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DAVID NACHMANSOHN

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A Biographical Memoir by

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DAVID NACHMANSOHN'S scientific lifepath was strongly influenced by his early studies on the biochemistry of muscle in Otto Meyerhof's laboratory. This experience led to an interest in the biochemistry of nerve activity, a field of study to which he would devote most of his scientific life. In so doing, he contributed—perhaps more than any other investigator—to our understanding of the molecular basis of bioelectricity.

David Nachmansohn was born in Jekaterinoslav, Russia (now Dnjetropetrowsk, USSR). His parents came from middle-class families among whom were many lawyers, physicians, and other professionals. Before David and his two sisters reached school age, the family moved to Berlin where they had many relatives. Thus, David's background and education were essentially, if not exclusively, German. His college education was strongly humanistic, with Latin, Greek, literature, and history as mainstays, some mathematics, and the rudiments of physics. Through his readings, perhaps primarily through his reading of the second part of Goethe's *Faust* when he was only seventeen years of age, he became interested in philosophy—so much so that he continued to attend courses and seminars in philosophy even while a medical student at Heidelberg in 1920.

When he entered the University of Berlin in the spring of 1918, David was strongly oriented toward the humanities. After Germany's defeat in World War I, however, the newly established republic faced grave social, political, and economic problems, and David was advised to study medicine, a profession that could provide economic independence. He accepted this advice and became a medical student; but as time went on, he became more and more interested in biology through his avid readings about the lives and scientific accomplishments of Bernard, Pasteur, Helmholtz, Ehrlich, and others. Eventually, he decided to devote his life to biomedical research and after his graduation in 1924 joined the laboratory of Peter Rona at the Charité for training in biochemistry.

The Charité was the university hospital of Berlin University Medical School in whose Department of Pathology Rona directed a division of biochemistry. There, Nachmansohn joined an exceptional company of bright young people: among them, Fritz Lipmann, Hans Adolph Krebs, Rudolph Schoenheimer, Ernst Chain, Karl Meyer, and Hans H. Weber. Nachmansohn's first paper, "Vital Staining and Adsorption," was published in collaboration with Krebs, an endeavor that began a lifelong friendship between the two. Nachmansohn also did some collaborative work with Weber that led to the publication of a paper entitled, "The Independence of Protein Hydration and Ionisation."

At Rona's, he became familiar with the work of the great Dahlem biochemists Meyerhof, Warburg, and Neuberg, which he found fascinating. Weber advised Nachmansohn to go to Otto Meyerhof at the Kaiser-Wilhelm Institut für Biologie in Berlin-Dahlem for further training. But when Nachmansohn approached Meyerhof, the eminent researcher informed him abruptly that he did not accept beginners—a position he reversed after speaking with the young Nachmansohn awhile. In Meyerhof's laboratory, Nachmansohn's postdoctoral contemporaries included Fritz Lipmann, Hermann Blaschko, Francis O. Schmitt, and this author. Karl Lohmann, who later discovered ATP, was Meyerhof's assistant, and Dean Burk was a visiting scientist. Hans Krebs was also in the same building, in Otto Warburg's laboratory. Nachmansohn often mentioned that it was Meyerhof who had had the most profound impact on his later work and scientific outlook.

Nachmansohn joined the Meyerhof laboratory in 1926. At that time, Grace and Philip Eggleton at the Cambridge biochemical laboratory had recently discovered a new phosphorylated compound in muscle they called "phosphagen" because it liberated inorganic phosphate during contraction. Soon thereafter, Fiske and Subbarow at Harvard Medical School showed the new compound to be phosphocreatine in which phosphate is linked to creatine through a phosphoamide bond.

