https://doi.org/10.1038/s41593-022-01241-z

Charles F. Stevens (1934–2022)

By Anthony M. Zador

Charles F. 'Chuck' Stevens, Distinguished Professor Emeritus at the Salk Institute, died peacefully in his home on 21 October 2022. He was 88. Chuck was a giant of modern neuroscience whose impact on science and on the lives of so many scientists is hard to overstate.

Chuck received his bachelor's degree in psychology from Harvard in 1956 and an MD from Yale Medical School in 1960. At Yale, he wrote his medical school thesis on 'Biological variability in two nerve membranes', presaging his interest in biological noise, a research theme he pursued throughout his career. He earned his PhD in Biophysics in 1964, working in the laboratory of Nobel laureate Haldan Hartline at Rockefeller University. He then went directly to a faculty position at the University of Washington in Seattle before moving to Yale Medical School and, in 1990, to the Salk Institute.

Chuck served on many boards, including at the Aspen Center for Physics, the Santa Fe Institute, and Cold Spring Harbor Laboratory, where he played a crucial role in shaping a burgeoning neuroscience group. In the early 1990s, he convinced the Sloan Foundation to fund the Sloan Centers for Theoretical Neuroscience; the Sloan Centers were crucial in bringing a generation of physicists, computer scientists, and other quantitatively trained researchers into neuroscience. He was elected to the National Academy of Sciences in 1982 and was an investigator with the Howard Hughes Medical Institute for many years.

Although Chuck headed an experimental lab throughout much of his career, he was really a theoretical neuroscientist at heart, before theoretical neuroscience was a respected and well-defined subfield. His PhD dissertation, 'A quantitative theory of neural interactions: theoretical and experimental investigations', lays out a mathematical theory of computation in the nervous system. Strikingly, it anticipates many subsequent debates — some still raging today, almost 60 years later — about rate versus temporal coding and population coding. Indeed, the thesis includes several chapters and appendices devoted to mathematical derivations and only a relatively small number of experimental figures.

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Chuck's interests in neuroscience were broad. Over the course of his career, he worked on a wide range of topics, including population coding, the mechanisms of neuronal excitability, single ion channels, synaptic physiology, and scaling laws. One of his first significant contributions, along with John Connor, was the discovery and characterization of a novel voltage-gated potassium current, the A current — the first new voltage-dependent current in the brain to be characterized since Hodgkin and Huxley. After he retired and shut down the experimental portion of his lab, he continued working on a variety of theoretical topics, including scaling principles and fly olfaction.

Perhaps his most important early contribution was the application of noise analysis to infer the conductance of the acetylcholine channel. In this theoretical tour de force, Chuck and his postdoc Charles Anderson recorded minute fluctuations in the endplate current at the neuromuscular junction. Using a simple physical model in which single acetylcholine channels open and close randomly, they were able to model the size and temporal spectrum of these fluctuations. Because each variable in the model had a physical interpretation, it could be measured independently. Several years later, Erwin Neher, while working as a postdoc in Chuck's lab, developed the single-channel recording method that allowed this conductance to be measured directly. Chuck declined to be an author on this paper, even though the work was conducted in his lab with his support. Neher was later awarded the Nobel Prize for this work. Although some were surprised that Chuck was not included in the award, he never expressed any regret. For Chuck, science was never a competition for glory or accolades.

Despite his many important contributions, Chuck did not obsess over choosing 'important' problems. His interests were so broad that it could sometimes appear that any question was of almost equal significance to him. Instead, his knack seemed to be in finding a beautiful solution to a problem; it was often the elegance of the solution that endowed the problem with 'importance'.

Chuck wrote several books. Each of these books was his attempt to synthesize a field for himself. Perhaps the most memorable is *A Primer of Neurophysiology*, which he published just a few years after starting his own lab. At ten simple chapters, this slim book has stood the test of time; a young scholar interested in neuroscience could do worse than to start here. He also wrote a book on physics (*The Six Core Theories of Modern Physics*) and even (at the age of 80) wrote himself a manual on the programming language R.

Chuck was exceedingly generous with this time. He could often be found in his office, door open, apparently happy to chat with anyone who happened to pop in. I first got to know him at Yale when I was an MD–PhD student. At the time, he had a standing offer to provide a one-on-one tutorial on any subject to any student who asked. He was a brilliant teacher, so it was odd that few students asked, but when I did, he kindly agreed to meet with me for several hours per week over several months. Together we went over classic papers in channel and synaptic biophysics. My experience was hardly unique. Chuck used to enjoy summering in pleasant locations — Cold Spring Harbor Laboratory, the Santa Fe Institute, the Aspen Institute — where he would work on theoretical problems and chat with the scientists he met. Given how generous he was with his time, it is a marvel that he ever got anything done.

Chuck tended to keep his lab small. He usually preferred to work closely with just a

single collaborator per project; most of his papers have just one other author. Author lists were almost always in alphabetical order, old school, so as to avoid disputes about author order. Chuck never organized lab meetings; instead, he would share the exciting results of one student or postdoc as he wandered around the lab chatting with the others.

Chuck had a well-earned reputation for the clarity of his lectures. People with no knowledge of neuroscience would marvel at how easily he could make even the most complex topic seem simple. He would start a seminar with a blank overhead projector and a felt tip marker and just start filling the transparencies with simple drawings and equations. By the end of the lecture he would have succeeded in conveying the nuances of the lab's latest findings, but each idea and result followed so readily from the last that at no point was there any danger of getting lost. His style was effective for the expert and layman alike. He also had excellent comedic timing. He once began a public lecture with an air of exaggerated pomposity: "The human brain consists of 100 billion neurons, 100 trillion synapses, connected by hundreds of thousands of miles of axons and dendrites," and then broke out in a grin as he continued to the punchline, "and we in neuroscience call that *job security*."

Chuck's legacy includes not just his tremendous scientific contributions, but his approach to doing science. At a time when science is increasingly seen as a competitive race, the pure joy that Chuck took in discovery serves as an inspiration. Chuck was a scientist's scientist, who continued to work until his very last days because that was what he wanted to be doing.

Chuck is survived by Jane, his wife of 66 years, along with two daughters and three grandchildren. One daughter predeceased him in 2013.

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Published online: 19 December 2022