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Obituary

Professor Sir Alan Hodgkin OM, FRS (1914–1998)

From an early age Alan Lloyd Hodgkin seemed destined to make a mark in the world. He came from a Quaker family whose members had made distinguished contributions to many fields of human activity including medicine, science, banking, art and making beautiful gardens. Alan spent schoolboy holidays in some of the most beautiful of these gardens including those of Glendurgen and Treworgan on the Helford River in the West Country. He was highly intelligent and had a strong constitution. His greatest boyhood interest was natural history and it was this interest that brought him to the Marine Biological Association's Laboratory (MBA) in Plymouth. He came first when a schoolboy, and later for a vacation course on which he said that he learnt more invertebrate zoology in a fortnight than in a whole year at Cambridge.

Greatly influenced by A.V. Hill and E.D. Adrian, he chose to specialize in physiology. William Rushton told me that the Part 2 Examination turned into an attempt to catch Alan out in at least one topic. The examiners failed, indeed his answers contained many new ideas. Along with his undergraduate studies he began research using apparatus which had belonged to his father's friend, Keith Lucas, who had been killed in 1916 in a flying accident. Keith Lucas had tackled a problem first stated clearly by the great German physiologists Johannes Müller and Hermann Helmholtz 'on the nature of the messages that go along nerve fibres'. Alan made good progress as an undergraduate and continued his experiments during his first postgraduate year (1937). He gave the first experimental proof that an electrical event at each point along a nerve fibre (axon) causes currents to flow which activate the next point along the fibre. In this way the impulse is propagated along the nerve fibre without decrement. Working with a crab nerve, he also showed the existence of a local response which is not propagated. This was recognized as outstanding work and he was invited to spend a year at the Rockefeller Institute in New York. It was there in 1938 that he met an 'extremely attractive and entertaining sort of person', Marni Rous, the daughter of an eminent pathologist Peyton Rous.

In 1929, J.Z. Young had discovered the giant nerve fibres or axons of squid that serve the main swimming muscles of squid. These axons have diameters of around a mm which is almost 100 times greater than a large frog axon. Alan was introduced to squid axons in Woods Hole by K.S. Cole and on returning to Britain lost little time before going with Andrew Huxley to Plymouth. There, in 1939, they succeeded in pushing a fine saline-filled electrode inside a fibre and made the astonishing discovery that, during the nerve impulse, the potential of the interior of the axon changed transiently from being about 50 mV negative with respect to the sea water in which the nerve had been placed, to being about 50 mV positive when it was expected to go to 0 mV. At this critical stage in their research the second Great War began and it was five years before they could continue this research.

Alan spent most of the war working on airborne radar. He played a major part in the development of very effective radar equipment for night fighters. He made many trial flights and a particularly important contribution to the design of scanning aerial systems. Later in the war he was transferred to the design of radar-controlled gun turrets for the defence of night bombers. Here the philosophy behind the project was less clear and Alan came to wonder whether the project was given high

Alan Lloyd Hodgkin, physiologist; born Banbury, Oxfordshire, 5 February 1914; Fellow of Trinity College, Cambridge 1936–1978, 1984–1998, Master 1978–1984; FRS 1948; Foulerton Research Professor, Royal Society 1952–1969, President 1970–1975; Nobel Prize for Medicine (jointly with Sir John Eccles and Sir Andrew Huxley) 1963; President, Marine Biological Association 1966–1976; John Humphrey Plummer Professor of Biophysics, Cambridge University 1970–1981; Chancellor, Leicester University 1971–1984; KBE 1972; OM 1973; married Marni Rous (one son, three daughters); died Cambridge 20 December 1998.

priority to show that something was being done to reduce the high casualty rate. It was recognized that 'serving as a rear gunner was a good way of committing suicide'. In the light of subsequent events he felt that it might have been best to advise that radio silence should be preserved and no attempt made to defend night bombers with small calibre machine guns.

During this period Alan made a visit to the USA and he and Marni decided to marry and did so on the 31 March 1944. Red tape was overcome by the happy chance of a friend of Marni's father having dinner with the appropriate official. The official was persuaded that true love should not be blighted and that there couldn't be a better way to demonstrate good Anglo–American relations than to allow Marni passage to England. She rejoined Alan in Malvern in May 1944, the last year of the war. Persuading Marni to marry him was Alan's greatest proof of genius. Marni brings calmness and fun, she has a low, enthralling voice and a wonderfully apt way with words. She pursued a career in publishing whilst taking care of their family and understanding the demands of a scientific life. They were both interested in, and sympathetic to, the vagaries and eccentricities of people and shared a wide interest in, and enjoyment of, art and books.

After five years of war service Alan was entitled to return to Cambridge and in June 1945 he did so. His later career was largely associated with three institutions: Trinity College, Cambridge, the Royal Society and the MBA in Plymouth. Here I shall concentrate on Alan and Plymouth. In 1946 he worked with crab nerves but in the summer of 1947 he resumed experiments on squid in Plymouth. Later in that year he was joined by Bernard Katz and by Andrew Huxley and he spent several months in Plymouth working on squid for almost all of the years from 1947 to 1970. He usually had one to three collaborators and he always attracted other scientists from the world over to study under his guidance. I well remember the pleasure their results gave to physiologists and how proud we were at international meetings when they gave accounts of their discoveries.