During this period, Meyerhof was interested in the energetics of muscular contraction. He worked to determine, as he had previously with various hexose phosphates, the heat of hydrolysis of phosphocreatine. It proved to be very high—of the order of 10,000 to 12,000 calories per mole—which contrasted with the low heat of hydrolysis of hexose phosphates (1,500 to 3,000 calories per mole). This finding enabled researchers to distinguish between high- and low-energy compounds in metabolism. (Some years later, it was shown that the breakdown of ATP to ADP and inorganic phosphate was the energy-yielding process more immediately related to muscular contraction, whereas the breakdown of phosphocreatine served to resynthesize the ATP. Lactic acid formation, most of which took place after contraction, was—like phosphocreatine breakdown—a recovery process aimed at restoring rapidly the relatively small ATP stores of resting muscle. Finally, the glycogen that gave rise to the lactic acid was resynthesized from lactic acid using the energy released by oxidation of a fraction of the lactic acid produced).

These developments fascinated the young David Nachmansohn and greatly influenced his later work.[1] During his early years in Meyerhof's laboratory, the function of phosphocreatine was unknown, and interest in this compound was very strong. It is therefore not surprising that Nachmansohn was given the assignment of looking for the relations among phosphocreatine breakdown, lactic acid formation, and the tension developed by muscle during isometric contraction in anaerobiosis. He also compared the phosphocreatine content of different kinds of muscle, especially muscles differing in the rapidity of their contraction. He found that rapidly contracting muscles contained much more phosphocreatine than slowly contracting ones, a fact that was consistent with, and in a way foretold, the function of phosphocreatine in muscular contraction.

Nachmansohn vividly described the atmosphere at Dahlem in the 1920s[2] when several Kaiser-Wilhelm research institutes were concentrated in a relatively small area: the Institute of Physical Chemistry, with Haber, Ladenburg, Polanyi, Freundlich, and Bonhoeffer; the Institute of Chemistry, with Beckmann, Willstätter, Otto Hahn, and Lise Meitner; the Neuberg Institute of Biochemistry; and the Institute of Biology, with Meyerhof, Warburg, Goldschmidt, Correns, and Hartmann. The young Nachmansohn was particularly stimulated by the "Haber Colloquia" in which Fritz Haber, the discoverer of the process for conversion of nitrogen and hydrogen into ammonia, attempted to bridge the

[1] Nachmansohn described these influences in an unpublished manuscript entitled "Molecular Aspects of Bioelectricity: An Autobiography."

[2] David Nachmansohn, "Molecular Aspects of Bioelectricity"; "Biochemistry As Part of My Life," *Annual Review of Biochemistry* 41(1972):1–27.

gap between physicists, chemists, and biologists so as to promote better understanding and cooperation among them. Nachmansohn credited these monthly colloquia, which were regularly attended by many members of the various institutes, with having greatly expanded his scientific and spiritual horizons.

Like so many others of Jewish origin, Nachmansohn left Germany when Hitler came to power. He was offered the opportunity of working at the Sorbonne, and in 1933 established himself in Paris with his wife, Edith, and their baby daughter, Ruth. From Paris, Nachmansohn made several visits to London, only a few hours away, to attend meetings of the British Physiological Society. As he explained in the 1972 autobiographical article in the *Annual Review of Biochemistry,* he could never have anticipated that, by attending those meetings, his scientific interests would take a new, unexpected turn. He could also not have predicted that this new turn would determine the direction of his scientific work for the rest of his life.

At that time, one of the main topics of discussion in the London meetings was the role of acetylcholine in nerve activity. Following the pioneering work of Otto Loewi and of Dale and his colleagues, Dale proposed that acetylcholine acts as a transmitter of nerve impulses across junctions (synapses) between neurons or between nerve and muscle, in contrast to the electric currents that propagate impulses along nerve and muscle fibers. This idea was supported by two main lines of observations: (1) the release of acetylcholine at synaptic junctions, as judged by its appearance in the perfusion fluid of certain ganglia, or striated muscle motor endplates, upon electrical stimulation of the afferent nerves; and (2) the powerful stimulating action of acetylcholine when applied locally to synaptic junctions, which was in striking contrast to its failure to elicit a response when applied to nerve fibers.

