NATIONAL ACADEMY OF SCIENCES

# GEORG VON BÉKÉSY

*1899—1972*

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*A Biographical Memoir by*

FLOYD RATLIFF



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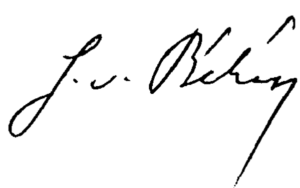

# GEORG VON BÉKÉSY

*June 3, 1899–June 13, 1972*

BY FLOYD RATLIFF

ON THE OCCASION of Georg von Békésy's election to the National Academy of Sciences in 1956, he gave the following replies to two items in a questionnaire sent to him by the Academy to obtain biographical information for its files:

"Major interest?" "Art."

"Major influences which determined the selection of your particular field of science?" "Pure accident."

These replies—"Art" and "Pure accident"—succinctly characterize much of the life and work of Georg von Békésy. His life was devoted almost as much to art as it was to science; and, although his love of art was carefully cultivated, the course of his scientific career was determined almost as much by chance as it was by design. He found his life work outside of his original chosen field during the economic depression in Hungary following World War I, and he was set on his wanderings half way around the face of the earth by the political turmoil there after World War II.

Professor Georg von Békésy died on June 13, 1972, at the age of seventy-three, in Honolulu. Born on June 3, 1899, in Budapest, he was the son of Alexander and Paula von Békésy. The Békésys were an old and distinguished family in Hungary, and Alexander von Békésy held a position in the Hungarian diplomatic service. Because of his father's various assignments, Georg von Békésy spent his early childhood in Budapest, Munich, and Constantinople. In 1916 he obtained his baccalaureate in chemistry at Berne, Switzerland, where his father was then a *chargé d'affaires* in the Hungarian Embassy. Following World War I, Békésy returned to Hungary and in 1923 received his doctorate in physics at the University of Budapest. Békésy began his scientific career in the laboratory of the Hungarian Post, Telephone, and Telegraph. He spent the next several years there (except for the year 1926–1927, when he worked in Berlin with K. Küpfmüller in the laboratories of Siemens and Halske). In 1932 he was appointed privat docent in the University of Budapest, where in 1940 he became Professor of Experimental Physics. For some time Békésy had two laboratories; for, after his appointment at the University, he continued his research in the government laboratory at the Hungarian Post.

During the foreign occupation of Hungary after World War II, Békésy found conditions intolerable for scientific research and in 1946 accepted an invitation to go to the Karolinska Institutet in Stockholm to work with Y. Zotterman. A year later, under the aegis of Professor S. S. Stevens, he came to the United States and joined the faculty of Harvard University. In 1949 he was given a special appointment there as Senior Research Fellow in Psychophysics, which enabled him thereafter to devote his full attention to research. Békésy held this post for nineteen years. At the age of sixty-seven, with the unhappy prospect of retirement facing him, Békésy resigned and moved to a new laboratory built for him at the University of Hawaii, where he accepted an appointment as Professor of Sensory Sciences—an endowed chair provided by the Hawaiian Telephone Company. He continued his research at Hawaii for six years—almost until the day of his death.

In 1961 Georg von Békésy was awarded the Nobel Prize in Physiology or Medicine "for his discoveries concerning the physical mechanism of stimulation within the cochlea." The following excerpt from the Presentation Speech by C. G. Bernhard of the Karolinska Institutet provides a fine characterization of Békésy's research on the mechanics of the ear:

"According to the saga, Heimdal was able to hear the grass grow. Our hearing ability is perhaps not of that kind, but our ear is anyhow almost sensitive enough to record the bounce of an air molecule against the eardrum, while, on the other hand, it can withstand the pounding of sound waves strong enough to set the body vibrating. Moreover, the ear is capable of a selectivity which permits a close analysis of sounds the various qualities of which determine the characteristics of the spoken word and of instrumental and vocal expressions in the universe of music.

"A sound which hits the ear makes the eardrum vibrate. Within the air-filled middle ear the vibrations are transmitted via a subtle system of levers, the ossicle chain, to the fluid of the inner ear, the cochlea. The footplate of the stirrup which serves as the innermost link of the ossicle chain is movably mounted in the opening of the oval window of the inner ear which faces the middle ear. The vibrations of the fluid engage in their turn the so-called basilar membrane, an oblong partition which divides the spiral-shaped cavity of the cochlea in its longitudinal direction. Along its entire length the membrane carries sense cells, receptors, like fine tapering columns with hairy points reaching up to a covering membrane. The receptor cells, or hair cells, transform the mechanical energy, represented by the vibrations of the basilar membrane, into the specific form of energy which triggers the nerve impulses. The frequency of these impulses serves as the code to the information carried on to the higher nerve centers.

"Von Békésy has provided us with the knowledge of the physical events at all strategically important points in the transmission system of the ear. This does not mean that the properties of the oscillating systems of the ear have not been an object of study and theoretical considerations by scientists before von Békésy. The field of physiological acoustics has a noble ancestry, in which the theories of von Helmholtz hold an authoritative position.

