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WILLIAM DUWAYNE NEFF
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A Biographical Memoir by

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William D. Neff

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BY JAY M. GOLDBERG AND NELSON Y.-S. KIANG

WILLIAM DUWAYNE ("DEWEY") NEFF WAS a plainspoken Midwesterner, who became committed to the study of hearing as an undergraduate and maintained that commitment throughout his career. Best known for his use of the ablation method to study the functions of the various levels of the auditory pathways, he combined behavioral, electrophysiological, and neuroanatomical techniques to define deficits in auditory function more elaborate than simple audiometry. Rather than concocting intricate theories, he was content to follow experimental facts wherever they led. Because of his sound judgment and no-nonsense style, he was asked to provide advice to numerous professional and governmental agencies. His straightforward, nonpedantic approach to science appealed to graduate students. It may very well be that the large number of graduate students that he trained is one of his most enduring legacies. Many of these graduate students went on to distinguished careers and, following in his footsteps, trained many successful scientists.

Dewey Neff was born on October 27, 1912, in Lomax, Illinois, to Lyman Neff and Emma Jacobson. A sister named Jenona had been born a year earlier. Dewey's father, like his own father and brothers, was a skilled carpenter, but for much of his adult life he worked as a lumberyard manager. The family spent the first 10 years of Dewey's life in Lomax, a small town on the Illinois side of the Mississippi River between Burlington, Illinois, and Fort Madison, Iowa. After short stays in Yates City and Brereton, Illinois, and a trip to South Dakota, the family settled in Freeport, Illinois, where the children graduated from the local high school (Jenona in 1929 and Dewey in 1930). In a privately published memoir (L. M. Neff, 1969) their father commented on the fact that the children attended schools in many different towns: "I always thought [this] was good for them. They learned to meet strangers and adapt themselves to changing conditions."

Dewey entered the University of Illinois in 1930 with the intention of becoming an architect. In those depression years he had to work his way through college, including spending one year working full time. As a result, it took him six years to complete his undergraduate education.

THE GRADUATE YEARS

During his undergraduate years, Dewey came under the influence of Elmer A. Culler, a professor of psychology, who persuaded him to continue as a graduate student in experimental psychology. Culler was a well-known physiological psychologist, whose research combined studies of animal learning and hearing. When Culler moved from Illinois to the University of Rochester, he persuaded Dewey to move with him. During his stay at Rochester, Dewey made lasting friendships with fellow graduate students Karl Kryter and J. C. R. Licklider, both of whom went on to distinguished careers of their own.

When Dewey began his graduate work, the dominant question facing hearing researchers was how tonal frequencies were represented in the cochlea and in central auditory pathways. Dewey was intrigued by a report from the Johns Hopkins University neurosurgeon, Walter E. Dandy (Dandy, 1934) on the hearing losses resulting from inadvertent lesions to the auditory nerve when the vestibular nerve was cut to relieve the symptomss of Ménière's disease. Hearing could be impaired at high frequencies, but never at low frequencies.

Dewey realized the potential import of Dandy's findings for the place theory of hearing, in which near-threshold tones of any particular frequency were supposed to activate only a restricted and specific set of auditory nerve fibers. Therefore, the question arose whether, in fact, Dandy had ever sectioned the hypothesized low-frequency fibers. The lack of histological controls prevented the question from being resolved in humans. For his doctoral dissertation, Dewey partially cut the auditory nerve in several cats and, compared their hearing preoperatively and posoperatively. The behavioral testing was based on a method developed by Brogden and Culler (Brogden and Culler, 1936). In addition, cochlear electrophysiology was performed at the time of sacrifice and postmortem histology was examined in collaboration with Prof. E. G. Wever of Princeton University. Dewey's results in cats were similar to those of Dandy's in humans. Partial section of the auditory nerve could produce a selective high-frequency hearing loss, but never one confined to low frequencies. The histology provided a rationale for the behavioral findings. In all animals, nerve fiber degeneration started at the cochlear base, where high frequencies are represented, and extended for varying distances toward the apex, the region most sensitive to low frequencies. There was no instance of restricted apical degeneration. From electrophysiology Dewey concluded that cochlear microphonics, which are now recognized to arise from hair cells, could be spared even in the virtual absence of innervating nerve fibers. World War II delayed full publication of the research until 1947. (Neff, 1947; Wever and Neff, 1947).