Acetylcholine was known to be rapidly hydrolyzed by an enzyme, acetylcholine esterase, which is strongly inhibited by the alkaloid, eserine. In fact, no acetylcholine was found in the perfusion fluid of stimulated ganglia unless the fluid contained eserine, an indication that the acetylcholine released by electrical stimulation was rapidly hydrolyzed.

It seemed to Nachmansohn that much more knowledge was needed on the nature, distribution, and concentration of acetylcholine esterase in various tissues and that such information might provide clues to the role of this enzyme in nerve activity. He began work on this problem in Paris in 1936 and soon found that acetylcholine esterase was present at high concentrations in many different types of excitable fibers of nerve and muscle and in brain tissue, in both vertebrates and invertebrates; it was hardly detectable, however, in such organs as the liver or kidney. In addition, the concentration appeared to be several-fold higher at the neuromuscular junctions than in the nerve fibers.

In his study of the literature on the neuromuscular junction, Nachmansohn came across an article by J. Linhard in which the electric organs of fish were described as modified muscle fibers, comparable to motor endplates, in which the muscular elements were either missing or present only in rudimentary form. He thought it would be of interest to determine the acetylcholine esterase content of electric tissue. Nachmansohn had happened to see live *Torpedo* at the 1937 Paris World's Fair; he managed to procure some for study and found the concentration of acetylcholine esterase in the electric organ to be exceedingly high. In his own words, "The result was simply stunning: 1 g of electric tissue (fresh weight) hydrolyzed 3–4 g of acetylcholine per hour, although the tissue is 92% water and only 3% protein."[3]

[3] David Nachmansohn, "Biochemistry As Part of My Life," *Annual Review of Biochemistry* 45(1972):1–27.

The importance of this discovery, which opened the way for the elucidation of the molecular mechanisms involved in the generation of bioelectricity, can hardly be overestimated. In collaboration with Egar Lederer, Nachmansohn soon used the electric organ of the *Torpedo* fish to purify acetylcholine esterase. (This work was reported in a 1939 paper published in the *Bulletin de la Société de Chimie Biologique* [*Paris*].) In addition, Nachmansohn carried out experiments on the same organ in June 1939 at the Marine Biological Station at Arcachon, near Bordeaux. Together with W. Feldberg (a pharmacologist from Dale's group) and A. Fessard (an electrophysiologist at the Sorbonne), Nachmansohn provided the first unequivocal evidence for the electrogenic action of acetylcholine; the results were published in 1940 in the *Journal of Physiology*.

His next paper on electric tissue, prepared in collaboration with C. W. Coates and R. T. Cox, was published from Yale in 1941 in the *Journal of General Physiology*. This paper dealt with the correlation between the electrical potential and the acetylcholine esterase content of different sections of the electric organ of the electric eel. The use of electric tissue later made possible the crystallization and biochemical characterization of acetylcholine esterase in Nachmansohn's laboratory as well as the isolation of choline acetylase and the acetylcholine receptor.

In 1939, John Fulton invited Nachmansohn to join his department at Yale University. He stayed in New Haven until 1942, when he moved to Columbia University and became associated with the Departments of Neurology and Biochemistry at the College of Physicians and Surgeons. In New Haven, he had already begun to work with the electric organ of the electric eel (which he obtained from the New York Aquarium) and found not only that the acetylcholine esterase concentration was as high as in *Torpedo* but that the electric tissue contained phosphocreatine and ATP in concentrations comparable to those in striated muscle. Furthermore, the electrical discharge was accompanied by phosphocreatine breakdown. These observations suggested to him that the energy required for resynthesis of the acetylcholine hydrolyzed during the electrical discharge was supplied by the same processes that provide the energy required for muscular contraction, namely ATP and phosphocreatine breakdown, lactic acid formation, and, in the last instance, carbohydrate oxidation.

