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NEWS

Muscles and movement: a memorial meeting to celebrate the life and work of Professor Roger Woledge (1938–2015)

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On a cold, damp late-April day in east London, the family, friends, colleagues and admirers of muscle physiologist Roger Woledge came together to remember his life and scientific contributions at a celebratory symposium at Queen Mary University of London (QMUL). Woledge died unexpectedly in March 2015 following a riding accident, but by the end of the day-long symposium supported by The Company of Biologists, we were left in little doubt of the great intellect and infectious enthusiasm that defined Woledge and his approach to life and research. While some of the delegates had come from just along the corridor, others had travelled from as far as Australia and the USA, to share recollections, anecdotes and their affection for this giant of modern muscle physiology. 'Roger had a depth of knowledge that was, to me, unsurpassed', said meeting co-organiser Tim West, who was a postdoc with Woledge and one of his key collaborators, Nancy Curtin, at Imperial College, London, in the late 1990s. Saying that Woledge's versatility was exceptional, West adds, 'He could talk about an enzyme in a dish, understand the kinetics of it and talk to experts about it. At the same time he could turn around and talk about muscle physiology and whole-animal kinematics with as deep an understanding.'

Introducing the symposium, Curtin detailed Woledge's early career as an undergraduate in the University College London (UCL) Physiology Department, where he was able to satisfy 'his itch for quantitative information' with his love for practical work. After graduating from UCL, Woledge joined the lab of Nobel Prize winning scientist A. V. Hill for a three year fellowship. 'The years that Roger spent with A. V. must have been a remarkably good match between mentor and student; there seems to have been just the right balance between instruction by A. V. in the lab and time when Roger worked on his own', Curtin said. However, she remembers that Hill did not encourage Woledge to apply for a PhD, because Hill did not believe in the degree. Instead, Doug Wilkie persuaded Woledge that he should register for a PhD while in his lab to work on the energetics of tortoise muscle, and Woledge eventually graduated in 1966, publishing his seminal paper in the *Journal of Physiology* two years later (Woledge, 1968). Referring to their life-long collaboration, Curtin said, 'He was not one of these people that got discouraged when things didn't work; he was quite optimistic. He also knew a lot, we complemented each other as we each had our own separate skills.' Ultimately, Woledge went on to head the department where he had been an undergraduate, in addition to directing the UCL Institute of Human Performance before his retirement from university administration in 2003, although he continued to publish in journals such as *Journal of Applied Biomechanics* and *Journal of Experimental Biology* until his death.

Over the course of the symposium, friends and colleagues recalled their discussions and collaborations with Woledge. Jack Rall from Ohio State University, USA, described Woledge's innate sense of fairness. Remembering discussions with Woledge about the challenges faced by Graham Hoyle and others in the 1980s as they attempted to gain acceptance for the role of a third 'S' filament in muscle contraction, Rall said that Woledge encouraged him to discuss the controversy in his recently published book, *Mechanism of Muscular Contraction* (Rall, 2014), 'as he felt that the third filament's proponents were being ignored unjustifiably', said Rall. Throughout the remainder of his talk, Rall recalled the early suppression of the role of the S filament, which had been evident in the first papers outlining the sliding filament model of muscle contraction, and then discussed the work of Koscak Maruyama and Kuan Wang, who independently identified the key S filament protein, now known as titin.

Roger Woledge riding his horse Luke at Shoeburyness Beach ca. 2012. Photo credit: Elizabeth Dollimore.

In the following talk, Earl Homsher from the University of California Los Angeles, USA, acknowledged his debt of gratitude to Woledge, talking about his insight into experimental design and modest approach when discussing experiments. 'For me, he was a leading force in muscle energetics at a time of confusion, and showed us how to use energetics to evaluate processes that occurred in muscle…. Roger's experiments and papers on energetics set the standard for muscle energetics research in the 1970s and, I think, to the present', said Homsher. Outlining the structure of the book *Energetic Aspects of Muscle Contraction* (Woledge et al., 1985) that he wrote in collaboration with Woledge and Curtin, Homsher described the immense investment of time that resulted in the chapter dedicated to the heat of chemical change – accounting for 108 of the book's eventual 357 pages. Homsher explains that the chapter was designed 'to tell you everything you wanted to