Dewey's results left two questions. (1) What would be the consequence of cochlear lesions restricted to the apex? (2) Why did partial sections of the auditory nerve in his experiments never produce selective apical nerve degeneration? In an attempt to answer the first question, Schuknecht and Neff (Schuknecht and Neff, 1952) found that cochlear lesions confined to the apex resulted in modest hearing losses limited to low frequencies. A potential answer to the second question was suggested by Kiang (Kiang, 1979) at a conference organized by Dewey's graduate students and postdoctoral trainees to honor him. Kiang speculated that Dewey's lesions were too medial. As such, they passed through the cochlear nucleus, rather than the auditory nerve and were located so as to sever the high-frequency innervation of the nucleus, but not the more laterally situated low-frequency innervation.

WARTIME

Following completion of his graduate work, Dewey was appointed as a research associate at Swarthmore College, where he collaborated with the famous Gestalt psychologist Wolfgang Köhler. The attack on Pearl Harbor occurred shortly after the start of Dewey's second year at Swarthmore. Within the month Dewey resigned his position and joined the Underwater Sound Laboratories in New London, Connecticut, where he worked on the selection and training of submarine crews (Cronbach and Neff, 1949) and auditory discrimination in sonar detection (Neff and Thurlow, 1949).

THE UNIVERSITY OF CHICAGO

In 1946 Dewey joined the faculty of the Department of Psychology at the University of Chicago. This was an exciting time at the university. A team led by Enrico Fermi had made important contributions to the Manhattan Project, including the first demonstration of a sustained nuclear reaction. Immediately after the war, Edward Teller returned to the University from Los Alamos and Harold Urey, a Nobel laureate in chemistry, came from Columbia University. Paul Weiss, a professor of zoology, was doing pioneering studies in developmental neurobiology, including the first demonstration of axoplasmic flow. Roger Sperry, having already done his limb re-innervation and optic tectum studies in Weiss's laboratory, was returning to the university after a postdoctoral fellowship with Karl Lashley at Orange Park. Ralph W. Gerard was a professor of physiology in whose laboratory pioneering work with microelectrodes was taking place. Kenneth S. Cole, having made fundamental observations on action potentials in the giant squid axon, was appointed a professor of biophysics and was perfecting electronic methods needed to control the voltage and current across the nerve membrane. Heinrich Klüver and Stephen Polyak were located on the top floor of Culver Hall, a musty old building. Klüver was continuing his studies of the behavioral effects of temporal lobe lesions in monkeys—the Klüver-Bucy syndrome—while Polyak, having completed his monumental monograph on the vertebrate retina, was now working on an even more ambitious monograph dealing with the entire visual system.

At the same time, a different breed of graduate student was arriving on campus: war veterans financed by the GI Bill. Compared with graduate students before or since, they were older and more mature, sobered by their war experiences. Many were married and already raising families. They had sublimated their personal agendas to the war effort and now wished to finish graduate school and begin their professional careers.

On arriving at the University of Chicago, Dewey taught a summer course in physiological psychology attended by some of these students. Here Dewey could expound his view that a multidisciplinary approach, then practiced in only a few laboratories, was required to make progress in hearing research and, more generally, in brain research. His own doctoral research had exemplified this perspective, combining behavioral testing, electrophysiology, and neuroanatomy. In addition, Dewey was of the opinion that to understand the functions of higher auditory centers, one had to expand the behavioral testing of animals beyond the measurement of hearing thresholds. Here he was inspired by work in the visual system, especially that done by Lashley and Klüver.

Dewey and the other psychologists doing animal research were assigned laboratory space in a cockroach-infested, two-story, prefabricated wooden structure, officially known as the Laboratory of Physiological Psychology, but commonly referred to as the "Prefabs." Dewey set up soundproofed experimental chambers to test animal hearing and histological facilities to prepare tissue for microscopic evaluation of lesions. He established an electrophysiological laboratory in space belonging to the Section of Otolaryngology in Billings Hospital. This was part of a continuing collaboration with otolaryngologists in the Surgery Department, including Chief of Otolaryngology John Lindsay, Henry Perlman and Harold Schuknecht (Lindsay et al., 1953; Schuknecht et al., 1951). Dewey's work with Schuknecht on selective cochlear lesions has already been mentioned and was the start of a lifelong friendship.