"Von Békésy's distinction is, however, to have recorded the events in this fragile biological miniature system. Authorities in this field evaluate the elaborate technique which he developed for this purpose as being worthy of a genius. By microdissection he reaches anatomical structures difficult of access, uses advanced teletechniques for stimulation and recording, and employs high magnification stroboscopic microscopy for making apparent complex membrane movements, the amplitudes of which are measured in thousandths of the millimeter.

"Among von Békésy's important contributions to our knowledge of sound transmission in the middle ear should be mentioned the elucidation of the vibration patterns of the eardrum and of the interplay of the ossicle movements. His technical and theoretical mastery has reached its peak in those investigations which led to the fundamental discoveries concerning the dynamics of the inner ear. Experimental and clinical data had confirmed von Helmholtz's assumption that the frequency of the sound waves determines the location along the basilar membrane at which stimulation occurs. The physical characteristics of the pattern of the membrane vibrations and the conditions for its appearance had, however, previously only been the object of theoretical considerations. Von Békésy succeeded in unveiling the features of the vibration pattern. He found that movements of the stirrup footplate evoke a wave complex in the basilar membrane, which travels from the stiffer basal part to the more flexible part in the apex of the cochlea. The crest of the largest wave first increases, thereafter quickly decreases. The position of the maximal amplitude was found to be dependent on the frequency of the stimulating sound waves in such a way that the highest crest of the travelling wave appears near the apex of the cochlea at low-frequency tones and near its base at high frequencies. The conditions for the appearance of these specific vibration patterns were determined in model experiments.

"Von Békésy then turned to the question of how the hair cells are stimulated. With a thin needle, the point of which touched the basilar membrane, different parts of the membrane could be set in vibrations in various directions. The point of the needle simultaneously served as an electrode for recording the electrical potentials from the receptor cells. It was found that a local pressure on the basilar membrane is transformed into strong shearing forces which act on the hair cells in various degrees.

"Thus, von Békésy has given us a clear picture of how the cochlea functions mechanically and his discoveries serve as a basis for our conception of the cochlea as a frequency analyzer."*

Fortunately for the student and researcher in the field of hearing, Békésy's writings on the main results of his many studies on hearing over the thirty-year period 1928–1958 were published in 1960 in a single volume, *Experiments in Hearing*, translated and edited by E. G. Wever. These papers are models of technical skill, elegance of experimental design, and clarity of presentation.

Békésy's physical measurements of the mechanical properties of the ear convinced him that some sort of neural "sharpening" mechanism must be required to account for the remarkable sharpness of pitch discrimination. The general form of Békésy's ideas was derived from the earlier work of Ernst Mach on

*C. G. Bernhard, "Presentation Speech," in *Nobel Lectures, Including Presentation Speeches and Laureate's Biographies. Physiology or Medicine, 1942–1962* (Amsterdam–London–New York: Elsevier Publishing Co. for the Nobel Foundation, 1964), pp. 719–21.

inhibitory interactions in the visual system. Békésy published a few preliminary observations on the possible role of inhibition in hearing as early as 1928; but extensive investigations (including work on skin senses, vision, and taste) were not carried out until much later, as he gradually became more and more interested in this aspect of his work. His researches in this field, prior to 1967, are well summarized in his book *Sensory Inhibition.*

This brief account of Békésy's life and work represents the sum and substance of the public record, excepting one autobiographical sketch published posthumously in 1974. Békésy generally left it to others to extol his virtues and proclaim his accomplishments.

Békésy was a solitary person. Although friendly, he was reserved; few people knew him intimately, and those who did respected his desire for privacy. Despite Békésy's usual solitary ways, however, when the occasion demanded he was outgoing and sociable. He had a keen sense of humor, and his lectures and conversations were always punctuated with some anecdote, wry comment, or little aphorism that went directly to the heart of the matter. For example: One day at the weekly colloquium in the Harvard Psychology Department (with which the Psycho-Acoustic Laboratory was affiliated), the guest speaker was at his worst and gave an extraordinarily long and dull lecture on a mathematical theory of behavior. Unfortunately, the audience responded in kind, and at equally great length, with pointless questions and irrelevant comments. When at long last it was all over, Békésy led me directly to the blackboard in his office, picked up a piece of chalk, and said, "This is the most important but least known equation in all of the social sciences. Always remember it, for as you have just seen, it completely describes a great deal of human behavior." And then—summing up the whole afternoon neatly—he wrote:

$$0 + 0 = 0.$$

Békésy often remarked that his was a lonely life, but he preferred it that way. His closest friends, from which he drew both solace and inspiration, were the art objects he had collected over the years. These filled his laboratory, secreted here and there in drawers and filing cabinets where one might ordinarily expect to find only tools, supplies, and records of data. But always at least one of these treasures was out on display on his work bench or desk where he might spend hours examining it and reflecting on its beauty. This was not a surprising aspect of Békésy's character, for he was truly creative himself, and his contributions to science were very close to art. Indeed, the private Békésy—known only to a few and even to them incompletely—can only properly be portrayed as the many-faceted person which he was: A true Renaissance man with very broad interests and great depth of knowledge in both the arts and the sciences.