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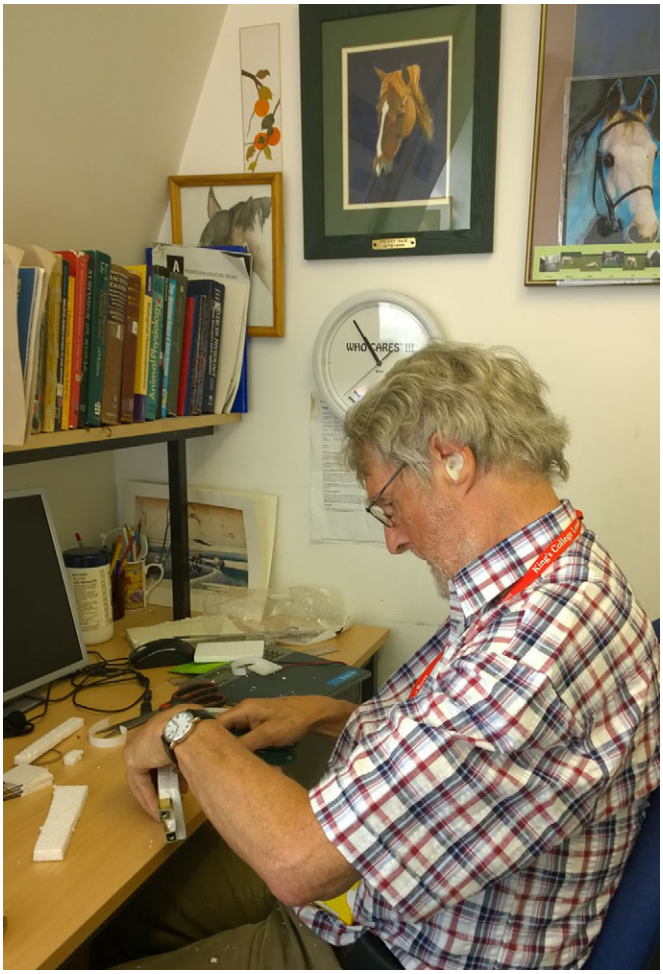
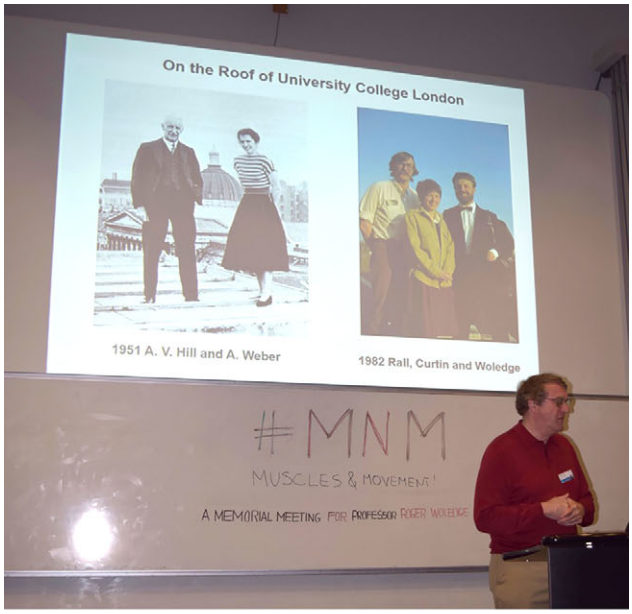
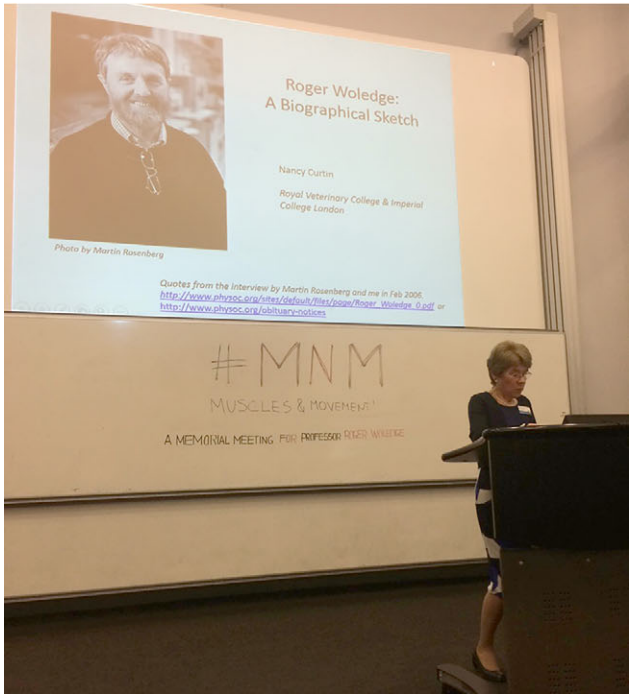


Roger Woledge doing what he loved best, building equipment at Kings College London. Photo credit: Michealjohn Kalakoutis.





Jack Rall (above) and Nancy Curtin (below) remembering Roger. Photo credit: Dylan Morrissey.

know about how to measure heat, chemical change and what was seen'.