As was the case for his mentor, Elmer Culler, much of Dewey's otolaryngology-related research was partly funded through various otological societies. More importantly, Dewey was able to use contacts he had made during his wartime service to secure funding from the Office of Naval Research (ONR). Nowadays most funding for neuroscience research comes from the National Institutes of Health (NIH) or from the National Science Foundation (NSF). The NSF was founded in 1950, and the Extramural Program of the NIH, although started in 1946, became an important source of funding only in the late 1950s. In the early postwar years the Defense Department became a major source of support for university research, and the ONR was a major source of funding for Dewey's work.

Many of the war veterans who were graduate students in psychology chose to do their doctoral research in Dewey's laboratory because he exuded a quiet confidence and displayed a generosity of spirit. He seemed to be a person who knew where he was going and would be happy for others to accompany him. In addition, his multidisciplinary approach to science had an intellectual appeal. With a coherent and, for its time, a well-funded research program, Dewey's laboratory appealed to prospective doctoral candidates as a place where they could successfully learn their craft. As one of his graduate students, Irving Diamond, said at a reunion some 45 years later: "You knew when you came to work in Dewey's lab that you were joining a winning team." As the last of the war veterans finished their graduate studies, Dewey was able to recruit younger, more traditional graduate students. By the time Dewey left the University of Chicago in 1961, he had successfully supervised the doctoral research of over 20 students.

There were usually several graduate students working with Dewey at any one time. Concentrating on ablation studies, Dewey and each student would settle on a thesis topic. It was then the student's responsibility to do the necessary behavioral testing, usually in cats, but in some cases in rhesus monkeys. Audiometric testing was done in a rotating cage, the device devised by Brogden and Culler. For more sophisticated auditory discriminations (e.g., tonal frequency or tonal pattern discriminations) animals were trained in a double-grill box, which required that the animals run between two compartments to avoid shock. Sound localization was studied in a semicircular arena in which the animal was trained, when released from a restraining box, to go to one of two food wells behind which a buzzer had sounded before release. Once an animal had reached a high level of performance, an ablation of some selected part of the auditory system was done under sterile surgical conditions. Dewey usually did the surgery with the student assisting. After a postoperative recovery, typically a few weeks to a month, the animals were retested and, if necessary, retrained to see if they could once again do the discriminative task. Following postoperative testing, an attempt was made to assess the extent of the lesion with evoked-potential methods, after which the animal was sacrificed and the brain was fixed by transcardiac perfusion as the first step in histological processing.

The main topic of interest for Neff and his students was the function of the auditory cortex, although work was also done on lower levels of the auditory pathways. The extent of cortical lesions was based on electrophysiological mapping done by Clinton Woolsey and his colleagues (Woolsey, 1960), among others. A major conclusion of the research was that animals were still able to make simple discriminations after removal of all known auditory cortical areas. This had already been suggested by Harlow Ades and his colleagues, who showed that hearing thresholds (Kryter and Ades, 1943) and intensity differential limens (Raab and Ades, 1946) were unaltered in animals after cortical ablations. Work in Dewey's group showed that frequency discriminations could be relearned after very large cortical removals (Butler et al., 1957), but the ability to perform more complex tasks, including tonal pattern discriminations (Diamond and Neff, 1957; Diamond et al., 1962) and sound localization (Neff et al., 1956) were permanently compromised. Even the simpler tasks, which could presumably be accomplished by lower auditory centers, had to be relearned after the cortical lesions.

The results demonstrated that in the absence of cortical receiving areas, the auditory system still has impressive capabilities. That trained discriminations were lost after cortical removals might imply that cortical processing has a ubiquitous role when the entire system is intact. The definition of that precise role still remains elusive. In addition, even permanent deficits may be related to the behavioral tasks used to demonstrate discriminative ability, rather than to the sensory discrimination per se. For example, later work showed that animals, after cortical removals, are capable of indicating the location of a sound by unlearned orientation head movements (Thompson and Welker, 1963; Poon, 1979) or simple learned responses (Heffner and Masterton, 1975) even though they are unable to walk toward the position of a previously presented sound (Neff et al., 1956; Heffner and Masterton, 1975). It remains unresolved as to whether this last deficit reflects a defect in sensorimotor integration, short-term memory, or attentiveness/distractibility.