Békésy's interest in art was undoubtedly fostered by the circle in which his family moved. During all of his early years he was surrounded by artists, sculptors, musicians, and other intellectuals who were friends and acquaintances of his parents. As a young man, Békésy studied music seriously; and it has always seemed strange to many people that in his later years the world's greatest authority on hearing was more interested in the visual arts than in the musical arts. The explanation is simple. Békésy found that he could not get music off his mind. After playing or listening to a good tune, he felt compelled to hum it or go over it in his mind for hours, or even days. This, he felt, interfered with sound, logical thinking. Because the perception of a work of visual art faded away at once—unless he made a conscious effort to recall it—he chose to make the study of art and archeology, rather than music, his avocation.

Békésy studied art not only for the great pleasure it gave him, but also for an effect that he believed it would have on his mind. Comparing one art object with another to determine quality and authenticity, he thought, greatly improved his ability to make judgments about the quality of scientific work too. Whether such transfer actually took place no one can say. But there is no question that art pervaded all of Békésy's science. The many superb instruments of his own design, the models and movies of various wave phenomena, the illustrations in the papers describing his experiments—indeed, even the experiments themselves—can all properly be called works of art. (Many of Békésy's private papers, films, and slides are now available for study in the Library of Congress.)

During his lifetime, Békésy collected a large number of works of art and rare books. Many were lost in World War I, others in World War II, and some were destroyed or damaged as a result of a fire in Memorial Hall at Harvard. In spite of all this, the collection gradually grew larger and more varied. But the collection was almost as private as was Békésy's personal life—few persons were ever privileged to see more than a mere fragment of it. Now, however, it is in the public domain. In his last will and testament, Békésy chose to honor the Nobel Foundation, which had earlier bestowed such great honor upon him, with a gift of that which was closest and dearest to him—the art objects that he had collected over the years and that had been both a source of inspiration in his work and a source of solace for a lonely man in times of need of comfort. The Georg von Békésy Collection of Art was placed on public exhibition for the first time, by the Nobel Foundation, on December 9, 1974.* His collection of books is now in the Library of the University of Hawaii.

As was mentioned above, Békésy's choice of a scientific career was, as he put it, "pure accident." But chance can only provide

*A biographical sketch of Békésy, which focuses on his interest in art, is included in the catalog: F. Ratliff, "Georg von Békésy: His Life, His Work, and his Friends," in *The Georg von Békésy Collection*, ed. by J. Wirgin (Malmö, Sweden: AB Allhem for the Nobel Foundation, 1974).

opportunity; it remains for the individual to seize upon it and exploit it. And when he does so time and again, as Békésy did, that is the mark of genius.

For example, it was largely a matter of chance that a man trained in chemistry and physics became interested in the psychophysiology of hearing and in the role of inhibitory interactions in sensory processes. To begin with, it was Békésy's youthful idealism and patriotism that prompted him to leave Switzerland, following World War I, and to return to Hungary to help rebuild the country. His doctoral research in physics at Budapest had been in a branch of optics now known as interference microscopy, and he tried to find a position in the field of optics. But times were very hard then and there were no jobs at all for a physicist with his background and experience. Békésy finally decided to find the best-equipped laboratory in Hungary and work there for nothing, if necessary. The only laboratory still well equipped after the war was the Hungarian Post and Telegraph. It had support because the government was forced by postwar treaties to maintain the telephone and telegraph line that crisscrossed the country. Although the laboratory had no proper position for a physicist, they did employ Békésy and give him a small salary.

Every day brought a new experience. One day telephone lines would fail, on another there would be radio problems, and so on. As a result Békésy was drawn into the problems of the rapidly developing field of communication engineering—particularly the electromechanical means of the transfer and processing of information.

At that time the international telephone lines were tested over a loop made by closing the circuit in another city. The input voltage of a series of pure tones fed into the origin of the loop at Budapest would be compared with corresponding output voltage when it arrived back at Budapest. The complete measurement took many minutes—sometimes hours, if there was much trouble with the lines. Békésy developed a new method that would check the lines in about one second. To learn how to do this, he spent many hours at night in the room where the cable heads came in, listening to conversations and trying to match the systems properly. Békésy paid close attention to everything he heard over the lines, including the inevitable "clicks" when phones were connected and disconnected. These clicks seemed to change as the status of a line changed, so he started using them as the test signal, and within a few days he had perfected his new, more efficient method. As Békésy pointed out in his Nobel Lecture, the basic idea was similar to a musician making a quick check of the tuning of his violin by plucking a string rather than by the more time-consuming bowing. In effect, Békésy "plucked" the telephone line instead of "bowing" it. The key to the whole problem was that the clicks each contained a wide spectrum of frequencies—thus each click sent the equivalent of innumerable "pure tones" along the lines in a single short pulse. This click method provided the key to Békésy's future research and led him to the study of the sense of hearing and the mechanics of the ear. But this came about more or less by chance, too.

The Hungarian government wanted to make further improvements in the international telephone system and asked the laboratory for advice on how the limited funds available for research should be spent. Békésy's opinion was that the money should be allocated to improving the weakest part of the system. With the click method it was easy to determine that the telephone receiver was the worst part of all—including even the international cables themselves. But this focus on the receivers immediately raised the further question: Is the receiver more or less sensitive than the ear? For it would be futile to improve the receiver if it were already more sensitive than the ear itself. By making the click comparison it was evident that the eardrum was a much, much better instrument than the ordinary telephone receiver. It was therefore essential to improve the receiver first.

