without the aid of microscopy few more knowledge could be gained in the next two centuries. The interested reader is encouraged to read upon this period [3, 4].

But we shall mention Duverney's theories on the physiology of hearing, which were postulated in the eighteenth century. To Duverney the ultimate organs of sound perception are the cochlea, the semicircular canals, and within the cochlea, the spiral lamina. He compares the latter to a musical instrument that serves to define the tones and distinguish between them. The beginning of the first turn is relatively wide, then, gradually, turns narrow. According to Duverney, one may assume that the wider parts vibrate more slowly and therefore are affected only by low-pitched tones, while the narrower parts vibrate more quickly, responding to high-pitched tones, perceiving and conducting them [5]. The theory proposed by Duverney proved not to be correct, since the perception of tones of high pitch is known to occur in the basal turns, those of low pitch in the upper turns. Furthermore, Duverney did not interpret the cochlea as the sole organ of ultimate sound perception but believed that the semicircular canals were of similar importance. Duverney's theory is described with detail in his enduring monument of the study of the ear entitled *Traité de l'Organe de l' Ouïe* [6]. We were able to find a copy of this historical document at the Texas Medical Center Library. In Figure 1, we show some of the dissections of the inner ear as depicted by Duverney.

THE NINETEENTH CENTURY

Marchese Alfonso Corti's work published in the beginning of the second half of the nineteenth century proved to be fundamental to better define the histology of the organ of hearing. He is the first histologist who studied the labyrinth with detail. He also provided a description of the spiral lamina. Corti not only made reference for the first time to the spiral ganglion but also advanced an exact picture of the cells that rest on the basilar membrane. Corti provided the first drawings of the existence of outer and inner hair cells, other "round epithelial cells" and the tectorial membrane [7].

Ernst Reißner made several important discoveries for our understanding of the organ of hearing. Corti failed to identify Reissner's membrane; however, Ernst Reißner with different methods and an improved technique described a membrane that separated the scala media from the scala vestibuli, Reissner's membrane [8].

Otto Friedrich Deiters also contributed significantly to the current knowledge of the histology of the inner ear. Deiters identified for the first time a type of cell, which was named after him, the Deiter cell; he described its intriguing relation to the outer hair cell and the supporting basilar membrane [9, 10].

The work of Corti, Reißner, and Deiter contributed for a better understanding of the histology of the inner ear. Further progress would be made by von Helmholtz as will be now discussed.

HERMANN VON HELMHOLTZ (1821-1894)

Hermann von Helmholtz not only contributed to a better understanding of the inner ear but also provided a description of the mechanical coupling of sound from the tympanic membrane to the oval window [11]. He describes how a tense tympanic membrane is easily shifted to vibration by the undulating air, and the mechanism for vibration transmission through the ossicular chain to the water of the labyrinth underlying the oval membrane in direct contact with the footplate of the stapes. Transmission of vibration would be more effective if both membranes were in contact with air on each side. Mechanical coupling of sound is favorable because of the smaller area of