Soon after Nachmansohn moved to Columbia, he tested the idea that electric tissue contains enzymes capable of utilizing the energy of ATP for the acetylation of choline, an idea that indeed proved to be the case. This was, in many respects, key because it was the first time that ATP was found to drive a synthetic reaction other than through phosphorylation. Nachmansohn soon found that choline acetylase, the enzyme(s) responsible for the acetylation reaction, required a coenzyme because the activity of the acetylase-containing extracts was lost after dialysis and was restored by the addition of boiled enzyme. The identity of this coenzyme remained obscure, however, until Lipmann and coworkers found that an enzyme catalyzing the formation of acetylsulfonamide from ATP, acetate, and sulfonamide also required a coenzyme (coenzyme A, or CoA for short) for activity. They elucidated the structure of this coenzyme in 1947.

The discovery of choline acetylase was published by Nachmansohn and Machado in the *Journal of Neurophysiology* in 1943. Ironically, three journals (*Science, Journal of Biological Chemistry,* and *Proceedings of the Society for Experimental Biology and Medicine*) refused to publish this eminent and trailblazing biochemical paper. The reviewers apparently could not believe that ATP would participate in reactions other than phosphorylations. In retrospect, they cannot be blamed for their skepticism because Nachmansohn's finding was totally unexpected. Acetylation was eventually found to result from the coupling of two reactions: (1) ATP + acetate + CoA $\rightarrow$ AMP + inorganic pyrophosphate + acetyl-CoA; and (2) acetyl CoA + choline (or sulfonamide) $\rightarrow$ CoA + acetylcholine (or acetyl-sulfonamide).

Work proceeded in a number of laboratories on the localization of acetylcholine esterase using biochemical assays (e.g., of the extruded axoplasm and the sheath of the giant axon of the squid) and electron microscopic observations. The results of these studies made it appear highly probable that the enzyme was a component of excitable membranes everywhere—not only of synaptic membranes but also of the membranes of axons and conducting fibers in general. In his Harvey Lecture entitled "Metabolism and Function of the Nerve Cell" (delivered in 1953 and published in 1955), Nachmansohn advanced the view that acetylcholine acts as a signal recognized within the membrane by an acetylcholine receptor protein; this results in a conformational change that leads to increased local permeability to ions and membrane depolarization, thus generating an action potential—an idea that proved to be correct. Ernest Schoffeniels, in Nachmansohn's laboratory, was able to isolate the electroplax, the single-celled elementary unit of electric tissue, which was found to be extremely rich in acetylcholine esterase and receptor protein.

If one considers that receptors are now recognized as the initial elements in the response of all cells to specific stimuli and that the concept originated with the acetylcholine receptor, it becomes evident that Nachmansohn set a biological landmark. This was also the first neurotransmitter receptor to be characterized biochemically, thanks to its accessibility in the vertebrate muscle endplate and its abundance in the specialized electric organ of electric fish.

The finding that acetylcholine esterase activity is very high in excitable membranes—including nerve fiber membranes—and that the localization of the acetylcholine receptor is the same as that of the esterase led Nachmansohn to postulate that the nerve impulse is generated through a depolarization of the membrane by acetylcholine released by the stimulus from an inactive complex with protein. The action potential thus generated would give rise to the release of acetylcholine in adjacent sites leading to propagation of the current along the fiber by successive acetylcholine bursts. Rapid hydrolysis of acetylcholine by the esterase and the ion pump mechanism coupled to the breakdown of ATP would restore membrane polarization at each point as the impulse travelled down the fiber.

Nachmansohn's theory, already suggested in earlier publications, was presented in detail in his book, *Chemical and Molecular Basis of Nerve Activity,* first published in 1959. A revised edition appeared in 1975 with considerably more experimental support for his ideas. The revised edition also contained two supplements, one by Nachmansohn on the properties and functions of proteins of the acetylcholine cycle in excitable membranes and one by E. Neumann that presented a molecular model for bioelectricity.