This study of the mechanics of the eardrum led naturally to the study of the middle ear and the investigation of the chain of bones—stirrup, hammer, and anvil—that conducts the sound from the eardrum to the inner ear. And likewise, this study led naturally to the inner ear itself and dealt with a very old problem—the form of the pattern of vibration produced on the basilar membrane in response to a pure tone. Others before Békésy, notably Helmholtz and Corti, had looked at the intact basilar membrane. Their technique was to chip away the surrounding bone. But the cochlea is imbedded in one of the hardest bones in the body; and by the time the cochlea was opened and the basilar membrane exposed to view, the membrane was usually displaced or disturbed in some way so that observations of its motions were inconclusive. Furthermore, the whole cochlea tended to dry out during the preparation, thus distorting the natural mechanical properties of the membrane.

With the elegant experimental techniques that were to characterize all of his later research, Békésy solved all of these technical problems at once. The solution was simple: do the dissection under fluids. The preparation was placed in a square bath with the fluid entering one side and flowing out the other. Then, by using a high-speed drill, it was possible to grind off very thin layers of bone. Each time the drill was used, a cloud of bone dust was formed in the bath; but, because the fluid was continuously flowing, the cloud cleared very quickly. With a special 200-power underwater microscope Békésy could observe the progress of the work closely and proceed very carefully. He was thus able to open nearly a full turn of the tip of the snail-shaped cochlea and thereby to expose to view a substantial portion of the intact basilar membrane. In this way the various patterns of vibration of the membrane produced by various pitches of sound could be observed directly.

In 1928 Békésy published his first and probably most significant paper on the pattern of vibration in the membranes of the cochlea of the ear. This one paper provided the foundations for his whole career: The basic experimental observations in it set the course of practically all of his subsequent studies on the mechanics of the ear, and the ideas that he expressed in it on how Ernst Mach's laws of contrast in vision might also be significant in hearing and in other senses set the course of his work on lateral inhibition, which was to occupy most of his later years. Chance played a role here, too; Ernst Mach's work came to Békésy's attention by "pure accident" one day when he was searching for a paper by Mach's son, Ludwig, on what is now known as the Mach–Zender interferometer.

It was Békésy who pointed out to me, about 1950, the similarity between Mach's ideas on inhibition and the inhibitory interaction that H. K. Hartline (Nobel Laureate in Physiology or Medicine 1967) had just discovered in the compound eye of the horseshoe crab *Limulus*. This observation of Békésy's gave that phenomenon added significance and established a framework for its investigation and interpretation over the next quarter of a century. It also stimulated Békésy to devote more and more of his own time in later years to a comparative study of inhibition and the contrast effects it produces in practically all of the senses. One of his last papers was concerned with the study of some contour and contrast effects found mainly in Oriental art, which he had come to admire so much during his last years in Hawaii. Indeed, the search for truth and the love of beauty were never far apart in Békésy's life and work. Commenting on his first view of the organ of Corti he wrote:

"I found the inner ear so beautiful under a stereoscopic microscope that I decided I would just stay with that problem. It was the beauty and the pleasure of beauty that made me stick to the ear."

## HONORS

1931 Denker Prize, German Otological Society
1937 Leibnitz Medal, Akademie der Wissenschaften, Berlin
1939 Guyot Prize for Speech and Otology, Gronigen University
1946 Academy Award, Academy of Science, Budapest
1950 Shambaugh Prize in Otology, Collegium Oto-Rhino-Laryngolicum
1954 Member, American Academy of Arts and Sciences
1955 Warren Medal, Society of Experimental Psychologists
1955 M.D. (*honoris causa*), Wilhelm University, Munster
1956 Member, U.S. National Academy of Sciences
1957 Gold Medal, American Otological Society
1959 M.D. (*honoris causa*), University of Berne
1961 Gold Medal, The Acoustical Society of America
1961 Achievement Award, Deafness Research Foundation
1961 Nobel Prize in Physiology or Medicine
1962 M.D. (*honoris causa*), University of Padua
1963 D.Sc., Gustavus Adolphus College
1965 D.Sc., University of Pennsylvania
1968 D.Sc., University of Buenos Aires
1968 D.Eng. (*honoris causa*), National University of Cordoba
1969 D.Sc., University of Hawaii
1969 M.D. (*honoris causa*), University of Budapest

## BIBLIOGRAPHY

*KEY TO ABBREVIATIONS*

Acta Oto-laryngol. = Acta Oto-laryngolica
Akust. Z. = Akustische Zeitschrift
Ann. Otol. Rhinol. Laryngol. = Annals of Otology, Rhinology, & Laryngology
Ann. Phys. = Annalen der Physik
Arch. Otolaryngol. = Archives of Otolaryngology
Elektr. Nachr.-Tech. = Elektrische Nachrichten-Technik
Forsch. Fortschr. = Forschungen und Fortschritte
J. Acoust. Soc. Am. = Journal of the Acoustical Society of America
J. Appl. Physiol. = Journal of Applied Physiology
J. Gen. Physiol. = Journal of General Physiology
J. Opt. Soc. Am. = Journal of the Optical Society of America
Percept. Psychophys. = Perception and Psychophysics
Phys. Z. = Physikalische Zeitschrift
Proc. Natl. Acad. Sci. USA = Proceedings of the National Academy of Sciences of the United States of America
Vision Res. = Vision Research
Z. Tech. Phys. = Zeitschrift für technische Physik


1928

Über den Einfluss der nichtlinearen Eisenverzerrungen auf die Güte und Verständlichkeit eines Telephonie-Übertragungssystemes. Elektr. Nachr.-Tech., 5:231–46.

