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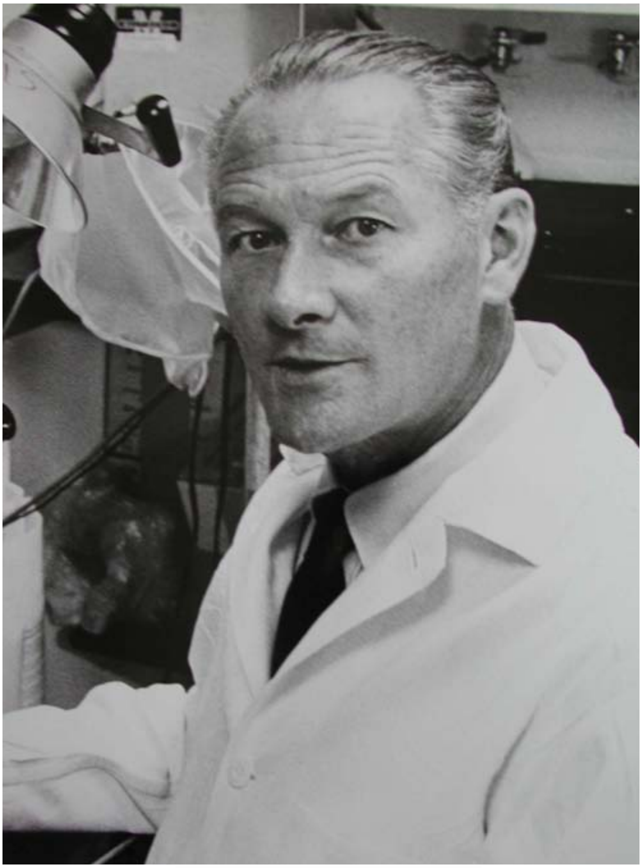

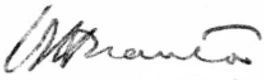

WALLE J. H. NAUTA

June 8, 1916–March 24, 1994

BY EDWARD G. JONES

WALLE NAUTA WAS ONE of the leading neuroanatomists of his generation and a key figure in neuroscience history as a consequence of his development of a revolutionary technique for tracing connections in the nervous system. It was a technique that dominated the field of neuroanatomy at a time when it was forming one of the seminal influences in the rise of neuroscience as an integrated discipline.

Nauta came from that once large but now almost vanished group of Dutchmen that for centuries had made its home in the East Indies. He was born on June 8, 1916, in Medan, Sumatra, a thriving commercial center on the Malacca Strait. His father, from Leiden, had gone there as a missionary of the Dutch Reformed Church but had soon turned to issues of public health, education, and better governance for the Indonesian people and it was into this milieu that Nauta was born. As was typical, he was sent to Holland for his later elementary schooling. The whole family returned to Holland in the late 1930s, thus escaping internment during the Japanese occupation of the East Indies during World War II. Reportedly, Nauta was never a particularly engaged student until he entered medical school at Leiden University, where he found his métier.

By 1937 he had completed the preclinical part of his medical training at Leiden and before proceeding to the clinical years he served for two years as a student assistant in the Anatomy Department. It was there that his interest in neuroanatomy began. He was commencing his clinical rotations in 1940 when the German army occupied the Netherlands. On completing his clinical studies in 1942, he was about to return to an instructorship in anatomy when Leiden University was closed by the occupying authorities on account of its being a hotbed of subversion. He therefore received his qualifying medical degree from the State University of Utrecht and began to work in the Pharmacology Department there. It was at this time that he married Ellie Plaat, another Dutch Indonesian who had been stranded in the Netherlands without resources by the outbreak of war. In order to support herself she had become a nurse. After graduation and until 1946 Walle Nauta was both a practicing physician and a researcher at the University of Utrecht. The war years were periods of great hardship and want for all Dutch citizens. As a physician, Nauta was fortunate in having a permit that enabled him to pass beyond checkpoints and thus treat farmers in the countryside in return for food. But it was still a period of great privation. At one point in the lab, where he had begun studying the effects of hypothalamic lesions on sleep in rats, supplies ran out and the rats had to be fed with milk from Mrs. Nauta, who was at that time nursing their first child. His doctoral thesis was completed and the degree awarded in 1945.

The Nautas, like all the Dutch people, suffered not only hunger but also indignity and sometimes worse at the hands of the occupying forces. Despite these experiences, Walle Nauta never stereotyped individual Germans, and it was typical of him that he and his family at the end of the war protected the local German administrator—who had turned a blind eye to the Nautas' harboring of a Jewish girl for most of the war—until his bona fides could be established and safe passage back to Germany secured. For protecting that Jewish girl the names of Ellie and Walle Nauta are inscribed on the Wall of the Just in Jerusalem. In a reversal of fortunes the Nautas were to send care packages to the German administrator after his return to his homeland.