Consistent with his belief in a multidisciplinary approach to the neurosciences, Dewey was instrumental in the founding in 1955 of the degree-granting Section of Biopsychology in the Biological Sciences Division. To be enrolled in the Biopsychology Section, graduate students had first to be admitted by the Psychology Department, which was in the Social Sciences Division. Once enrolled, the student's curriculum and research had a large biological sciences component and the Ph.D. was awarded in the Division of Biological Sciences. The philosophy of the program as stated in the university announcements was as follows:

> It is expected that the research [person] trained in biopsychology may . . . devote . . . attention to problems falling between the discipline of psychology and the traditional disciplines, such as physiology, anatomy and zoology. The student is expected, therefore, to become substantially grounded in the physical and biological sciences, in addition to the general field of psychology. Emphasis is placed . . . upon understanding the role of neural and extra-neural mechanisms of the internal environment in the regulation of behavior.

This nascent neurosciences program served as the focus for the training of his graduate students while Dewey remained at Chicago and continued well into the 1990s.

BOSTON

After spending 15 years in Chicago, Dewey was persuaded to move in 1961 to Bolt, Beranek and Newman (BBN), a high-technology company founded in 1948 by two Massachusetts Institute of Technology (MIT) professors in acoustics, Richard Bolt and Leo Beranek, and a former student of theirs, Robert Newman. Originally an acoustical consulting company, BBN obtained many prestigious commissions in architectural acoustics, including the innovative Kresge Auditorium at MIT, the Shed at Tanglewood, and Avery Fisher Hall at Lincoln Center. By the late 1950s the company was looking to diversify. Dewey's graduate student friends Karl Kryter and J. C. R. Licklider had been recruited to the company. Both had changed their interests from their original training in auditory physiology and psychophysics. Kryter had become an expert in the effects of noise on human performance (Kryter, 1970) while Licklider grew interested in the relation between humans and computers and is credited with helping to develop computer networking, which eventually led to the Internet (Waldrop, 2001).

In recruiting Dewey the company had hoped to expand into the field of auditory physiology. Dewey brought with him two of his recent graduate students, Norman Strominger and Philip Nieder. They set up an experimental suite with a surgery, animal facilities, and testing rooms, and began several promising experiments. Unfortunately, at this time the federal government decided not to support basic research at commercial companies. Since Dewey's research in a corporate environment depended on federal funding, it was clear to him that he had to move on. In 1963 he welcomed the opportunity to join the faculty of Indiana University at Bloomington. The next year he was made director of the newly formed Center for Neural Sciences.

INDIANA UNIVERSITY

In his new position Dewey faced two challenges: (1) to build the Center for Neural Sciences and (2) to reestablish his research program. Dewey attracted several people to the center: Jorgen Fex, an auditory physiologist who pioneered the study of auditory efferents, came from the Karolinska Institute after stints in Australia and the National Institutes of Health; Conrad Mueller, a visual scientist best known for his work on Limulus eye, came from Columbia University; Willem van Bergeijk, a physicist interested in the evolution of hearing, arrived from Bell Laboratories; Ilsa Schwartz, an auditory neuroanatomist, came from a postdoctoral fellowship at Albert Einstein Medical School; and Boyd Campbell, a comparative neuroanatomist, moved from Walter Reed Army Medical Center. Through no fault of Dewey's, the center did not flourish. Van Bergeijk met an untimely death. Fex left to become director of the Laboratory of Neuro-otology at the National Institutes of Health. Schwartz left to take an offer at the University of California, Los Angeles. Campbell left to resume clinical training. Of the people Dewey recruited, only Mueller remained at Indiana University.

Dewey did resume his own research. With his first Indiana graduate student, J. I. ("Pete") Casseday, he studied the role of acoustic commissures in sound localization. Building on the graduate research of Colston Nauman Moore, done at Chicago, they were able to show that sound localization was unperturbed by section of the corpus callosum or the commissure of the inferior colliculus, but was impaired by section of the trapezoid body, the main fiber bundle allowing for the integration of binaural inputs in the superior olivary complex (Moore et al., 1974; Casseday and Neff, 1975). Two other graduate students worked with Dewey on studies of relatively simple auditory behaviors. Paul Poon confirmed that animals could indicate the location of a sound by unlearned orientation head movements (Poon, 1979), while C.-K. ("Joseph") Chan defined some of the brain stem pathways involved in various acoustic reflexes (Chan, 1983).