Zur Theorie des Hörens; die Schwingungsform der Basilarmembran. Phys. Z., 29:793–810.

1929

Zur Theorie des Hörens; über die Bestimmung des einem reinen Tonempfinden entsprechenden Erregungsgebietes der Basilarmembran vermittelst Ermüdungsercheinungen. Phys. Z., 30:115–25.

Zur Theorie des Hörens; über die eben merkbare Amplituden- und Frequenzänderung eines Tones: die Theorie der Schwebungen. Phys. Z., 30:721–45.

1930

Zur Theorie des Hörens; über das Richtungshören bei einer Zeitdifferenz oder Lautstärkenungleicheit der beiderseitigen Schalleinwirkungen. Phys. Z., 31:824–35, 857–68.

Über das Fechnersche Gesetz und seine Bedeutung für die Theorie der akustischen Beobachtungsfehler und die Theorie des Hörens. Ann. Phys. (Folge 5), 7:329–59.

Sur la théorie de l'audition. L' Année Psychologique, 31:63–96.

1931

Bemerkungen zur Theorie der günstigsten Nachhalldauer von Räumen. Ann Phys. (Folge 5), 8:851–73.

Über die Messung der Schwingungsamplitude fester Körper. Ann. Phys. (Folge 5), 11:227–32.

1932

Über die Ausbreitung der Schallwellen in anisotropen dünnen Platten. Phys. Z., 79:668–71.

Zur Theorie des Hörens bei der Schallaufnahme durch Knochenleitung. Ann. Phys. (Folge 5), 13:111–36.

Über den Einfluss der durch den Kopf und den Gehörgang bewirkten Schallfeldverzerrungen auf die Hörschwelle. Ann. Phys. (Folge 5), 14:51–56.

1933

Über die Schallfeldverzerrungen in der Nähe von absorbierenden Flächen und ihre Bedeutung für die Raumakustik. Z. Tech. Phys., 14:6–10.

Über die Hörsamkeit der Ein- und Ausschwingvorgänge mit Berücksichtigung der Raumakustik. Ann. Phys. (Folge 5), 16:844–60.

Über den Knall und die Theorie des Hörens. Phys. Z., 34:577–82.

1934

Über die Hörsamkeit kleiner Musikräume. Ann. Phys. (Folge 5), 19:665–79.

Über die nichtlinearen Verzerrungen des Ohres. Ann. Phys. (Folge 5), 20:809–27.

Über die Hörsamkeit von Konzert- und Rundfunksälen. Elektr. Nachr. Tech., 11:369–75.

1935

Physikalische Probleme der Hörphysiologie. Elektr. Nachr.-Tech., 12:71–83.

Über akustische Reizung des Vestibularapparates. Pflüger's Archiv für die gesamte Physiologie des Menschen und der Tiere, 236: 59–76.

Über akustische Rauhigkeit. Z. Tech. Phys., 16:276–82.

1936

Über die Herstellung und Messung langsamer sinusförmiger Luftdruckschwankungen. Ann. Phys. (Folge 5), 25:413–32.

Über die Hörschwelle und Fühlgrenze langsamer sinusförmiger Luftdruckschwankungen. Ann. Phys. (Folge 5), 26:554–66.

Fortschritte der Hörphysiologie. Z. Tech. Phys., 17:522–28.

Zur Physik des Mittelohres und über das Hören bei fehlerhaftem Trommelfell. Akust. Z., 1:13–23.

1937

Über die Photoelektrische Fourier-Analyse eines gegebenen Kurvenzuges. Elektr. Nachr.-Tech., 14:157–61.

Über subjektive harmonische Teiltöne. Akust. Z., 2:149.

Über die mechanische Frequenzanalyse einmaliger Schwingungsvorgänge und die Bestimmung der Frequenzabhängigkeit von Ubertragungssystemen und Impedanzen mittels Ausgleichsvorgängen. Akust. Z., 2:217–24.

1938

Über die Entstehung der Entfernungsemfindung beim Hören. Akust. Z., 3:21–31.

Psychologie und Fernsprechtechnik. Forsch. Fortschr., 14:342–44.

1939

Über die Piezoelektrische Messung der absoluten Hörschwelle bei Knochenleitung. Akust. Z., 4:113–25.

Über die mechanisch-akustischen Vorgänge beim Hören. Acta Otolaryngol., 27:281–96, 388–96.

Über die Vibrationsempfindung. Akust. Z., 4:316–34.