At the end of the war Nauta, now again at Leiden and in the Anatomy Department, contemplated a career in ophthalmology but felt that the circumstances prevailing at that time precluded this, and so he sought a permanent position in anatomy. He claimed that as a student assistant at Leiden he had been attracted to the hypothalamus by the work of Walter R. Hess on the sleep-waking cycle, by Philip Bard's studies of "sham rage," and by the mounting evidence for its endocrine and neurosecretory relationships. And he recognized that many of the issues raised by these reports demanded anatomical answers that could not be pursued with contemporary neuroanatomical techniques. His fluency in several languages gave him the opportunity to look for a position beyond the Netherlands, and in 1947 he was appointed to a lectureship at the University of Zürich, Switzerland. While many might imagine that it was the presence in Zürich of Walter Hess—perhaps the most prominent investigator of the hypothalamus at that time—that had attracted Nauta, Hess in fact had rejected Nauta's work as lacking behavioral relevance, and Nauta became a lecturer in the Department of Anatomy under the direction of Professor Gian Töndury.

In his four years at Zürich Nauta established himself as a very popular teacher, something that was to characterize him for the remainder of his career and something that was particularly important in Zürich, since his income depended upon student attendance at his lectures and labs. But it was also here that his obsession with developing an improved neuroanatomical tracing technique came to the fore. The direct investigation of neural connections in the hypothalamus, in which most fiber tracts are not myelinated, had always been hampered by the lack of a practical experimental method for revealing unmyelinated fibers belonging to particular functional systems. At the hands of earlier neuroanatomists such as Cajal, the study of normal fibers impregnated by the Golgi technique had yielded some basic information on local connectivity; but the sheer tangle of fibers in their fine meshworks in the hypothalamus made imperative a more selective technique for labeling fibers that began or ended among identified neuronal groups, some of them—such as the hippocampus—far removed from the hypothalamus. For nearly three-quarters of a century the identification of fiber tracts experimentally had meant placing a surgical lesion in one part of the brain of an animal and then following the anterograde (Wallerian) degeneration of axons away from the cell bodies affected by the lesion, or identifying the cells projecting their axons to the region lesioned by their retrograde reaction to destruction of their axon terminations. Unfortunately, in the 1940s the single available anterograde stain—that of Marchi—revealed only the degenerating myelin sheaths of myelinated fibers, which were generally lacking in the hypothalamus, and the cells of origin of many fiber systems afferent to or within the hypothalamus itself were protected from retrograde degeneration, probably because of their widespread axon collaterals. What was needed was a stain that would selectively pick out degenerating axoplasm, hopefully against a background in which staining of normal fibers unaffected by the experimental lesion was suppressed. In this way any fibers, myelinated or unmyelinated, could be traced from the point of lesion to their regions of termination. It was to this that Walle Nauta assiduously applied himself during his years in Zürich. Fortunately, he enjoyed both enormous popularity as a teacher and the unstinting support of Professor Töndury, because, from the point of view of publications, it was far from a productive enterprise.

The Nauta method, as we all came to call it, had its origins in the reduced silver methods of Bielschowsky and Cajal, in which metallic silver is deposited in axons in thin histological sections by reduction of a weak solution of silver nitrate. Regrettably, this lacks specificity, and all processes of all nerve cells, axons and dendrites, are impregnated. A modification—that of Paul Glees—described in 1946, could reveal the endings of those fiber systems in which the terminal boutons on degenerating axons enlarged and assumed a ring-like configuration as the result of what was later revealed as a neurofilamentous hyperplasia. However this technique did not suppress staining of that obscuring mass of normal fibers, and was plagued with false positives. Nauta had had some success in identifying degenerating terminal ramifications with other forms of silver stain (1947), such as that of Bodian (1936) but he saw in the Bielschowsky method, in which silver is precipitated from an unstable ammoniacal salt, a better chance of revealing degenerating fibers in their entirety (1993). The Nauta stain in its first prototype (1951) did reveal quite clearly the fragmenting axons undergoing anterograde degeneration, but it suffered from a failure to suppress the co-staining of the intact and still obscuring normal fibers. The suppression of the normal fibers was to come in a later iteration (1952; 1954,2; 1955), in which by mordanting the sections in potassium permanganate and potassium bisulfite, the later deposition of silver in normal fibers could be suppressed.

In retrospect it became clear that this was obtained at the cost of also suppressing staining of many of the finer degenerating fibers. However, until further improved by other hands (see below), the suppressive Nauta-Gygax method became the method of choice for experimental neuroanatomical studies for more than a decade. That period was one in which all the major connections of the central nervous system were reinvestigated at a level of resolution never before possible.