In the light of the work of Hodgkin and Huxley and their collaborators, especially that of Richard Keynes, we can now describe the nerve impulse in terms of the opening and closing of known numbers of specialized channels in the cell membrane which separates the axon's internal from the external body fluids. This 'gating' of the channels is governed by changes in the electrical potential across the membrane. The opening and closing of the channels determines the movements of ions, particularly sodium, potassium, calcium and chloride, in exactly known quantities and timing, into and out of axons. These ionic currents then trigger the spread of the impulse by the mechanism that Alan had demonstrated in his earlier work. It was further proved that, without calling on any source of chemical energy, but using the energy stored in the differences in ion concentrations between the protoplasm and the external fluids, the large squid axons can conduct about a million impulses. The use of chemical energy takes place well after the impulse when sodium is pumped out of the axon in exchange for potassium. Finally the extraordinarily successful Hodgkin–Huxley equations linked measurements of the currents which were found with different voltages across the cell membrane with the voltages and currents found during nerve impulses for a variety of ionic compositions of the medium.

This sustained and brilliant work was most important for major parts of physiology and medicine and in 1963 Alan shared a Nobel Prize with Andrew Huxley and John Eccles. The giant axon could be considered not only as a nerve fibre but simply as a cell and the light that it throws on membrane physiology forms an indispensable foundation for all work on biological membranes such as those of our own hearts, brains and glands. It was, for example, a necessary foundation in our understanding of: the processes by which nerve cells interact with other nerve cells; the excitation and contraction of muscles; the regulation of other tissues in which transmitter substances such as adrenaline, dopamine and calcium play a role.

Alan Hodgkin, although having periods of intense thought when he was abstracted from the world, preferred working with a few dedicated colleagues. He had remarkable physical and intellectual stamina and he had a passion for experiments. The squid were caught each day and came into the Laboratory at teatime in the afternoon. The experiments often went on until almost breakfast time. For one period I managed to rearrange the times of fishing so that the squid arrived at lunchtime. Trevor Shaw said "please stop this—instead of working from teatime to breakfast, I now work from lunch to breakfast time". Alan could be emotionally involved in the outcome of an experiment. When sensibly he should have rested he could not resist waiting for just one more reading. To make himself repeat experiments that almost anyone else would have found entirely satisfactory he gave himself the task of making the 'perfect' experiment for publication. He sometimes said "experiments never give the best or the worst results you can imagine, but only the dullest". In his research this was clearly not true. Following great successes, the squid workers had blow-outs at Pedro's or The Horn of Plenty. In doing this Alan said they were following the advice given by Marni's father: "when you think you have made a discovery, celebrate by having a good dinner, and then when you find you have not made a discovery, at least you have had a good dinner".

He was an exceedingly thoughtful and generous man. To give some examples: against the advice of the Vice Chancellor of the University, in order to increase the security of his instrument-maker and his part-time secretary, he gave up his Royal Society Chair and accepted the Plummer Chair in Cambridge; he gave a very substantial Prize which he had been awarded, to the widow of a young colleague with whom much of the work had been done; when Trevor Shaw and Peter Baker succeeded in squeezing out the protoplasm from the inside of a squid nerve fibre and then, by replacing the protoplasm with an artificial solution, restoring near normal functions, they were very keen that Alan should join them in exploiting this discovery. Alan agreed to join them but he was most insistent that all of the credit for the discovery be given to Shaw and Baker who had, as Alan said "struck gold"; when a young man appeared in very informal dress for a visit of the Emperor of Japan to the Royal Society, Alan, who was at this time the

President of the Royal Society, offered to lend him one of his own suits.

The researches of Hodgkin and his colleagues were high amongst the projects of the MBA for which the Association received support and the Association always had a full time member of its staff e.g. Trevor Shaw and Hans Meves, as well as scientists like Peter Caldwell on Fellowships, heavily involved with the squid programme. Alan himself was from 1951 to 1965 (for as many years as was consistent with the Articles of the Association) an elected member of the governing Council. From 1966 to 1976 he was the President of the MBA's Council and then a Vice President. Although he was always kindly, people were afraid of his penetrating questions during annual inspections. Alan showed an interest in the well-being of all of the Association's staff including some, e.g. those working on specimen supply, who had often been neglected in the past. He particularly admired the work of Quentin Bone and Malcolm Clarke and he strongly backed the increased support given to the group of geochemists led by Michael Whitfield. He used his great prestige to protect the Association from the ever increasing bureaucracy in the administration of science. During his term as President the recommendations of the Rothschild Report were being implemented. He had great fears, fully justified by events, that this would be harmful to basic research work.

In 1970 Alan became President of the Royal Society and in 1978 Master of Trinity College, Cambridge and reluctantly he had to give up work in Plymouth. He transferred his efforts to a successful study in Cambridge of the mechanism by which a receptor cell of the retina can signal the absorption of a single photon by one of its billion or so photosensitive molecules.

Alan was about 6 ft tall and he stooped slightly. He had an expressive face, sometimes attentive, sometimes far away and sometimes he had an inquiring pixie-like look, usually when he was about to trump your ace in conversation. He could not but be conscious of his intellectual powers but somehow made their exercise encouraging rather than intimidating. Amongst his most remarkable qualities were his intuition on scientific questions and his sensibility to those immediately around him. Whilst he applied rigorous standards in science he was kind to people. Thus, in some respects Alan was not always entirely truthful; for example, when you brought a theory to him which was evidently erroneous, he would say "that is an interesting idea, I thought it was true myself for a long time. In the end I found there were some objections to it." Alan was patriotic and although appreciative of excellent work no matter who had done it, he was especially pleased when the discoverer was British. He was distressed that England was so much less beautiful than it had been when he was a child.

No account of Alan Hodgkin's life would be in the slightest degree balanced without a tribute to Marni on whom Alan's happiness and cheerfulness depended. Through a long, painful, disabling and disheartening illness, he was sustained by Marni and continued to work 'whilst this machine was in him'.

Sir Eric Denton