Exp Brain Res (2010) 200:193–195
DOI 10.1007/s00221-010-2165-y

OBITUARY

Anders Lundberg (1920–2009)

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Published online: 28 January 2010

Anders Lundberg passed away in his home in Gothenburg, Sweden, on 18 May 2009. He was nearly 89 years old. During his long and remarkable scientific career, Anders Lundberg literally revolutionized our understanding of how the spinal cord and brain interact to generate and control movement.

Lundberg studied at Lund University in the 1940s. He received his MD degree in 1947, but his interest was already focused on research and as a student he had begun to work on the autonomic nervous system at the Department of Physiology with Georg Kahlson. From 1946 he was affiliated with the Nobel Institute of Neurophysiology at the Karolinska Institute in Stockholm under the directorship of Ragnar Granit where he analyzed electrical properties of axons. This work resulted in his PhD-thesis (1948) entitled "Potassium and thermal sensitivity of mammalian nerves". Half a year later, he left for New York to continue this line of research in the laboratory of Raphael Lorente de Nó, at the Rockefeller Institute where he spent 1.5 years. There he was also introduced to a leading spinal cord physiologist, David Lloyd, and to Yves Laporte, who joined Lloyd's group at the same time. Laporte was to become Anders Lundberg's life-long friend. Lundberg had many discussions with Lloyd and Laporte about spinal cord physiology and the classic work of Sir Charles Sherrington on spinal reflexes. These discussions were to have a major influence on Lundberg's future research.

After his post-doctoral sojourn in the United States, Lundberg returned to Stockholm, but soon was appointed as Associate Professor in Lund where he started up several projects. Using the newly introduced microelectrode technique, he was the first to investigate the electrical properties of salivary glands and described changes in their membrane potential associated with salivation [1]. He continued his research on autonomic ganglion cells and the neuromuscular junction. However, he also started studies on the spinal cord that thereafter was his major interest. In collaboration with Yves Laporte, he started by exploring properties of the dorsal spinocerebellar tract neurones using intra-axonal recordings in the dorsolateral funiculus of the spinal cord, benefiting from both Laporte's and Lloyd's experience in spinal cord physiology. Their findings attracted international attention and in 1956, Lundberg was invited by Sir John Eccles to his department in Canberra as Senior Research Fellow.

Together with Sir John Eccles, his daughter Rosamond Eccles and several of those who joined the Canberra group, Lundberg undertook systematic analysis of synaptic actions of primary afferents on spinal motoneurons and interneurons

Anders Lundberg was one of the founding editorial board members for EBR when it began its life in 1976 under the editorship of John Eccles. He was also one of the most prolific contributors to the journal with a total of 49 papers, including a series of 16 on the topic of "integration in descending motor pathways controlling the forelimb in the cat". He continued as an editor of the journal until volume 16 when he persuaded his younger colleague Hans Hultborn to take his place. Hans is one of the authors of the obituary. –John Rothwell

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using the technique of intracellular recording developed in Canberra. This work provided a new basis for our knowledge on mechanisms of spinal reflexes and their descending control, and resulted in 16 major papers (1957–1961) [2] (cf also page 11 in [3]).

Sir John Eccles describes Lundberg's visit as follows: "So impressed was I with the performance of Anders Lundberg that I tried … to get him to stay in the position of a Readership in my Department, which I would have had made specially for him" [4]. However, Lundberg choose to return to Lund and set out on a research program to analyze the supraspinal control of spinal segmental reflexes and the role of this control in voluntary movements. Two years later, he was appointed as a Full Professor of physiology at Göteborg University. He took office in 1961 after having been unanimously placed at the top of the list of candidates. A quote from a letter of recommendation by Sir John Eccles reflects the standing of Anders Lundberg at the age of 39. Sir John Eccles described him as "…one of the leading physiological investigators in the world. In fact I regard him as the person of his generation, who is closest in neurophysiological thought to my old master, Sir Charles Sherrington" [4].

During the next 30 years, Anders Lundberg indeed established himself as the international leader in his field. In Göteborg he built up from scratch, but with a generous support from the Swedish Medical Research Council, a neurophysiological research department with several laboratories working in parallel. The electronic and mechanical workshops constructed all equipment, as microdrives, microelectrode amplifiers and stimulators, needed to ensure the highest technical standard of the planned experimental work.

In his own words Lundberg defined as the aim of his studies "…a better knowledge of the neuronal machinery of movement, in particular of the feed-back control by primary afferents and interactions between different neuronal systems…" The corner stone of his work was the accumulating evidence that both reflex and descending commands reach motoneurons via the same interneurons. This idea was indeed revolutionary. Because only a very small proportion of synaptic contacts between sensory fibers or descending tract fibers and motoneurons turned out to be direct, spinal interneurons and their networks became the main subjects of his interest. He focused first on finding out which sensory fibers and which descending tract neurons provide input to various categories of these interneurons. Striking convergence of sensory fibers from different receptors, in particular, high threshold muscle, skin and joint receptors on some interneurons, revealed the degree of processing occurring at the level of these interneurons. It also provided a substrate for different motor synergies and for their selection by descending tract neurones, via the corticospinal, cortico-rubrospinal, vestibulospinal and reticulospinal tracts.