Nachmansohn's ideas, however, were not accepted by neurophysiologists. His molecular theory of nerve conduction is still highly controversial, despite the fact that a variety of experiments by Nachmansohn and others (detailed in the 1975 edition of his book) would appear to nullify objections to his theory. The fact, for instance, that acetylcholine when applied locally stimulates at synaptic junctions or motor endplates but has no effect on axons, may be explained by impermeability of the intact axonal membrane to quaternary ammonium ions. Acetylcholine, therefore, stimulates axons when applied at the Ranvier node sites where the myelin sheath is much thinner. It also stimulates when applied to areas of a nerve fiber where the phospholipids of the myelin sheath have previously been hydrolyzed by treatment with phospholipase. By the same token, curare—which competes with acetylcholine for binding to the receptor—blocks transmission of the nerve impulse across synapses but does not affect conduction when applied locally to the surface of nerve fibers. It does, however, block conduction when applied at Ranvier nodes or to the surface of fibers previously treated with phospholipase.

Physostigmine (eserine), a tertiary ammonium base, and prostigmine, a quaternary ammonium base, are both inhibitors of acetylcholine esterase, and the former—but not the latter—can depress conduction when applied to a single frog sciatic nerve fiber. Moreover, the excitable membrane of certain axons (e.g., those of the walking leg of the lobster) appears to be incompletely protected; these axons can be stimulated by the local application of acetylcholine. Organophosphates such as diisopropylfluorophosphate (DFP) or tetraethylpyrophosphate (TEPP) are irreversible inhibitors of acetylcholine esterase and block conduction across synapses and along nerve fibers.

Both the inhibition of acetylcholine esterase and the conduction block can be reversed by pyridine-2-aldoxime (PAM)—an organophosphate antagonist developed in Nachmansohn's laboratory by Irving Wilson as a war gas antidote. (It may be mentioned parenthetically that organophosphates are used commercially as insecticides. PAM has found a nonmilitary application in the systemic treatment of insecticide poisoning. Some local anesthetics are structural analogs of acetylcholine and compete with the latter for receptor binding, blocking electrical activity in the conducting and synaptic parts of excitable membranes.

Despite these results, the current belief is that the acetylcholine system is intercellular and not intracellular. Acetylcholine is thought to be liberated only at cholinergic nerve endings in the synaptic cleft and to bind to the receptor on the postsynaptic side, functioning, therefore, exclusively as a synaptic transmitter. Axonal conduction is believed to involve primarily electric field effects on conformational transitions of protein-ion channels. The high concentration of acetylcholine esterase and acetylcholine receptor in axonal membranes is nevertheless a remarkable fact that remains unexplained.

Nachmansohn's work attracted a great number of students and investigators, and his laboratory at the College of Physicians and Surgeons was for many years a place of much excitement and feverish activity. Nearly four hundred papers, the majority original research papers, were published from his laboratory between 1947 and 1977. In addition, Nachmansohn was an indefatigable traveler and lectured extensively in the United States and abroad.

In the spring of 1980, former students, collaborators, and friends of David Nachmansohn organized an international symposium at the University of Liège to honor him on his eighty-first birthday.[4] It was apparent at this meeting that the field of endeavor he had pursued so vigorously for many years had been expanded in many directions by his former associates and their students. Particularly noteworthy was the tremendous progress in our knowledge of the molecular structure of acetylcholine esterase and of the acetylcholine receptor.

The importance of Nachmansohn's acetylcholine receptor

[4] *Molecular Aspects of Bioelectricity: Festschrift and Proceedings of the International Symposium and Poster Session in Honor of David Nachmansohn on the Occasion of his 81st Birthday, Liège, May 25–27, 1980 under the Auspices of the Université de Liège, Belgium, and the Max-Planck-Institut für Biochemie, Martinsried, München, Germany.* Ed., Ernest Schoffeniels and Eberhard Neumann. Oxford: Pergamon Press, 1980.