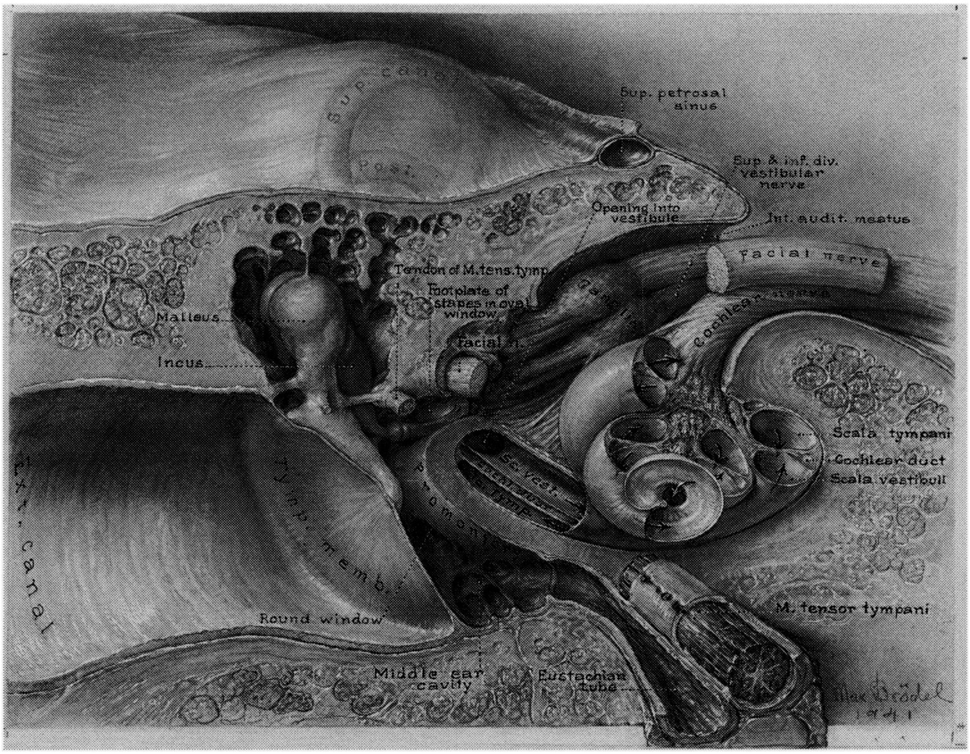

Figure 2. An illustration of the structure of the Ear as drawn by Max Brödel in the twentieth century. Reproduced with permission. Original art in the Max Brödel Archives, Art as Applied to Medicine, the Johns Hopkins University School of Medicine, Baltimore, Maryland.

the oval membrane in comparison to that of the tympanic membrane.

But his most important contribution is undoubtedly his interpretation of the analysis of sound in the inner ear. He believed the cochlea was tonotopically organized, that different parts of the cochlea would register different frequencies of sound [12]. This tonotopical organization posited that tuned fibers in the basilar membrane, on which the organ of Corti rests, vibrate in response to particular sound frequencies, just as a specific piano string will begin to vibrate in response to a sound at just the right frequency. He was correct that different frequencies are "heard" by different sections of the organ of Corti, with the parts nearest the ossicles sensitive to high tones and the parts farthest from the ossicles sensitive to low tones, but there were still many unanswered questions about how the cochlea functions. His unequivocal masterwork is "*Die Lehre von den Tonempfindungen als Physiologische Grundlage für die Theorie der Musik*", in which Helmholtz describes his resonance theory. The acoustical theory or resonance theory of von Helmholtz was widely accepted by the physiologists of that time.

GEORG VON BÉKÉSY (1899-1972)

One of the most important contributions to our understanding of hearing physiology is the work of von Békésy [13, 14]. His work provides for the first time a model of the micromechanical properties of the cochlear partition. With ingenious experiments he observed with a stroboscope that sound generated traveling waves along the cochlea. Using pure-tone stimuli, he found that each point along the cochlear partition vibrates at a frequency equal to that of the stimulus. The resulting pattern of vibration appears as a wave traveling from the base to the apex. The basis for the features of the traveling wave is the compliance of the basilar membrane. At the basal end, the membrane is stiff; the stiffness decreases systematically from base to apex. Sounds of higher frequency have a traveling wave with maximum amplitude closer to the base; the opposite is true for sounds of lower frequency. However, von Békésy assumed that little mechanical frequency analysis was done by the inner ear. Therefore the cochlear partition would be a passive system transducing a traveling wave into a nerve action potential. In Figure 2, we provide an illustration of the structure of the ear as drawn by Max Brödel in the twentieth century.

THE LAST DECADES

Even though von Békésy initiated a revolution in hearing physiology, many more answers to the mechanisms of sound transduction have been found in the last three decades. Georg von Békésy assumed that the cochlear partition was a passive system, however, soon thereafter it became apparent that such a system could hardly provide the high frequency selectivity and hearing thresholds of the cochlea. Some experimental evidence supported the theory of an active cochlear partition. The incoming traveling wave would be amplified by the organ of Corti and this would be fundamental for helping in producing the low hearing thresholds and frequency selectivity of the human ear. By the end of the 1970s, Flock found actin-like proteins in hair cells [15]. Later Kemp described the presence of sound coming from the ear, which he named acoustic emissions and suggested that outer hair cells might be generating mechanical energy [16]. This hypothesis gained robust acceptance in the 1980s when Brownell described a motile response in outer hair cells from the organ of Corti [17-19]. Until then outer hair cell function remained unclear. The function of the outer hair cell in hearing is now perceived as that of a "cochlear amplifier" that refines the sensitivity and frequency selectivity of the mechanical vibrations of the cochlea [20].

Many more advances in the physiology of hearing have been achieved, the interested reader can obtain more information elsewhere [21, 22].

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