NATIONAL ACADEMY OF SCIENCES

ERNEST GLEN WEVER

1902—1991

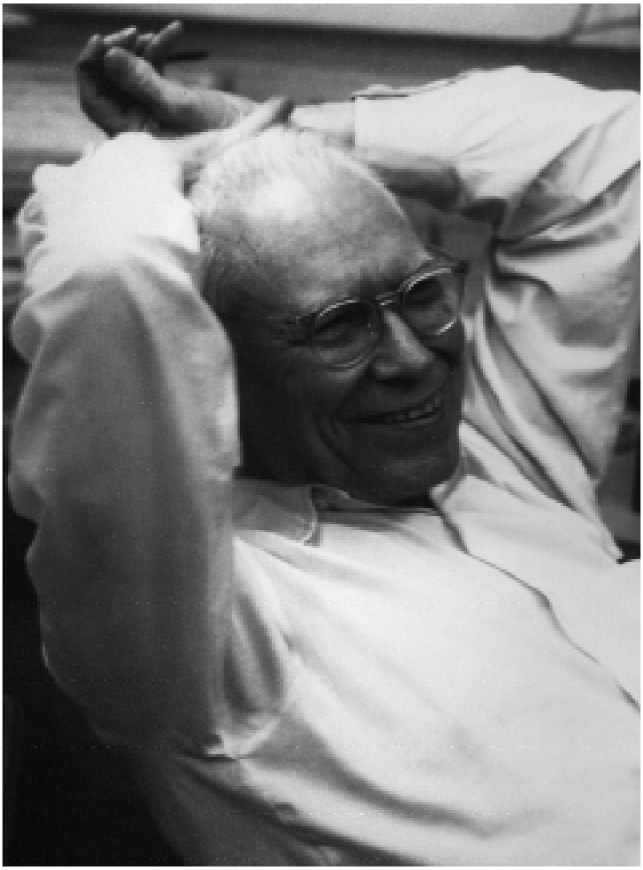
A Biographical Memoir by

JACK VERNON

Any opinions expressed in this memoir are those of the author(s) and do not necessarily reflect the views of the National Academy of Sciences.

Biographical Memoir

COPYRIGHT 1997
NATIONAL ACADEMIES PRESS
WASHINGTON D.C.



ERNEST GLEN WEVER

October 16, 1902–September 4, 1991

BY JACK VERNON

WE WERE DRIVING from Princeton, N.J., to Hibernia, N. J., when I asked Glen Wever, "What do we know about hearing in bats?" He answered, "About all we know is what Donald Griffin has written; that is, they detect and catch their prey by echo location, a term invented by Griffin. We really know nothing about their hearing ability except that it must be amazing; after all, they do with their ears what the rest of us do with our eyes." This conversation took place over forty years ago.

Glen Wever and I were driving to Hibernia to try to locate an abandoned zinc mine that we had heard was the home of hibernating bats. We were on a bat-collecting trip, the first of many to follow, from which we hoped to acquire some bats (Myotis Lucifugus, as it turned out) for experimental purposes. We planned to record the AC cochlear potentials from the bats' inner ears, which, at that time, had never been done. A filling-station attendant in Hibernia directed us to the zinc mine, where we found the entrance blocked with a heavy steel plate and a sign that read "KEEP OUT."

Left to my own devices, I think I would have obeyed the sign, but Glen said, "I think we can just manage to crawl

under that barricade." We proceeded to do just that. One of the keynotes of Glen's life was to bypass barricades—to find ways to get around (or under) those things that stood in the way of his progress. A mere steel plate, fortunately, was not about to deter his appointed round of bat collection.

Once in the zinc mine, which had been carved from solid granite, we found it was exceptionally clean, free of any human debris and filled with cool air. Outside it was a hot July day, but inside the mine it was cool enough to require jackets and gloves. When we had walked about half a mile or so into the mine we began to see clusters of bats hanging from the ceiling. Our plan was to acquire a few bats with which to start our experiments. At this point we had little idea about the anatomy of the bat's ear and reasoned that surgical practice would be required. Upon surveying the clusters of bats Glen suggested that possibly a cluster might represent some sort of family, social or community organization, and that we should take only one bat from each cluster and thus produce as little disturbance as possible to any social organization the bats might have. That is yet another example of how Glen Wever's mind and sensitivity worked.