Returning to Woledge's classic 1968 paper, where he compared tortoise and frog muscle contractions, Chris Barclay from Griffith University, Australia, described the delicate force and heat measurements that allowed Woledge to show that the muscle was so efficient that the amount of heat produced was barely measurable. Barclay explained, 'In fact, no muscle that has been studied has an efficiency that is any higher than tortoise. So it might be slow, it might be powerless, but it is the efficiency champion.' Following on, Alberto Minetti from the University of Milan, Italy, presented an entertaining discussion of the biomechanics of assisted human jumping, illustrated with a remarkable Pathé movie from 1927 of John Higgins bounding over six chairs in a single leap. Referring to Woledge's calculation of muscle–tendon power output, where he determined the limits of power production (Galantis and Woledge, 2003), Minetti explained how Higgins was able to amplify muscle power production by throwing weights from his hands at a critical point in the jump to generate thrust through a form of 'muscle-driven rocket propulsion' to achieve this unprecedented feat.

Reflecting on Woledge's passion for comparative studies, Alan Wilson and Tim West from the Royal Veterinary College, UK – one of the three labs where Woledge was spending his retirement – then presented a two-handed discussion of the physiology of muscle and its implications for predator interactions in the wild. Referring to Curtin's earlier talk where she had described Woledge as being 'on holiday' when indulging his passion for comparative physiology, West joked, 'At the RVC he was on holiday all the time, there were lots of animals to keep him interested'. While Wilson detailed their work collecting muscle biopsies from wild animals in Botswana, in parallel with measurements of the animals' movements as they pursued prey, West explained how power measurements derived from individual muscle fibres provide a good picture of the power outputs generated by the intact muscles.

In the final lectures of the day, Woledge's colleagues Di Newham from King's College London, UK, and Dylan Morrissey from QMUL discussed his contributions to our understanding of human muscle energetics and applications in geriatric medicine and sports

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science. ‘Roger liked making things’, said Newham, recalling how Woldege often designed and built his own equipment. Describing how Woledge showed that force production in older people was not simply a matter of muscle loss, Newham said, ‘Roger was one of the first people to say, “It’s not just quantity, it’s the quality of muscle that changes with aging, it’s the reduced force per cross-sectional area”’. Newham also recalled how she had collaborated with Woledge to look at the effects of swaying on the incidence of falls in the elderly. ‘This was a lovely example of Roger’s ability to analyse data’, she remembers, while describing how Woledge showed that there was a greater variability in the degree to which the elderly sway while walking, resulting from an increase in the variability of step width, which had not been apparent from measurements taken when the individuals were stationary. Concluding the session, Morrissey provided a clear impression of the breadth of Woledge’s contributions to physiotherapy, saying, ‘The impact and clinical reach of Roger’s work was really quite extensive’. Recalling his persistence, Morrissey provided examples of analyses that Woledge returned to – ‘like a dog with a bone’ – adding that one of the legacies of this approach was a suite of incredibly robust analysis tools that are still available.

Another highlight of the day-long symposium was the session dedicated to Young Investigators, where six early-career scientists presented brief summaries of their work, with several paying tribute to Woledge’s contributions. ‘Having a session to recognise young investigators seemed like the thing to do’, said West, adding that, ‘Roger liked to motivate young-uns’. Early in the day, Michaeljohn Kalakoutis from King’s College London presented his Aurora Scientific Young Investigator Award winning study, which had been inspired by an analysis conducted with Woledge that showed how the force measured from human skinned muscle fibres was affected by methodological differences between laboratories. After identifying that most laboratories used one of two activation solutions when measuring muscle force, Kalakoutis then compared the contractile response of muscle fibres in the two solutions. Muscle fibres bathed in the solution containing imidazole and potassium chloride that lacked glutathione generated a poor contractile performance relative to muscle fibres bathed in the solution containing TES buffer, glutathione and potassium propionate. ‘This shows that the use of different activating solutions is a likely cause of the variability in the specific force values reported from human skinned fibres in the published literature’, said Kalakoutis.

Throughout her talk, winner of the Codamotion Young Investigator award, Paulina Kloskowska from QMUL, referred affectionately to Woledge as ‘Prof’. Recalling how she had collected an enormous number of measurements from athletes and amateur sportspeople in an attempt to understand the causes of groin pain, Kloskowska described how she presented the avalanche of data to Woledge, who reacted by saying ‘Let’s create a simple solution’. However, what may have appeared as a simple solution to Woledge resulted in a bafflingly sophisticated analysis tool: ‘I was looking at the screen and I had no idea what was going on, but we were able to analyse our data,’ Kloskowska laughs.

Drawing the day to a close, Woledge’s daughter, Elizabeth Dollimore, reflected on her father’s zest for life and his ability to turn adversity into success. Recounting several anecdotes (including a family shopping trip that almost ended in disaster when confronted by a stream in flood – Woledge improvised stepping stones to provide safe passage), Dollimore also recalled how her father despised bullying and was a great supporter of his colleagues. ‘He really believed in collaborations… he never seemed to want to keep his data analysis to himself; rather, he seemed to want to share it’, said Dollimore. In addition, she recalled how Woledge was also a great enabler, saying, ‘Roger supported ideas. He said, “Yes, you can do this”’. Concluding events at the end of a day of celebration, Morrissey payed tribute to all the contributors and invited everyone at the meeting to ‘toast Roger over a glass of wine’.

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