Über die Empfindlichkeit des stehenden und sitzenden Menschen gegen sinusförmige Erschütterungen. Akust. Z., 4:360–69.

1940

Über die Stärke der Vibrationsempfindung und ihre objektive Messung. Akust. Z., 5:113–24.

Über die Sicherheit und Reproduzierbarkeit künstlerischer Urteile beim Rundfunk. *Arbeitstagung des deutschen Fachbeirates für Sing- und Sprechkultur in Wien,* April.

The neural terminations responding to stimulation of pressure and vibration. Journal of Experimental Psychology, 26:514–19.

1941

Über die Messung der Schwingungsamplitude der Gehörknöchelchen mittels einer kapazitiven Sonde. Akust. Z., 6:1–16.

Über die Elastizität der Schneckentrennwand des Ohres. Akust. Z., 6:265–78.

Über die Schallausbreitung bei Knochenleitung. Zeitschrift für Hals-, Nasen- und Ohrenheilkunde, 47:430–42.

Über das Hören der eigenen Stimme. Anzeiger der Akademie der Wissenschaften, Wien (Mathematisch-naturwissenschaftliche Klasse), 78:61–70.

1942

Über die Schwingungen der Schneckentrennwand beim Präparat und Ohrenmodell. Akust. Z., 7:173–86.

1943

Über die Resonanzkurve und die Abklingzeit der verschiedenen Stellen der Schneckentrennwand. Akust. Z., 8:66–76.

Über die direkte mikroskopische Ausmessung der Resonanzschärfe und Dämpfung der sogenannten Ohrenresonatoren. Forsch. Fortschr., 19:364–65.

1944

Über die mechanische Frequenzanalyse in der Schnecke verschiedener Tiere. Akust. Z., 9:3–11.

Über die Frequenzauflösung in der menschlichen Schnecke. Acta Oto-laryngol., 32:60–84.

1947

The variation of phase along the basilar membrane with sinusoidal vibrations. J. Acoust. Soc. Am., 19:452–60.

The sound pressure difference between the round and the oval windows and the artificial window of labyrinthine fenestration. Acta Oto-laryngol., 35:301–15.

A new audiometer. Acta Oto-laryngol., 35:411.

Über die neuen Audiometer. Archiv der elecktrischen Übertragung, 1:13–16.

The recruitment phenomenon and difference limen in hearing and vibration sense. Laryngoscope, 57:765–77.

1948

On the elasticity of the cochlear partition. J. Acoust. Soc. Am., 20: 227–78.

With W. A. Rosenblith. The eárly history of hearing: observations and theories. J. Acoust. Soc. Am., 20:727–48.

Vibrations of the head in a sound field, and its role in hearing by bone conduction. J. Acoust. Soc. Am., 20:749–60.

1949

The structure of the middle ear and the hearing of one's own voice by bone conduction. J. Acoust. Soc. Am., 21:217–32.

The vibration of the cochlear partition in anatomical preparations and in models of the inner ear. J. Acoust. Soc. Am., 21:233–45.

On the resonance curve and the decay period at various points on the cochlear partition. J. Acoust. Soc. Am., 21:245–54.

Über die Mondillusion. Experientia, 5:326.

The moon illusion and similar auditory phenomena. American Journal of Psychology, 62:540–52.

1950

Interchangeable pencil-type micromanipulator. Science, 111:667–69.

Suggestions for determining the mobility of the stapes by means of an endotoscope for the middle ear. Laryngoscope, 60:97–110.

1951

With W. A. Rosenblith. The mechanical properties of the ear. In: *Handbook of Experimental Psychology,* ed. by S. S. Stevens, pp. 1075–1115. New York: John Wiley & Sons, Inc.

The coarse pattern of the electrical resistance in the cochlea of the guinea pig (electro-anatomy of the cochlea). J. Acoust. Soc. Am., 23:18–28.

Microphonics produced by touching the cochlear partition with a vibrating electrode. J. Acoust. Soc. Am., 23:29–35.

DC potentials and energy balance of the cochlear partition. J. Acoust. Soc. Am., 23:576–82.

1952

Resting potentials inside the cochlear partition of the guinea pig. Nature, 169:241–42.

Micromanipulator with four degrees of freedom. Transactions of the American Microscopical Society, 71:306–10.

DC resting potentials inside the cochlear partition. J. Acoust. Soc. Am., 24:72–76.

Gross localization of the place of origin of the cochlear microphonics. J. Acoust. Soc. Am., 24:399–409.

Direct observation of the vibrations of the cochlear partition under a microscope. Acta Oto-laryngol., 42:197–201.

1954

Note on the definition of the term: hearing by bone conduction. J. Acoust. Soc. Am., 26:106–7.

With E. G. Wever and M. Lawrence. A note on recent developments in auditory theory. Proc. Natl. Acad. Sci. USA, 40:508–12.

Some electro-mechanical properties of the organ of Corti. Ann. Otol. Rhinol. Laryngol., 63:448–68.

1955

Subjective cupulometry. American Medical Association. Arch. Otolaryngol., 61:16–28.

Paradoxical direction of wave travel along the cochlear partition. J. Acoust. Soc. Am., 27:137–45.