We returned to Princeton, and the next day began working on the bats. The first thing we discovered was that we had very few surgical tools small enough to be effective with a bat, whose total body weight was 7 grams. In our initial surgical effort I managed to drop a pair of fine pointed jeweler's forceps, which bent one tine so that it laid over the other tine. Glen looked at what I thought was now a useless tool and said, "I bet you have just made a pair of scissors adequate for bat surgery." He was correct; those bent forceps became the mainstay in our subsequent bat surgeries. Investigation of the electrophysiological aspects

of the bat's inner ear revealed that its ear is highly and specifically tuned to 30,000 Hz, which is the primary pitch of this bat's echo location scream.

That episode with the bent forceps illustrates yet another of Glen's many positive and outstanding characteristics. If the needed tool was not available, he made it. Glen made not only tools but other things as well. For example, early on in his career he typed his own manuscripts and quickly discovered that he did not know when he was about to run off the bottom of a page, so he equipped his typewriter with a rotating wheel that would indicate the spacing of the typing according to its page location. Sometime later a typewriter salesman saw the device and shortly thereafter his company advertized the "Page Gage." Did Glen sue or demand royalties from the typewriter company? No, he did not. There was not a litigious bone in his body and thoughts of that sort simply would never occur to him. I once asked him why he did not take the typewriter company to court since it had obviously stolen his idea and was realizing a profit from it. He replied, "But the device still works just fine for me." His original need had been fulfilled and that was as far as he wished to pursue the matter.

Glen Wever's entire being was aimed at investigations and expositions of the ear. He had little or no interest in social activities or, indeed, in any activities that would detract from his investigative goals. Fortunately, for many of us those goals were aimed at the ear and hearing. His first book, *Theory of Hearing*, published in 1949 by Princeton University Press clearly lays out the investigative roadway that Glen was to travel the rest of his life. That book, by the way, was reported to be the first manuscript ever received by Princeton University Press that was totally free of error. Glen was never too busy or too distracted not to be totally accurate and totally complete.

Glen Wever began his investigative life in the early days of electronics, when the radio was new and when it was not possible to go to an electronic supply house or catalog and purchase such things as biological amplifiers or attenuators or anything needed to conduct hearing research. Therefore, he studied electronics, taught himself, and made his own amplifiers and attenuators. Great chunky things they were, driven by automobile batteries, but they were perfect. He found that the noise floor of amplifiers could be greatly reduced by using very precise components within carefully measured tolerances. I don't know for sure, but I would bet that no present-day bioamplifier is any quieter than those made by Glen Wever so many years ago.

Early on in his work he became interested in the microanatomy of the ear as a way to compare different species and different conditions within a given specie. At about that time Stacy Guild at Johns Hopkins had perfected the thin-section celloidin-embedding technique of tissue preparation. Glen spent a month studying with Stacy Guild in order to learn the technique first hand. From that time on, animals studied in his laboratory were characterized by the electrophysiological response of the inner ear as well as the morphology of that ear.

Around 1930 Glen Wever and Charles Bray, both faculty members in the Department of Psychology at Princeton University, discovered the bioelectric signals generated in the inner ear in response to sound stimuli. That discovery started a host of investigations about the inner ear that continue to this day. The discovery of the inner ear's electric potentials is a very special story requiring special attention.

