

Ron published many scientific papers and reviews in journals of the highest quality, including *The Journal of Physiology*. The Department hosted a number of very successful international conferences and took a leading part in the periodic visits of The Physiological Society to Leeds. With Tissa Kappagoda, he published a Physiological Society monograph entitled *Atrial Receptors*.

Ron served on the Editorial Board – and became Chairman – of *The Journal of Physiology* as well as other prestigious journals. He was Chairman of the Cardiovascular Commission of the International Union of Physiological Sciences for a number of years.

He became a Member of The Physiological Society in 1956, serving on the Committee from 1968–73. Following his great friend Robert Comline, he became Treasurer, the Senior Officer of The Society at the time, from 1980–86, after which he was elected Honorary Member.

In the Department and in every aspect of his career, Ron created an atmosphere characterised by a rigorous attention to detail and positive vigorous discussions with everyone: he generated a very relaxed atmosphere with frequent highly enjoyable and bibulous get-togethers and parties. There was constant positive critical debate and analysis allied to experimental confirmation: in the early days, ideas of Karl Popper were frequently invoked. He stimulated many young scientists from a wide range of backgrounds and countries to pursue high-flying careers in laboratory experimental work in physiology and its related areas of anaesthesia, surgery and cardiology, and the pharmaceutical industry.

We all owe him a huge debt. He had a remarkable ability to enthuse individuals of whatever background and to gain their trust and loyalty which he richly rewarded.

Note: in preparing this account, I had help from Roger Linden, Michael Snow, Peter McWilliam, David Mary and Ann Silver. I am very grateful for their assistance. Any omissions, errors or misinterpretations are solely my responsibility.

## Margaret Hay Gladden

21 December 1940–3 April 2010



Margaret had a long and productive research career, spanning four decades, which she managed to combine with raising four children. She was born, an only child, in Lancashire, the daughter of an industrial chemist from whom she inherited an interest in designing equipment to solve or overcome laboratory problems.

She was also active outside science, being an international rower in her youth and later playing an organising role in the Quakers and being an active supporter of the Liberal Democrats, putting her interest in gardening to use by hosting fund-raising garden parties. She returned to Quakerism as it has been in a Welsh branch of her ancestry in earlier times, possibly during George Fox's lifetime. She was a delightful colleague and had a love of driving at high speeds, which could be alarming if you were driven by her, as she surfed traffic, whilst elaborating Quaker principles.

She was also a thoughtful feminist and deplored the tendency for scientific controversies to break out amongst her male colleagues (outside of Glasgow) so very quickly, preventing genuine scientific dialogue. As she regarded men as the weaker sex, she was invariably kind and encouraging to her younger male colleagues. Whilst active in spindle physiology, her work was informed throughout by her medical training and she was aware of the need for research to assist eventually in the care of patients.

After retirement, Margaret continued to pursue her research into the effects of opiate anaesthetics on the output of fusimotor axons with the same characteristic dedication. As well as working on spindle physiology, she latterly acquired an additional interest, prompted by her compassionate nature: she was currently exploring the role that spindle 'reset' might play in alleviating some of the symptoms of motor dysfunction. This involved work in schools putting a promising form of therapeutic massage on a more scientific basis, as a means of helping to improve motor function in children with cerebral palsy.

As Guy Bewick relates below, she was still planning experiments at the time of her death. Margaret published over 70 papers, mostly in *The Journal of Physiology* and almost entirely on the subject of muscle spindles, though with an occasional foray into Victorian medical education and the use of networked computers in physiology teaching. Before the tyranny of citation analysis took hold, the proceedings of symposia used to be highly regarded and Margaret co-edited the proceedings of three such symposia.

After qualifying in medicine from London University in 1965, simultaneously taking her MRCS and LRCP, she took a DCh, also from London, in 1968. She then transferred to Geoffrey Kidd's laboratory in Liverpool where she held a MRC junior research fellowship and from where she was to publish her first papers that set the theme for most of her subsequent research: the relationship between structure and function in the innervation of skeletal muscle, especially the spindle. Her thesis was on the development of innervation in tenotomised muscle in the rat, and she was awarded the degree of PhD by Liverpool University in 1971.