Nauta's approach in developing his stain seems to have been largely empirical and to have consisted of little more than trying out again and again different combinations of oxidizing and reducing agents both before and during the silver reduction phase. Serendipity helped when one day an unusually successful result was traced to the use of formalin from an old bottle in which the concentration of formic acid would have been particularly high. Citric acid, for unknown reasons, also proved to be advantageous, especially in slowing down the rate of silver precipitation so that the background of the sections remained transparent under the microscope. Nauta was assisted in his attempts to understand the mechanisms of his stain by Lloyd F. Ryan, a U.S. Air Force major, later the European project manager for a General Electric Company defense contract, and a skilled photographer; and by Paul A. Gygax, a doctoral student in organic chemistry at the Swiss Federal Institute of Technology and later a chemist with the I. G. Farben Company, but it is probably fair to say that the mechanism for achieving selective suppression of one set of fibers and enhanced staining of another has never been satisfactorily elucidated. Nauta himself once remarked to the author of this biographical sketch that only Gygax understood it. I recall a student of mine invariably bowing three times in the direction of Boston before embarking on the silver deposition phase of the stain. Whether this was respect, disrespect, or merely superstition was never quite clear.

Knowledge of the stain began quickly to leak out and Nauta's demonstration of it at a meeting in Paris was met with an enthusiastic response in anticipation of the enormous possibilities it offered for a much higher resolution of neuroanatomical connectivity than had previously been available. On the strength of this he was invited by David McKenzie Rioch—who was at the Paris meeting and was forming the Research Division of Neuropsychiatry at the recently renamed Walter Reed Army Institute of Research in Washington, D.C.—to visit the division, and after a successful visit to join it as an investigator. This Nauta did in 1952, remaining there until moving to the Massachusetts Institute of Technology in 1964. During Nauta's time at Walter Reed and under the direction of Rioch, the Division of Neuropsychiatry became remarkable for the breadth and quality of its research; from it emerged some of the most distinguished neuroscientists of the recent past. Among those who were there during Nauta's time were John Boren, Joseph Brady, Boyd Campbell, Sven Ebbesson, Ford Ebner, Michael Fuortes, Robert Galambos, William Hodos, David Hubel, Harvey Karten, JacSue Kehoe, John Mason, William Mehler, James Petras, George Moushegian, Enrique Ramón-Moliner, Felix Strumwasser, and Eliot Valenstein. Many of these worked in Nauta's laboratory; others formed part of a very successful section of neurophysiology.

It was after moving to Walter Reed that Nauta's first papers on neural connectivity, as carried out with his new technique, began to appear. The first, with one of his Zürich colleagues, Verena Bucher, on efferent connections of the visual cortex in the rat came in 1954; his seminal paper on the distribution of the fibers of the fornix in the rat came in 1956. By this time the technique was coming into widespread use and it was to remain the principal method of experimental neuroanatomy until superseded by methods based upon axoplasmic transport in intact axons that came into use in the 1970s. Among the improvements made by others were those that gave enhanced visualization of the terminations of a degenerating axonal system, one of the most significant of them being made by Robert P. Fink and Lennart Heimer working in Nauta's laboratory at MIT and derived in large part from the original nonsuppressive Nauta-Gygax technique (Fink and Heimer, 1967).

Nauta's own output of publications was relatively small but all were influential and some of the most important appeared as chapters in books rather than as research reports. It would seem that at Walter Reed many experiments were done that never found their way into major publications. Perhaps the fact that there were relatively few publications was determined not only by a distaste for the customary rush to publication but also by a meticulous and perfectionist approach to writing that made the preparation of papers for publication unusually laborious.

Nauta's early papers commonly came at key moments when the field was ready for an examination of the connections of a particular part of the brain, and these publications served as an impetus to other work and as fundamental accounts against which all other studies had to be measured. His work on the distribution of the fornix (1956,1), on the connectivity of the amygdala (1956,2; 1961; 1962) and basal ganglia (1966,1), and on the spinothalamic tract (1960,2) all stand in this category. Some were published as solo authored papers, others with his associates at Walter Reed, of whom there were many, although not all became coauthors. Later studies on the connections of the habenula, substantia nigra, and basal ganglia, mainly carried out with students, reflected a concentration on the motor system and its relationships with the limbic system and less involvement with the hypothalamus. His broad knowledge, which extended beyond the mammalian brain, was reflected in occasional forays into the field of comparative neuroanatomy as well (1970,1; 1973,2). Many other studies that came out of his laboratory at MIT could probably have justifiably borne his name as a coauthor, but it was typical of him that in invariably promoting the interests of his students even at the expense of his own, his name did not appear.