Wever and Bray initially were attempting to record from the auditory nerve of the cat when one of those happy accidents occurred. Their laboratory was in a soundproof

room in the basement of Eno Hall. Their stimulating equipment and the animal preparation (a cat with an electrode in its VIII nerve) were set up in a dark room down the hall from the soundproof chamber in which the listener was located. Cables connected the two areas. The plan was that Glen would speak into the cat's ear while Bray would listen for the nerve responses coming from the speaker located in the soundproof chamber. Glen recalls that Bray came running out of the chamber so excited that he, Glen, could hardly understand a word he was saying. What he said was that he had heard every word Glen had said. The unexpected feature was the faithful reproduction of the human voice and not the expected neurological signals. Clearly the recording of the human voice had come from the cochlea and not from the VIII nerve on which their electrodes had been placed. This event, which was read before the National Academy of Sciences (1930) was the original recognition of the AC cochlear potential, which came to be recognized as the analog production of the inner ear in response to sound stimuli. These AC potentials of the ear also became known as the cochlear microphonic (they should have been designed the "Wever-Bray effect"), a designation that came about as the result of a misunderstanding. E. D. Adrian, a highly respected physiologist, remarked that the signals reported by Wever and Bray were probably artifacts, which he termed "microphonics," like those sounds produced in early radios when one tapped on the tubes of the radio.[1] Actually what Adrian said was, "I conclude that the effect is due to some kind of microphonic action by which vibrations produce changes in the potential between different points in the inner ear." In that same article, Lord Adrian went on to say, "But whatever its explanation, the Wever-Bray effect is certainly a remarkable phenomenon, and it may well prove to be of great importance to theories of

hearing." Despite such statements, the term "Cochlear microphonic" has stuck and is, to this day, in common use. Wever always referred to the electrical potentials of the ear as the "AC cochlear potentials," and in his honor I have always done the same, as do most of his other students. For his work in discovering the bioelectric potentials of the ear he received the first Howard Crosby Warren Gold Medal from the Society of Experimental Psychologists in 1932.

Glen Wever was born in Benton, Illinois. He received an A.B. degree from Illinois College in 1922 and an M. A. and a Ph.D. in experimental psychology from Harvard in 1924 and 1926, respectively. His doctoral thesis was conducted under the leadership and recommendation of E. G. Boring, who, at that time, published a classic paper entitled "Auditory Theory."[2] Interestingly enough, Wever did not do his doctoral thesis in the area of audition but rather in the area of vision. It was a figure-ground investigation utilizing a Gestalt orientation. After graduation he spent a year on the faculty of the University of California at Berkeley, after which he accepted an invitation from Professor Herbert Langfeld to be an instructor in the Department of Psychology at Princeton University.

While at Berkeley, Wever had a student named Stanley Truman who needed a thesis topic, and Glen suggested that he do a figure-ground-type study in audition, wherein subjects were required to make pitch discriminations in the presence of background noise. That study was a pivotal affair for Wever, for in order to have the necessary auditory equipment he contacted Wegel and Lane of Bell Telephone Laboratories in New York, making them aware of the equipment deficiencies in his laboratory. Then when Wever moved to Princeton it was but a short fifty miles to New York to visit Wegel and Lane in person. They provided him much of the electronic equipment he needed to conduct his work.

They provided, on "permanent loan" such things as an audio-oscillator, an audio-attenuator, a loudspeaker, and an audiometer—things Wever desperately needed for his investigations. No doubt Wegel and Lane often looked back on that era with pride, since it was they who made it possible for Glen Wever to do much of the wonderful things he did in the area of hearing.

In 1946 Dr. Julius Lempert, an otologist in New York City, invited Wever to spend one day a week with him to consider hearing problems in humans. That was the beginning of an exposure to a clinical orientation; however, it was limited to New York and did not invade the Princeton laboratory, although it was this orientation that led Wever and Merle Lawrence to extensive studies of the middle-ear mechanism.

Glen Wever remained at Princeton for the rest of his life, rising through the ranks to full professor in 1941. While there he held two distinguished endowed chairs, the first being the Dorman T. Warren Professorship from 1940 to 1950. It was because of Professor Warren that Eno Hall, the first college building in the United States to be exclusively dedicated to psychology, was constructed. The second endowed chair was the Eugene Higgins Professorship from 1950 to 1970, when he became professor emeritus.

During World War II Wever served as a consultant to the National Defense Research Council, where he suggested that sailors being considered for sonar operation be given tests predictive of musical ability. This suggestion reflects the influence of his wife Suzanne Rinehart Wever, a highly skilled musician. The use of this selection procedure, as well as improved training methods, resulted in greatly improved sonar performance. One story has it that Wever told the Navy its selection procedures for sonar operators were so

poor that any suggestion he made would be an improvement.

