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OBITUARY

Roger C. Woledge 1938–2015

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Roger C. Woledge 1938–2015 (photo by Dr. Martin Rosenberg)

Professor Roger Woledge was a muscle physiologist who was at the forefront of the major movements in muscle energetics research from the 1960s until his death in 2015. His published works span 54 years (1961–2015) and provide a direct link between the classical work on muscle thermodynamics, as epitomised by the work of A.V. Hill, Roger's first research supervisor, and the modern era of muscle physiology, in which muscle energetics is firmly associated with the molecular events underlying contraction. In the 1970s Roger was in the vanguard of an amazingly vigorous period of research undertaken by several groups attempting to balance muscle biochemistry, the source of energy for contraction, with the energy produced by contracting muscles as heat and work. This work, like all his research, was characterised by careful but innovative experiments and precise, quantitative analysis. Roger Woledge made a great contribution to muscle research but remained of quiet demeanour. He brought not only considerable technical skill but also a sense of the fun and excitement of finding things out through experiments.

Roger Woledge studied in the Department of Physiology at University College London (UCL) from 1956, graduating BSc with First Class Honours in 1959. He was then awarded a Medical Research Council Scholarship for research training which was carried out under the supervision of A.V. Hill. Hill had dominated British muscle physiology for the first half of the 20th Century and, although officially retired, he oversaw the start of Roger's career in muscle research. Hill didn't believe in the need to do a PhD but Doug Wilkie convinced Roger that this was the necessary path and subsequently supervised Roger's doctoral work on the energetics of tortoise muscle. During this time Roger was the Sharpey Scholar in the Department of Physiology (1962–1965). The PhD work resulted in one of the field's iconic papers in which the slow contractile properties and high efficiency of tortoise muscle are described. Tortoise muscle was, and remains, the most efficient muscle studied, and this paper introduced the now widely adopted idea that high power output and high efficiency are mutually exclusive properties of striated muscle. Roger interpreted the contrasting energetic properties of frog muscle (the classical preparation) and tortoise muscle in terms of Huxley's 1957 two-state cross-bridge model. The use of such models became a hallmark of his work, especially in later collaboration with Chris Barclay reviewing and interpreting a range of experimental studies.

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From the late 1960s until the early 1980s muscle energetics research was dominated by attempts to reconcile the magnitude of biochemical changes in contracting muscle with the amounts of energy produced as heat and work. It had been recognised for many years that there was probably more heat and work produced than could be accounted for by immediate ATP turnover. Roger, mostly in collaboration with Nancy Curtin, played a central role, accurately measuring both biochemical changes and energy output under a variety of experimental conditions. A crucial aspect of solving the problem was accurate determination of the expected heat and work, which required knowing the molar enthalpy of phosphocreatine breakdown under physiological conditions and this too was determined by Roger using in vitro calorimetry. It was eventually demonstrated that a large part of the energy output that could not be explained by immediate ATP turnover was, in fact, due to the heat that accompanied the binding of Ca^{2+} to troponin and parvalbumin. The presence of parvalbumin in muscles was not known when these experiments started. Roger extended the analysis of muscle thermodynamics from the cellular level to the molecular level by working with Takao Kodama and using calorimetry to quantify the thermodynamics of steps within the actin-myosin reaction. In the 2000s, Roger revisited the biochemistry-energy link in collaboration with Mike Ferenczi, Tim West and Nancy Curtin. They took advantage of newly-developed fluorescent probes for the ATP metabolites Pi and ADP to examine the millisecond-scale energetic events within the cross-bridge cycle at the start of contraction. This work represented an amalgam of the earlier work on cellular energetics, calorimetry of the actin-myosin interaction and mathematical modelling of the cross-bridge cycle. This approach echoed the theme of the monograph "Energetic Aspects of Muscle Contraction" co-authored with Earl Homsher and Nancy Curtin and published in 1985; it was the publication in which Roger took most pride.

In the 1980s, Roger, again working with Nancy Curtin, switched his attention to fish muscle, considering both the fundamental energetics of these muscles and energy turnover by muscle during contractions that mimic the in vivo events during swimming. Much of the initial work was done at the Marine Biological Association in Plymouth during short visits which Roger enjoyed enormously calling them his "science holidays". Part of the motivation for that work was to extend the small range of muscles about which there was detailed knowledge. At the time of his death, Roger was part of a team headed by Alan Wilson at the Royal Veterinary College, which was further expanding the range of muscles with experiments designed to determine whether the speed of very fast-moving animals, such as cheetahs, was reflected in the energetic properties of their muscles.

Roger was head of the Department of Physiology at UCL (1988–1994) and then Director of the UCL Institute of Human Performance (1994–2003). He became involved in many strands of work on human muscle performance. Work with Stuart Bruce and Suzanne Philips notably showed that hormone replacement therapy could slow the decline in women's muscle strength with age. In addition to his research achievements, Roger was a gifted teacher. For several years he had a key role in the UCL final year BSc "Muscle Course", which was a starting point for many muscle physiologists. He particularly enjoyed devising projects and discussing results with students. At the UCL Institute of Human Performance he started a very successful MSc degree for physiotherapists. In recognition he was awarded an Honorary Fellowship of the Chartered Society of Physiotherapy. After formal retirement, Roger continued to assist supervising research students and to work on human muscle at both King's College London and Queen Mary London. Some of this work involved biomechanical analysis for which his mathematical and modelling skills were invaluable.

Roger Woledge's achievements were many and substantial and yet he remained a modest person. A phrase used to describe his father, Prof Brian Woledge who was head of the Department of French at UCL from 1938 until 1971, was that he did not indulge in meretricious self-aggrandisement; this applied equally well to Roger. As a colleague and as a teacher, he was inspiring and his ready sense of humour made all interactions great fun. In both the research and teaching laboratory, he liked nothing better than tinkering with equipment, making things just that little bit better, if perhaps sometimes in the spirit of Heath Robinson! He was interested in a wide range of subjects beyond muscle physiology and always took a quantitative approach, whether it was estimating the size of a lifetime's supply of tea, calculating the exact time of sunrise and sunset during the darkest days of the English winter, or mapping his regular horse rides using GPS. Horse riding was a passion that had stayed with him since childhood and it was, perhaps, fitting that his last activity in life was riding in Epping Forest. Roger will be greatly missed by his many friends and colleagues but he has left a wonderful legacy of research work and fond memories of good times in his company.

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