Human skin perception of traveling waves similar to those on the cochlea. J. Acoust. Soc. Am., 27:830–41.

Beitrag zur Frage der Frequenzanalyse in der Schnecke. Archiv für Ohren-, Nasen- und Kehlkopfheilkunde, vereinigt mit Zeitschrift für Hals-, Nasen- und Ohrenheilkunde, Kongressbericht, 167: 238–55.

1956

Current status of theories of hearing. Science, 123:779–83.

Preparatory and air-driven micromanipulators for electrophysiology. Review of Scientific Instruments, 27:690–92.

Simplified model to demonstrate the energy flow and formation of traveling waves similar to those found in the cochlea. Proc. Natl. Acad. Sci. USA, 42:930–44.

1957

Sensations on the skin similar to directional hearing, beats, and harmonics of the ear. J. Acoust. Soc. Am., 29:489–501.

The ear. Scientific American, 197(2):66–78.

Neural volleys and the similarity between some sensations produced by tones and skin vibrations. J. Acoust. Soc. Am., 29:1059–69.

1958

Pendulums, traveling waves, and the cochlea: introduction and script for a motion picture. Laryngoscope, 68:317–27.

Funneling in the nervous system and its role in loudness and sensation intensity on the skin. J. Acoust. Soc. Am., 30:399–412.

1959

Similarities between hearing and skin sensations. Psychological Reviews, 66:1–22.

Synchronism of neural discharges and their demultiplication in pitch perception on the skin and in hearing. J. Acoust. Soc. Am., 31:338–49.

With J. Lempert. Improvement of sound transmission in the fenestrated ear by the use of shearing forces. Laryngoscope, 69:876–83.

Neural funneling along the skin and between the inner and outer hair cells of the cochlea. J. Acoust. Soc. Am., 31:1236–49.

1960

*Experiments in Hearing.* Translated and edited by E. G. Wever. New York: McGraw-Hill Book Co. 745 pp.

Neural inhibitory units of the eye and skin: quantitative description of contrast phenomena. J. Opt. Soc. Am., 50:1060–70.

Experimental models of the cochlea with and without nerve supply. In: *Neural Mechanisms of the Auditory and Vestibular Systems,* ed. by G. L. Rasmussen and W. F. Windle, pp. 3–20. Springfield: Charles C Thomas, Publishers.

The influence of inhibition on the sensation pattern of the skin and the eye. In: *Symposium on Cutaneous Sensitivity,* ed. by Glenn R. Hawkes, pp. 50–62. Fort Knox, United States Army Medical Research Laboratory Report no. 424.

1961

Pitch sensation and its relation to the periodicity of the stimulus. Hearing and skin vibrations. J. Acoust. Soc. Am., 33:341–48.

Are surgical experiments on human subjects necessary? Laryngoscope, 71:367–76.

Über die Gleichartigkeit einiger nervösen Prozesse beim Hören und Vibrationssinn. In: *Proceedings of the Third International Congress on Acoustics,* pp. 13–20. Amsterdam: Elsevier.

Concerning the fundamental component of periodic pulse patterns and modulated vibrations observed on the cochlear model with nerve supply. J. Acoust. Soc. Am., 33:888–96.

With E. G. Wever, W. E. Rahm, Jr., and J. H. T. Rambo. A new method of perfusion for the fixation of tissues. Laryngoscope, 71:1534–47.

Abweichungen vom Ohmschen Gesetz der Frequenzauflösung beim Hören. Akustische Beihefte, Acustica, 11:241–44.

1962

The gap between the hearing of external and internal sounds. In: *Biological Receptor Mechanisms,* ed. by J. W. L. Beament, pp. 267–688. (Symposium No. 16, Society for Experimental Biology) London: Cambridge Univ. Press.

Comments on the measurement of the relative size of the DC potentials and microphonics in the cochlea. J. Acoust. Soc. Am., 34: 124.

Can we feel the nervous discharges of the end organs during vibratory stimulation of the skin? J. Acoust. Soc. Am., 34:850–56.

Concerning the pleasures of observing, and the mechanics of the inner ear. In: *Les Prix Nobel en 1961*, pp. 184–208. Stockholm: P. A. Norstedt & Söner, AB.

Synchrony between nervous discharges and periodic stimuli in hearing and on the skin. Ann. Otol. Rhinol. Laryngol., 71:678–92.

Lateral inhibition of heat sensation on the skin. J. Appl. Physiol., 17:1003–8.

1963

Letter to editor and contributors of the Békésy commemorative issue of the Journal of the Acoustical Society of America. J. Acoust. Soc. Am., 35:120.

Hearing theories and complex sounds. J. Acoust. Soc. Am., 35:588–601.

Three experiments concerned with pitch perception. J. Acoust. Soc. Am., 35:602–6.

Concluding remarks of the round table discussion on the frequency analysis of the normal and pathological ear. (Sixth International Congress of Audiology, Copenhagen) International Audiology, 2:26–29.

Interaction of paired sensory stimuli and conduction in peripheral nerves. J. Appl. Physiol., 18:1276–84.

Modification of sensory localization as consequence of oxygen intake and reduced blood flow. J. Acoust. Soc. Am., 35:1183–87.