In 1950 the National Institutes of Health established grants dedicated to the construction of research facilities. One such grant was awarded to Professor Wever, which resulted in the construction of the Auditory Research Laboratories at Princeton. The laboratory, built in the region of Princeton's football stadium, was soon evacuated in order to permit expansion of the stadium. The laboratories were then constructed on the north side of Princeton's Forestall Campus. The unique feature of the Forestall Laboratory was Wever's design. Each laboratory was established as a separate small building rather than being separate rooms in a single building. The concept of separate buildings provided excellent sound isolation, and, in an effort to provide electromagnetic radiation isolation, the outside wall of the internal sound chamber was lined with copper sheeting and the inside wall of its outside chamber was lined in a similar fashion. These chambers provided excellent isolation and conditions for recording the low-voltage electrophysiological signals of the auditory system.

During his lifetime Glen Wever received many awards and honors, starting in 1932 with the first award of the Howard Crosby Warren Gold Medal from the Society of Experimental Psychologists. This award was in recognition of the initial recordings of the AC cochlear potentials of the inner ear. Toward the end of his career he received the Award of Merit from the Association for Research in Otolaryngology, indicating that his contribution to science was not a one-shot affair but rather an ongoing lifetime of contributions. Other awards included the Shambaugh Prize of the Collegium Oto-Rhino-Laryngologicum, the Silver Medal of the Acoustical Society of America, and an honorary degree from the University of Michigan.

In the 1950s Wever was appointed chairman of Princeton's psychology department, a task he found unpleasant. His first and only love was research involving the ear, and the duties of a chairman were viewed as an intrusion into his primary efforts. The politics of academe were of no interest to Glen; indeed, social interactions of any sort were of very slight interest except for those with colleagues where the exchange could be about the ear and hearing.

Wever was not a "joiner"; nevertheless, he was a member of the American Academy of Arts and Sciences, the American Psychological Association, the Society of Experimental Psychologists, the Acoustical Society of America, the American Otolaryngology Society, and the Association for Research in Otolaryngology. He rarely attended the meetings of these societies.

In 1949 Wever published *Theory of Hearing*, which became a primary source of auditory information for many generations of investigators. In 1954 he and Merle Lawrence published *Physiological Acoustics*, which proved to be another critical resource. He worked with Georg von Bekesy (the Nobel laureate) translating Bekesy's manuscript, *Experiments in Hearing*,[3] from German into English. It was in that book that Bekesy (undoubtedly thinking about Glen Wever) suggested that each scientist needs a capable enemy. He said "An enemy is willing to devote a vast amount of time and brain power to ferreting out errors both large and small, and without any compassion. The trouble is that really capable enemies are scarce, most of them are ordinary." That book by Bekesy provided yet another invaluable resource for investigators of the auditory system. Prior to that time Wever's book *Theory of Hearing* had been published. Note that he did not title it "Theories of Hearing"; it is clear that for him there was only one theory, and one has to admit to this day that Wever's theory is the most thorough treatment

of hearing. More modern theories in this area are usually restricted and narrow in scope, dealing with limited aspects of auditory phenomena.

On May 16-18, 1982, a conference was held at Princeton University to honor Glen Wever. The conference was composed of students and colleagues who had been associated with and influenced by Glen Wever. The purpose was to say "thank you" to Glen for all he had done for so many of us. The culmination of the conference was a published volume of the presentations made at the conference.[4]

The conference and book were composed of twenty-three presentations, which ranged in topics from "Five Years of Cochlear Potentials" by Merle Lawrence to "Interpretation of the Sharply Tuned Basilar Membrane Response Observed in the Cochlea" by Shyam Khanna, to "Rate Function in Cutaneous Vibratory Perception" by Carl Sherrick, "Comparative Morphology of Stereocilia" by James Saunders, "Echo Location in Bats" by James Simmons, "Dolphin Hearing and Sound Production" by Sam Ridgeway, "The Vestibular Apparatus and Space Motion Sickness" by Donald Parker, "The Relation Between Noise and Health" by Ernest Peterson, and "Possible Physiological Correlates of Subjective Tinnitus" by Jack Vernon, to name a few. That memorial book contained twenty-one chapters, all but one written by Wever's previous students or colleagues.