Recognition, nevertheless, came steadily to Walle Nauta. He was elected to the National Academy of Sciences (in 1967), the American Philosophical Society, and the American Academy of Arts and Sciences, and received a number of honorary degrees from U.S. and foreign universities. He was a recipient of the Karl Spencer Lashley Award of the American Philosophical Society, the Henry Gray Award of the American Association of Anatomists, the Ralph W. Gerard Award of the Society for Neuroscience, and the Bristol Myers Award for neuroscience research. He was a founding member of the Society for Neuroscience and one of its early Presidents (1972-1973); he was a long-standing affiliate and active participant in the Neurosciences Research program in whose symposia and other activities he took great pleasure.

Nauta's approach to the brain was that of a generalist, not as one devoted to any single system, although the limbic system and motor control systems could always be seen as particular interests. His lectures revealed not only an enormous depth of neuroanatomical knowledge but also the capacity to form linkages between the systems of the brain: sensory-motor, motivational, visceral, cortical-subcortical. And he was never averse to promoting research not his own in his public lectures. His broad knowledge was kept fresh by a deep commitment to teaching. Nauta never separated his research, as so many do, from the teaching enterprise. He also remained rooted in medical neuroanatomy, and during his period at Walter Reed he regularly taught in the medical neuroanatomy course at the University of Maryland. His partners in this course were Hans Kuypers, another Dutchman who had been a student at Leiden from the end of World War II, and William Mehler, who were not only intimate friends but two of the premier neuroanatomists of their generation.

When Nauta moved to MIT in 1964 he became professor of neuroanatomy in the Department of Psychology, at that time headed by Hans Lukas Teuber, who had been instrumental in his recruitment. Nauta became Institute Professor in 1973 and remained in that position until his retirement and transfer to emeritus status in 1986. He taught neuroanatomy throughout his time at MIT, and his lectures were extremely popular among graduate students and others. Among those who benefited from his support and tutelage were many of today's neuroscientists, including Robert Beckstead, Valerie Domesick, Patricia Goldman-Rakic, Ann Graybiel, Elizabeth Grove, Susan Haber, Lennart Heimer, Miles Herkenham, Harvey Karten, Christiana Leonard, Gene Merrill, and Gerald Schneider, to name but a few. Nor was his influence unfelt at another institution located across the Charles River. But he seems to have yearned for medical neuroanatomy and was delighted when the joint Harvard-MIT M.D.-Ph.D. program was launched, because it gave him the opportunity to interact again with medical students.

Walle Nauta had a deep sense of social responsibility and obligation to his fellow man but the days of hardship during the Second World War had left their mark on him, and he had little tolerance for those whose sense of entitlement was far greater than their experience of the world.

He was convinced that there was real evil in the world and that it was often necessary to resort to any means, even military force, to overcome it. In this he was apt to be labeled a conservative, but if so, it was a conservatism born of adversity and it belied a deeper sense of humanity.

Walle Nauta enjoyed ships and sailing, possibly on account of his childhood travels to and from Indonesia, and he sometimes claimed that his interest in cross-sectional anatomy derived from his parallel interest in the deck plans of ships and from a family tradition as shipbuilders. The name Nauta is said to be derived from *nauta hollandis*, or Dutch sailor, a reminder of a medieval past when Dutch seamen raided the Baltic forests for timber for shipbuilding. Sailing was always a passion with Walle Nauta. As a young man he received numerous awards for sailboat racing and had he not had to face his medical school examinations in 1938, he would have competed for a place in the Dutch Olympic sailing team. It is claimed that his competitive instincts were never as forcefully revealed as when he was in command of his Thistle-class sailboat in which he raced on outer Boston harbor until well into his sixties. He was still sailing a Sunfish for recreation in his seventies.

Walle Nauta represented a type of neuroscientist that is no longer with us. A classical neuroanatomist with an enormous depth of knowledge who could work on any part of the brain, but one who was also in touch with modern developments in neuroscience and able to cast his neuroanatomical studies in a modern context. With a strong base in medicine, as so few basic scientists have today, he never lost sight either of the necessity of casting one's research in the context of the diseased nervous system. He was perhaps the epitome of nonreductionism, not a prevailing motif in today's neuroscience. Yet his influence was broad, not only on account of his modernizing, almost single handedly, the whole field of experimental neuroanatomy but also because of the influence that he had over so many students and fellow scientists as a collaborator or teacher or as an author of some of the most fundamental papers in neuroscience.

I AM INDEBTED TO DR. Haring J. W. Nauta and Dr. Harvey J. Karten for assistance in preparing this memoir.

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