1964

Rhythmical variations accompanying gustatory stimulation observed by means of localization phenomena. J. Gen. Physiol., 47:809–25.

Olfactory analogue to directional hearing. J. Appl. Physiol., 19: 369–73.

Die gegenseitige Hemmung von Sinnesreizen bei kleinen Zeitdifferenzen. Naturwissenschaftliche Rundschau, 17:209–16.

Sweetness produced electrically on the tongue and its relation to taste theories. J. Appl. Physiol., 19:1105–13.

Duplexity theory of taste. Science, 145:834–35.

1965

The effect of adaptation on the taste threshold observed with a semi-automatic gustometer. J. Gen. Physiol., 48:481–88.

Cochlea mechanics. In: *Theoretical and Mathematical Biology,* ed. by Talbot H. Waterman and Harold J. Morowitz, pp. 172–97. Waltham, Mass.: Blaisdell Publishing Company.

Inhibition and the time and spatial patterns of neural activity in sensory perception. Ann. Otol. Rhinol. Laryngol., 74:445–62.

Temperature coefficient of electrical thresholds of taste sensations. J. Gen. Physiol., 49:27–35.

Loudness recruitment. Transactions of the American Otological Society, 53:85–92.

1966

Taste theories and the chemical stimulation of single papillae. J. Appl. Physiol., 21:1–9.

Pressure and shearing forces as stimuli of labyrinthine epithelium. Arch. Otolaryngol., 84:122–30.

1967

Mach band type lateral inhibition in different sense organs. J. Gen. Physiol., 50:519–32.

Some similarities in sensory perception of fish and man. In: *Lateral Line Detectors,* ed. by P. Cahn, pp. 417–35. Bloomington: Indiana Univ. Press.

Foreword. *Lateral Line Detectors,* ed. by P. Cahn, pp. vii–ix. Bloomington: Indiana Univ. Press.

*Sensory Inhibition.* Princeton: Princeton Univ. Press. 265 pp.

1968

Brightness distribution across the Mach bands measured with flicker photometry, and the linearity of sensory nervous interaction. J. Opt. Soc. Am., 58:1–8.

Problems relating psychological and electrophysiological observations in sensory perception. Perspectives in Biology and Medicine, 11:179–94.

Location of maxima and minima in sensation patterns influenced by lateral inhibition. J. Appl. Physiol., 25:200–206.

Feedback phenomena between the stringed instrument and the musician. Rockefeller University Review, 6:1–9.

Mach- and Hering-type lateral inhibition in vision. Vision Res., 8: 1483–99.

1969

Ein Modell der mechanischen und nervösen Vorgänge des Innenohres. Nova Acta Leopoldina, Nummer 184, 33:103–19.

Similarities of inhibition in the different sense organs. American Psychologist, 24:707–19.

Inhibition as an important part of sensory perception. Laryngoscope, 79:1366–86.

The Doctor of Medicine and the Doctor of Philosophy. (Dr. Julius Lempert Memorial Issue) Arch. Otolaryngol., 90:687–89.

Resonance in the cochlea? Sound, 3:86–91.

The smallest time difference the eyes can detect with sweeping stimulation. Proc. Natl. Acad. Sci. USA, 64:142–47.

1970

Travelling waves as frequency analysers in the cochlea. Nature, 225:1207–9.

Apparent image rotation in stereoscopic vision: the unbalance of the pupils. Percept. Psychophys., 8:343–47.

Enlarged mechanical model of the cochlea with nerve supply. In: *Foundations of Modern Auditory Theory,* ed. by J. V. Tobias, vol. 1, pp. 307–41. New York: Academic Press, Inc.

Success and failure of teamwork in biology and medicine. Perspectives in Biology and Medicine, 14:69–81.

Improved musical dynamics by variation of apparent size of sound source. Journal of Music Theory, 14:141–64.

1971

Localization of visceral pain and other sensations before and after anesthesia. Percept. Psychophys., 9:1–4.

Auditory backward inhibition in concert halls. Science, 171:529–36.

Two different ways of making progress in physics and medicine. In: *Oral-Facial Sensory Motor Mechanisms,* ed. by Ronald Dubner and Yojiro Kawamura, pp. 1–6. New York: Appleton-Century-Crofts.

1972

The missing fundamental and periodicity detection in hearing. J. Acoust. Soc. Am., 51:631–37.

Lines that do not increase their width under a magnifying glass. Proc. Natl. Acad. Sci. USA, 69:885–87.

Mach bands measured by a compensation method. Vision Res., 12:1485–97.

Compensation method to measure the contrast produced by contours. J. Opt. Soc. Am., 62:1247–51.

1973

Sense organs and their sensitivity. Advances in Oto–Rhino–Laryngology, 19:1–30.

1974

Prefatory chapter: some biophysical experiments from 50 years ago. Annual Review of Physiology, 31:1–16.

Introduction, Chapter 1. In: *Auditory Systems, Handbook of Sensory Physiology*, vol. V/1, ed. by W. D. Keidel and W. D. Neff, pp. 1–8. Berlin, Heidelberg, New York: Springer Verlag.