In his retirement years Wever continued as a senior research psychologist at Princeton, completing two of an intended trilogy of books. The completed books were *The Reptile Ear* (1978) and *The Amphibian Ear* (1985). The third book was to be on the hearing of fish but was not completed due to health problems.

The Amphibian Ear provides many examples of Wever's ability to organize things and present them in an established and logical manner. He starts the book by explaining

that the word "amphibian" means "both lives"; that is, a life above the water and in air and a life below water, which we generally consider to be impossible. The book contains a very scholarly account of amphibian characteristics, the origin of amphibia, theories of amphibian ancestry, and the function of hearing in amphibia. The experimental methods by which amphibian hearing has been investigated reveal the thoroughness with which Wever undertook tasks of this sort: (1) anatomical description of the hearing apparatus, (2) behavioral observations of the animal's acoustic responses and discriminations, and (3) electrophysiological responses of the inner ear. Most investigators would have been content with any one of these three approaches but not Glen; for him it was necessary to do the complete evaluation. The traditional view of the development of the vertebrate ear held that the course of evolution began with the fishes, extended through the amphibians to the reptiles, and then proceeded to birds and mammals. As a consequence of Wever's book, *The Amphibian Ear*, the traditional evolution view will be challenged. We will always consider it a serious loss that Wever was unable to finish his book on the hearing of fish.

Glen Wever was a dedicated scientist in the finest sense of that word, and he will be greatly missed by those of us who knew him best.

NOTES

1. *J. Physiol.* 71(1931):28-29.
2. E. G. Boring. Auditory theory.
3. G. von Bekesy. *Experiments in Hearing.*
4. R. Fay and G. Gourevitch, eds. *Hearing and Other Senses: Presentations in Honor of E. G. Wever.* Groton, Conn.: Amphora Press, 1983.

SELECTED BIBLIOGRAPHY

1930

With C. W. Bray. Action currents in the auditory nerve in response to acoustical stimulation. *Proc. Natl. Acad. Sci. U.S.A.* 16:344-50.

With C. W. Bray. The nature of acoustic response: The relation between sound frequency and frequency of impulses in the auditory nerve. *J. Exp. Psychol.* XIII:373-87.

1949

Theory of Hearing. New York: Wiley.

1954

With M. Lawrence. *Physiological Acoustics*.

1955

With J. A. Vernon. The threshold sensitivity of the tympanic muscle reflexes. *Arch. Otolaryngol.* 62:204-13.

1956

With J. A. Vernon. Sound transmission in the turtle's ear. *Proc. Natl. Acad. Sci. U.S.A.* 42:292-99.

1957

With J. A. Vernon. The auditory sensitivity of the Atlantic grasshopper. *Proc. Natl. Acad. Sci. U.S.A.* 43:345-48.

1960

With J. A. Vernon. The problem of hearing in snakes. *J. Aud. Res.* 1:77-83.

1961

With J. A. Vernon. Cochlear potentials in the marmoset. *Proc. Natl. Acad. Sci. U.S.A.* 47:739-41.

With J. A. Vernon. Hearing in the bat, Myotis Lucifugus, as shown by the cochlear potentials. *J. Aud. Res.* 2:158-75.

1963

With J. A. Vernon, E. A. Peterson, and D. F. Crowley. Auditory responses in the Tokay Gekko. *Proc. Natl. Acad. Sci. U.S.A.* 50:806-11.

1965

The degenerative processes in the ear of the Shaker mouse. *Ann. Otol. Rhinol. Laryngol.* 82:277-80.

1978

The Reptile Ear: Its Structure and Function. Princeton, N.J.: Princeton University Press.

1985

The Amphibian Ear. Princeton, N.J.: Princeton University Press.