

Sir Alan Lloyd Hodgkin 1914–1998

by Denis Baylor and King-Wai Yau

Sir Alan Hodgkin, one of the great physiologists of the twentieth century, died at Cambridge, England on December 20, 1998. He was 84.

He was born in Banbury, England and educated at Gresham's School, Holt, and Trinity College, Cambridge. Early in his career, his scientific genius manifested itself in a now-classic piece of work demonstrating that conduction of the nerve impulse requires the spread of electrical current between active and inactive regions of the nerve fiber. During the Second World War, he made key contributions to the development of radar for night fighters, and although a biologist, he became Principal Scientific Officer for radar development by 1944. This work, as well as his earlier life and subsequent career, is detailed in his book *Chance and Design, Reminiscences of Science in Peace and War*.

In 1937–1938, he spent a year in the United States at the Rockefeller Institute for Medical Research and became acquainted with K. S. Cole, who introduced him to the voltage-clamp method. In the late 1940s, Hodgkin, Andrew Huxley and Bernard Katz used this method in a brilliant series of experiments that elucidated the ionic mechanisms underlying the nerve impulse. These experiments, along with an elegant and original quantitative description of the voltage-dependent membrane conductances, remain a landmark in our understanding of how neurons work. For this work, Hodgkin and Huxley were awarded the Nobel Prize for Medicine or Physiology in 1963 (shared with John Eccles). The ion channels whose existence Hodgkin and Huxley inferred have now been purified, cloned and sequenced and form a standard part of biological doctrine taught at the high school level. Hodgkin's and Huxley's picture of how ion channels



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behave has proved to be remarkably prescient and robust.

Subsequently, Hodgkin turned his attention to the sodium pump and showed that its function depends on the consumption of ATP. He discovered that potassium ions move through potassium channels in single file and characterized the membrane conductances that underlie excitability in muscle fibers. He also made the first direct measurements of the activity of the sodium–calcium exchanger, which is an important pathway for calcium extrusion in cells.

In the early 1960s, Hodgkin collaborated with Michaelangelo Fuortes in a study of the light response of photoreceptor cells in the eye of the horseshoe crab *Limulus*. From a kinetic analysis of the light response, they made the then-heretical suggestion that light activated ionic conductances in the membrane via a series of biochemical cascades continue to be studied to the present day. The collaboration with Fuortes sparked his interest in vision, which he studied for the rest of his career. Between 1970 and the late 1980s, when he retired, his laboratory pioneered biophysical investigations of signal transduction in retinal rods and cones, again setting new standards for experimentation and analysis.

For many scientists, particularly those who had the privilege of knowing and working with him, Hodgkin represented the epitome of scientific excellence. A renowned physiologist once remarked, "I

have several heroes, but Alan is the one I always try to imitate." His unparalleled analytic powers grew out of formidable mathematical skills, largely self-taught, as well as a remarkable intuition. Whereas some think of him as a theorist because of the quantitative flavor of many of his papers, he was in reality a consummate experimentalist. He relished good measurements and enjoyed complete immersion in them, down to the smallest details. When experimental results were in conflict with a theory, he immediately rejected the theory and started over, no matter how elegant the theory might have seemed. In spite of his hunger to understand nature, he did not try to force an answer when there wasn't one.

For Hodgkin, science was an intensely personal experience to be enjoyed in all its aspects. He therefore preferred to work on a single project at a time and to have a very small research group. His insistence on taking on a fair share of all aspects of the work was itself an inspiration. Discussions of the latest results were serious and focused, and although he was patient with coworkers and receptive to their ideas, he was impatient with error and sloppy thought. He had an unerring sense of what would stand the test of time and what would fall by the wayside. His negative impression, indicated by a characteristic wrinkling of the nose, was a bad omen indeed.

Hodgkin received many other honors, including Knight of the British Empire, the Order of Merit and membership in the Royal Society as well as many foreign academies. While serving as President of the Royal Society and Master of Trinity College, Cambridge, he managed to keep his research going at full throttle. In spite of his many accomplishments and honors, he remained a modest person with simple tastes. He had a delightful dry sense of humor.

His professional success and enjoyment of life owed much to a wonderfully supportive family. His devoted wife Marion (Marni), the daughter of Nobel laureate Peyton Rous, had prior knowledge of the demands of the scientific way and backed Hodgkin in all things. He is survived by Marni and four accomplished children.

Scientists of Hodgkin's talent and distinction are rare indeed.

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