Dewey summarized his own studies on auditory cortex in a brief review (Neff, 1977) and wrote a comprehensive survey of behavioral studies in the auditory system (Neff et al., 1975).

NATIONAL SERVICE AND AWARDS

In addition to his wartime service Dewey served for a year (1953-1954) in London as a scientific liaison officer for the Office of Naval Research. He was a long-standing member of the Committee on Hearing and Bioacoustics of the National Research Council, as well as a member of the Executive Council of the Acoustical Society of America and of the Psychonomics Society. He served on the Editorial Boards of the *Journal of Neurophysiology* and the *Annual Review of Psychology*. Along with Wolf Keidel, he edited volume V ("Auditory System") of the *Handbook of Sensory Physiology*. He was the sole editor of a series, *Contributions to Sensory Physiology*, which published reviews on sensory processing; eight volumes were published between its founding in 1965 and 1983. In recognition of his contributions, Dewey was elected to the National Academy of Sciences in 1964 and the American Academy of Arts and Sciences. He received the Annual Award of the Beltone Institute for Hearing Research and the Award of Merit of the Association for Research in Otolaryngology.

IN SUMMARY

During Dewey's professional career, much of experimental psychology moved from emphasizing speculative doctrines, as exemplified by various learning theories, to obtaining more empirical descriptions of the brain, behavior, and the relation between the two. He and his students never established a school of thought wedded to specific dogmas but concentrated on obtaining rigorous experimental results with proper controls and making limited generalizations. A list of his graduate students at Chicago and Indiana and the titles of their Ph.D. dissertations are included at the end of this memoir, and it will be evident that they moved in many directions, contributing in diverse ways to the neurosciences.

On balance, one of Dewey's most lasting contributions may be his students. He created an environment where young people could find themselves and develop their individual strengths. He was patient, encouraging, and available to members of his laboratory including students, technical staff, and visitors. The comforting atmosphere universally felt by the people who worked with him was directly related to his social skill in providing education under the guise of friendly chats. He was able to attract some of the best students available and they always benefited from his relaxed yet rigorous instructional style. These personal qualities also made him a highly regarded, informed advisor to his peers and to a variety of scientific organizations.

Dewey had a daughter, Carol, and a son, Peter, by his first wife, Ernestine, a professor of English, and a total of five grandchildren. His second wife, Palmer, contributed to auditory research by studying the effects of muscular dystrophy on the middle-ear reflexes. His professional family was large and his influence remains strong on all who were fortunate enough to know him.

DOCTORAL DISSERTATIONS OF STUDENTS TRAINED BY W. D. NEFF

University of Chicago

Arnott, G. P. Impairment following ablation of the primary and secondary areas of the auditory cortex, 1953.

Butler, R. A. The role of the auditory cortex in frequency discrimination, 1951.

Diamond, I. T. The function of the auditory cortex: The effect of ablation of the auditory cortex on the discrimination of temporal frequency patterns, 1953.

Gerken, G. M. The evoked electrocortical response to acoustic stimulation and its relation to behavioral conditioning, 1959.

Goldberg, J. M. Frequency discrimination after central nervous system lesions, 1960.

Hahn, J. F. Effects of partial ablations of visual areas I and II on visual form discrimination in the cat, 1952.

Hind, J. E. An electrophysiological study of tonotopic organization in the auditory cortex of the cat, 1952.

Jerison, H. J. Effect of auditory cortex ablation on tone pattern discrimination in the rhesus monkey, 1954.

Kennedy, T. T. K. An electrophysiological study of the auditory projection areas of the cortex in monkey (Macaca mulatta), 1955.

Kiang, N. Y.-S. An electrophysiological study of cat auditory cortex, 1955.

Lindquist, S. E. Stimulation deafness: A study of temporary and permanent hearing losses resulting from exposure to noise and to blast impulses, 1949.

Nauman, C. Sound localization: The role of the commissural pathways of the auditory system of the cat, 1958.

Nieder, P. C. Electrophysiological recording and stimulation studies of the auditory system of unanesthetized cats, 1960.

Odoi, H. An investigation into the functions of the visual cortical areas in the cat, 1951.

Oesterreich, R. E. The role of higher neural auditory centers in the discrimination of differential sound intensities, 1960.

Rosner, B. S. Higher auditory nervous centers, 1950.

Stoughton, G. S. S. The role of the cortex in retention of a conditioned response to auditory signals, 1954.

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