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RESEARCH****Review****The beginning of intracellular recording in spinal neurons:  
Facts, reflections, and speculations<sup>☆,☆☆</sup>**Douglas G. Stuart<sup>a,\*</sup>, Robert M. Brownstone<sup>b</sup><sup>a</sup>Department of Physiology, University of Arizona, Tucson, AZ 85721-0093, USA<sup>b</sup>Department of Surgery (Neurosurgery) and Anatomy & Neurobiology, Dalhousie University, Halifax, NS, Canada B3H 1X5

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## ABSTRACT

Intracellular (IC) recording of action potentials in neurons of the vertebrate central nervous system (CNS) was first reported by John Eccles and two colleagues, Walter Brock and John Coombs, in Dunedin, NZL in 1951/1952 and by Walter Woodbury and Harry Patton in Seattle, WA, USA in 1952. Both groups studied spinal cord neurons of the adult cat. In this review, we discuss the precedents to their notable achievement and reflect and speculate on some of the scientific and personal nuances of their work and its immediate and later impact. We then briefly discuss early achievements in IC recording in the study of CNS neurobiology in other laboratories around the world, and some of the methods that led to enhancement of CNS IC-recording techniques. Our modern understanding of CNS neurophysiology directly emanates from the pioneering endeavors of the five who wrote the seminal 1951/1952 articles.

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Abbreviations: AP, action potential; AHP, afterhyperpolarization; CNS, central nervous system; CPG, central pattern generator; EPSP, excitatory PSP; EC, extracellular; Ext, extensor; Fl, flexor; IN, interneuron; IC, intracellular; IPSP, inhibitory PSP; MN, motoneuron; PSP, postsynaptic potential; SC, spinal cord

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## 1. Introduction

In the first article ([Barbara and Clarac, 2011](#)) of this sequence of five historical articles on spinal motoneuron (MN) and motor unit (MU) neurobiology ([Stuart et al., 2011](#)) it was emphasized that theories on the human body's control of its musculature date back in antiquity to at least the ideas of Hippocrates [~460–380 BC] and Aristotle [384–322 BC], with substantial further advances awaiting the observations of Galen [129–216 AD] and after another long

hiatus, work in the renaissance period of the 14th to the 17th C, including, in particular, that of Leonardo da Vinci [1472–1519], Andreas Vesalius [1514–1564], René Descartes [1596–1650], and Giovanni Borelli [1608–1679]. In the articles that follow there is another long hiatus up to the 19th C, and then a focus on the 20th and early 21st C.

By the very early 20th C, it was accepted by most neuroscientists despite the vitriolic objections of Golgi ([Barbara, 2010](#)) that animal behavior resulted from brain networks that were comprised of individual neurons, as depicted so

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