idea for our understanding of the generation of bioelectricity in molecular terms may be gauged from the review by Changeux (a former collaborator with Nachmansohn) and his associates,[5] and a recent report[6] prepared for the National Institute of Mental Health by panels of scientists in various areas of neurobiology and related fields. In these publications, the monomeric form of the receptor is described as a transmembrane, allosteric protein with an approximate molecular weight of 250,000, containing two acetylcholine (agonist) binding sites and consisting of four types of polypeptide chains of apparent molecular weights: 39,000 (α), 48,000 (β), 58,000 (γ), and 64,000 (δ) in a ratio of $\alpha_2,\beta,\gamma,\delta$. The receptor has several functional states: In the resting state, it has low affinity for agonists, and the ion channel is closed; in the active state, the binding sites are occupied by agonist and the channel is open. On binding two molecules of acetylcholine, the receptor undergoes rapid transitions (on a submillisecond time scale) between the resting and the active state. These fluctuations last a few milliseconds until hydrolysis of the acetylcholine causes its dissociation from the receptor.

After his retirement in 1967, Nachmansohn continued to work, travel, and lecture extensively. He was an enthusiastic supporter of the Zionist cause and made many visits to Israel. He was very active on behalf of the Hebrew University and the Weizmann Institute and was for many years a member of the board of governors of the latter institution. Nachmansohn was a firm believer in the world fraternity of science and was among the first scientists of German-Jewish origin to visit Germany after the war, working with strong determination for the reestablishment of scientific ties between

[5] J.-P. Changeux, A. Devillers-Thiéry, and P. Chemoulli, "Acetylcholine Receptor: An Allosteric Protein," *Science* 225(1984):1335–45.

[6] *The Neuroscience of Mental Health*. U.S. Department of Health and Human Services Publication no. (ADM)84–1363. Rockville, Md.: 1984.

Germany and the West. He also promoted intensely scientific rapprochement between Germany and Israel. In the 1970s Nachmansohn devoted himself to the study of the role played by German-Jewish scientists in the explosion of scientific knowledge that took place in the first quarter of this century. This effort culminated in the publication of his book, *German-Jewish Pioneers in Science: 1900–1933*.[7]

Because of his interest in art and history, David Nachmansohn was a stimulating travel companion. My wife and I enjoyed his company on many a visit to Israel, Italy, Sicily, and Greece, profiting from his scholarly knowledge of the classical world. David had strong convictions and defended them stubbornly, but he never let scientific preoccupations interfere with his enjoyment of life. He was refined in his tastes and gentle and understanding with his friends.

I AM GREATLY INDEBTED to Arthur Karlin (Columbia University) and Jean-Pierre Changeux (Institut Pasteur) for helpful suggestions.

[7] David Nachmansohn, *German-Jewish Pioneers in Science: 1900–1933* (New York: Springer, 1979).

HONORS

Nachmansohn became a member of the National Academy of Sciences in 1965. He was also a member of the American Academy of Arts and Sciences, the German Academy of Natural Sciences (Leopoldina), and an honorary member of the Weizmann Institute of Sciences of Israel and the Berlin Medical Society. He was a recipient of the Pasteur Medal (Paris), the Neuberg Medal (New York), the Medal of the Société de chimie biologique (Paris), the Albrecht von Graefe Medal of the Berlin Medical Society, the Nicloux Medal (Paris), and the Gold Medal of the Spanish Council for Scientific Research. He received an honorary M.D. degree from the Free University of Berlin and honorary D.Sc. degrees from the University of Liège (Belgium) and Tufts University (Boston).

An international symposium on the molecular basis of nerve activity was held at the Free University of Berlin, in October 1984, in memory of David Nachmansohn. That this symposium was sponsored jointly by the Max-Planck-Gesellschaft zur Forderung der Wissenschaften, the Société française de chimie biologique, the Weizmann Institute of Sciences, the Deutsche Forschungsgemeinschaft, the Senator for Science and Research of the City of Berlin, the Free University of Berlin, and the Gesellschaft für Biologische Chemie, attests to the high esteem in which David Nachmansohn was held by his colleagues and friends.

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