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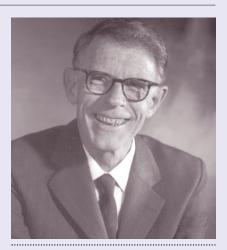
David Keynes Hill (1915–2002)

David Hill, physiologist and biophysicist, died on 18 August 2002. His father was A. V. Hill (known simply as A.V.), a pioneer of biophysics who received a Nobel prize for his measurements of the heat produced by muscles. His mother was Margaret, sister of the economist Maynard Keynes, and of the surgeon and bibliophile Geoffrey Keynes who married a granddaughter of Charles Darwin. A. V. Hill is remembered chiefly for his mathematical formulations, both of the excitation of nerves by applied electric current, and especially of the relations between the force against which a muscle contracts, the speed at which it shortens, and the rates at which it liberates energy as work and as heat.

As a boy, David often acted as an assistant in his father's experiments. Like his father, he was an undergraduate at Trinity, Cambridge, which he entered in 1934 with a major scholarship. In his first two years, he studied physics and chemistry as well as physiology. He then registered as a medical student because in those days a medical qualification was a prerequisite for an academic career in physiology. After doing the necessary anatomy and the final-year physiology course, he had one year of research before the outbreak of the Second World War.

In that year he continued his father's work on isolated muscles from frogs, using for his heat measurements the equipment that A.V. had developed at University College London. He re-examined the absorption of heat that occurs during the first minute after a contraction, and showed that it is caused by the resynthesis of adenosine triphosphate (the immediate source of the energy dissipated during contraction) by transphosphorylation from phosphoryl creatine, and not by a stage in the formation of lactic acid from carbohydrates as had previously been supposed. He also measured the time courses of three other processes during recovery after a contraction that had not been previously measured because of their small size and slow time course: oxygen consumption, production of heat and changes in pH. This was a remarkable achievement for a young scientist in so short a time and on the strength of it David was elected to a research fellowship at **Trinity College.**

On the outbreak of war, he started clinical study but soon joined a group at the Postgraduate Medical School at the Hammersmith Hospital in London. Here he worked on the effects of crush injuries,



Innovator in muscle research

which were expected to be among the most serious consequences of air raids.

A. V. Hill had led the team developing anti-aircraft gunnery in the First World War, and it was on his advice that in 1940 the physicist Patrick Blackett was appointed as scientific adviser to Anti-Aircraft Command. A.V. then provided him with three physiologists as assistants, including his son David and myself. All of us had an adequate background in physics for our work, which involved adapting the gun-control equipment to operate with the crude data provided by the radar sets of that time, working on a wavelength of 3 metres. This entailed many visits to gunsites, both at practice firings and during air raids.

From 1942, David held various other posts in operational research for the Army, finally becoming personal assistant to Brigadier B. F. J. Schonland, scientific adviser to Field Marshal Montgomery. He was the first British scientist to examine an unexploded V2 rocket, and he obtained information about ballistic missiles that would have been launched by magnetic propulsion into Britain if the launching sites had not been overrun by Allied troops.

After the war, David returned to his research on muscle, first at Cambridge, then (1948–49) as physiologist at the laboratory of the Marine Biological Association in Plymouth, and finally as biophysicist back in Hammersmith (vicedean, 1970–76). Here his prime duty was overseeing the development of electronics and of instruments for observations on human patients, but he had time to continue his research. Until 1971 he continued in the same general field as his own and his father's pre-war work, using physical techniques on isolated muscles and nerves but with an emphasis on the intracellular structure of muscle (neglected by A.V.) and using many original techniques. A group of his papers reported optical changes in nerve and muscle. Another series of investigations on muscle used ultraviolet microscopy and radioactive tracers both to localize the adenine nucleotides and phosphoryl creatine in relation to the muscle-fibre striations and to follow the intracellular tubular system that communicates with the external fluid. This system serves to conduct the influence of excitation inwards from the surface membrane of the muscle fibre to activate the contractile material. He discovered a 'short-range elastic component' in the response of resting muscle to stretch, which implied that a number of cross-bridges between the thick and thin filaments exist even in the resting state but are broken when the relative displacement of the filaments exceeds a few nanometres. Almost all of his papers up to 1971 were under his authorship alone.

From 1971 until 1977, David collaborated with R. H. T. Edwards and his group in studies on human muscle, measuring force, heat production and chemical changes, the latter research requiring samples taken from their own muscles by needle biopsy. From 1977, he continued his work on muscle with P. A. Merton, activating their own muscles by heroic procedures such as stimulating them with electric shocks through the skin and by strong magnetic fields applied to the brain.

In 1949, David had married Stella, sister of the immunologist John Humphrey, and they had three daughters. Following his retirement in 1982, David experimented in photography, and, after he and his wife made their final move to Yorkshire, he made himself extremely skilled in woodwork. He died after a long illness in which he became progressively less mobile, though he retained his faculties and remained cheerful until the end.

I got to know David Hill well as an undergraduate: my own career followed his closely from my arrival at Trinity College one year after him. After he left Cambridge in 1948 we kept in touch until his death. His friendship was of great importance to me, especially when I first arrived at Trinity, younger than most of my contemporaries and very shy. He was exceptionally kind, gentle, modest and generous. He will be greatly missed. **A. F. Hustey**

A. F. Huxley is at Manor Field, 1 Vicarage Drive, Grantchester, Cambridge CB3 9NG, UK.