From Liverpool, Margaret moved to Glasgow, joining Ian Boyd's laboratory in the then Institute of Physiology as a research fellow and successively as lecturer (1973), senior lecturer (1983) and reader (1991). The early seventies was a time when the dual model of the

spindle was coming under increasing pressure from new observations in histochemistry, EM and physiology. This had been formulated by combining Peter Matthews' division of fusimotor actions into dynamic and static categories with Ian's nuclear bag and nuclear chain fibre systems. Despite being overthrown by the late seventies, the simplicity of the dual model might account for the sorry fact that it continues to be described in many current textbooks. Margaret's part in the overthrow began when she extended the late Sibyl Cooper's observations on the distribution of elastic fibres in spindles and showed that the prominent elastic fibres of the polar regions of spindles were concentrated around just one of the (usually) two nuclear bag fibres. This nuclear bag fibre, now known as the bag<sub>2</sub>, was innervated by static fusimotor axons, whereas the bag fibre without such a concentration of elastic fibres was innervated by dynamic fusimotor axons and is now known as the bag<sub>1</sub> fibre. These results were obtained using a preparation of the tenuissimus muscle with intact nerve and blood supply that seems to have been introduced by Margaret to Ian's lab following her visit to Toulouse, where it was developed by Yves Laporte and the late Paul Bessou.

The recognition that there were not two, but three, types of intrafusal muscle fibre (bag<sub>1</sub>, bag<sub>2</sub> and chain) focussed attention on the pattern of their motor innervation, especially the specifically fusimotor ( $\gamma$ ) static axons. On the one hand it resolved the conundrum that dynamic axons always activated bag fibres whereas static axons might activate bag fibres or chain fibres, or both together; on the other it raised the question as to why the static axons needed two very different effectors. Together with Peter McWilliam, Margaret soon reported that bag<sub>2</sub> and chain fibres could, to some extent at least, be separately activated by cortical or midbrain stimulation. In her continuing work with Ian, until his untimely death in 1987, Margaret pursued the idea that there might be two, or even three, kinds of static  $\gamma$  axon. The idea was repeatedly

criticised by David Barker's group in Durham and with further evidence against it from Yves Laporte's group, now in Paris, it appears that even before 1987 Margaret had her own doubts as she candidly related when she abandoned the idea in a review she presented at a symposium held in Glasgow in honour of Ian's memory as part of the IUPS congress in 1993.

In Glasgow in the early nineties, Margaret focused her attention on central and reflex activation of  $\gamma$  motoneurons, but she also developed an interest in the other sensory innervation of the spindle, the secondary endings supplied by group II afferents. Much of this work was carried out in collaboration with Yves Laporte's group. Her last major collaboration was with Elżbieta Jankowska of Göteborg on group II and interneuronal inputs to  $\gamma$  motoneurons; her last full paper to be published in *The Journal of Physiology* was in 2002 on coupling of Ia and II afferent output by static  $\gamma$  axons, so returning once again to the constant theme of the relationship between structure and function in the spindle.

#### **Peter McWilliam writes:**

I first met Margaret when I came to Glasgow in 1971. She had immense technical expertise and endless patience with all things at the micro level. She also had endless patience with people and with me in particular as I was always wanting to try new things in the lab. Although Ian was my formal PhD supervisor, his duties as head of department meant that I relied on Margaret for much of the day-to-day supervision. Our greatest piece of work together was working out the motor innervation of the mammalian muscle spindle. This involved developing a preparation where we could isolate and observe a single spindle under the microscope whilst maintaining its nerve and blood supply so that we could also isolate the multiple individual afferent and efferent axons to the spindle. The experiments would take 30–36 hours and involved us working in shifts.

Margaret and I eventually enjoyed a memorable eureka moment at about 5:00 am on a fine summer's morning

when we suddenly realised exactly how the intrafusal fibres of a spindle were innervated by the static and dynamic  $\gamma$  motor fibres. In later years it was great to see our wiring diagram of the spindle reproduced in several text books.

Margaret always had tremendous energy and stamina for these long experiments which stemmed from her rowing. She competed at international level and I have memories of her taking time off to compete in the coxless pairs at the European Championships. One year she gave birth to her first child (a daughter, I think) midway through a series of long experiments. As I recall she completed an experiment about 48 hours before the baby was born despite the rest of us in the lab imploring her to take things easy. Mum and baby were back in the lab about a week later! She always had a smile and a kind word for all she met.

#### **Guy Bewick writes:**

I met Margaret through Bob Banks, at Durham University, a fellow muscle spindle physiologist. We all met previously at local and national meetings, but more particularly over the last 2–3 years. We invited Margaret to become a regular attendee in our group discussions on an MRC project Bob and I are collaborating on. She took a very active part in proceedings, always looking so hale and healthy, and it was a great surprise to hear of her strokes. We greatly appreciated her contributions to our meetings, especially her enthusiasm and depth of knowledge in her field of research. Her wealth of experience was invaluable and she will be greatly missed both as a scientist and as a warm and generous colleague.

Margaret is survived by her former husband John Womersley and her children, Hugh, Gillian, Rona and Howard.

**Robert M Banks, Michael Lucas, Jim Morrison and Ian McGrath with thanks to Peter Ellaway, Peter McWilliam and Guy Bewick**