These studies led to three particularly important groups of findings: (1) a cellular basis of alternative reflex pathways to motoneurons that enabled the CNS to select the most appropriate reflex pathways in a task- and context-dependent manner, (2) the neural control of locomotion and (3) the role of cervical propriospinal and spinal interneurons in the control of reaching and grasping movements.

Lundberg's interest in the locomotion stemmed to a large extent from his desire to "…*find* a functional meaning for the pattern of Ia connexions from large muscle spindle afferents to motor nuclei." [5]. It also originated from his interest in Graham Brown's and Sherrington's work on spinal stepping, with evidence for intrinsic spinal networks being responsible for the basic locomotor rhythm. Lundberg's work on locomotion included both a kinematic and EMG analysis of patterns of activation of hind limb muscles in intact animals, but was closely linked to his ongoing studies in reduced preparations. The latter explored effects of descending monoaminergic pathways and systemically applied NA precursor (L-DOPA). The results revealed the existence of a neuronal network released by monoamines which had features expected of neuronal networks subserving locomotion and the cellular substrate of Graham Brown's "half-center hypothesis" (see Lundberg's 1968 Nansen Memorial Lecture in Oslo, on the neural control of stepping [5]; see also [6] for a more detailed description of Lundberg's contribution to the field of locomotion).

Anders Lundberg devoted the last period (1976–2000) of his scientific career to the role of interneurons in the cervical spinal cord in the control of forelimb movements in the cat. This work was initiated by the discovery that propriospinal neurons located in the C3–C4 spinal segments can mediate excitation and inhibition to forelimb motoneurons from virtually all the descending motor systems [7]. These findings in reduced, immobile animals opened an exceptional opportunity to investigate the function of a defined set of spinal interneurons during voluntary movements in awake, behaving animals. Behavioral experiments with selective spinal cord lesions demonstrated that the C3–C4 propriospinal neurons can mediate the command for goal-directed forelimb reaching, whereas more caudal segmental interneurons carry the command for grasping with the digits [7]. The C3–C4 propriospinal neurons and brainstem neuronal systems that converge onto them can also be used to update a descending command from the motor cortex en route to the motoneurons, with minimal delay, if the target position suddenly changes during the movement. In his last own review, Anders Lundberg emphasized the usefulness of this neuronal system to understand voluntary motor control also in primates [7], and indeed other

research groups were inspired to explore the role of the C3–C4 propriospinal neurons both in humans and in monkeys [8, 9].

Lundberg wrote several important reviews on these issues, but he also asked his visiting collaborators and his own postdoctoral fellows to author some (for example [10]). Several of the hypotheses on spinal mechanisms of movement ensuing from his work subsequently found support in reduced animal preparations in which some forms of motor behavior could be reproduced (fictive locomotion and fictive scratching), in behavioral studies on animal or by indirect techniques in humans (see [9]).

The achievements of Anders Lundberg were highly valued and he was awarded several prizes, including the Alvarenga Prize (1963), the Eric K. Fernström Nordic Prize in Medicine (1978) and the Wakeman Award for research of relevance for spinal cord injury from Duke University (1986). He was elected foreign member of the Royal Danish and Norwegian Academies of Sciences (1976 and 1981) and the French Academy of Sciences (1989) and was awarded a doctor honoris causa degree from the Université Libre de Brussel (1975).

During Lundberg's career, he mentored 14 PhD students and during the years in Göteborg, he was joined by nearly 50 collaborators from abroad, from PhD students to visiting professors. Those who worked closely with Anders Lundberg witnessed his enormous enthusiasm and intensity. His students experienced that he already from the start considered them as full collaborators rather than students, that he encouraged their independence and had very high expectations from them. He supported them in all possible ways to allow them to develop their own research lines. He also made personal sacrifices in the form of unpaid leaves of absence in order to free-up financial resources for temporary positions for collaborators and colleagues.

Anders Lundberg retired in 1986, after 25 years at Göteborg University but remained an active scientist for a long time afterwards. He supervised his last PhD student until 1990, co-authored his last publication in 2000, and participated in scientific discussions with former students and collaborators up to his departure.

Anders Lundberg was an outstanding scientist who was highly respected among colleagues all over the world. The words: "He has reached long and found much. His kind comes to the world not often in centuries" may apply to him as much as to Sherrington [11] and Eccles [12].

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