

Vernon Mountcastle: Father of neuroscience

Terrence J. Sejnowski¹

Computational Neurobiology Laboratory, Howard Hughes Medical Institute, The Salk Institute for Biological Studies, La Jolla, CA 92037

The first annual meeting of the Society for Neuroscience was held in 1971 in Washington, DC. Vernon Mountcastle, the first elected president of the fledgling society, planned every detail of the inaugural meeting and was at the front door to greet everyone into what would eventually become a major scientific discipline. The Society would grow rapidly as researchers in Departments of Anatomy, Physiology, Pharmacology, Psychiatry, Psychology, Neurology, Neuroethology, Neurochemistry, Neurobiology, and Neuro-engineering found common ground in probing brains and behavior. Mountcastle, already a legend for his discoveries in neurophysiology, foresaw a future for neuroscience that transcended the traditional disciplines.

Mountcastle arrived at The Johns Hopkins School of Medicine in 1938 as a medical student and never left, except for participating in the invasions of Anzio and Normandy as a surgeon during World War II. He would succeed Philip Bard as the Director of the Department of Physiology in the School of Medicine in 1964 (see the Society for Neuroscience interview with Vernon Mountcastle in 1997; www.youtube.com/watch?v=dYssHNjydOg). Mountcastle's seminal discoveries of cortical processing in monkeys during that period were foundational.

Lord Adrian's recordings from single sensory endings and nerve fibers set the stage for the next generation to probe the central nervous system with single neuron resolution. Mountcastle pioneered recordings from single neurons in the somatosensory system. He undertook a series of experiments, recording from single mechanoreceptive nerve fibers from the skin of the hand and comparing the sensitivity of the response with psychophysical measurements. Carefully quantifying the thresholds of these fibers led to direct comparisons between the physical stimulus, the neural signals, and the perceptual correlates.

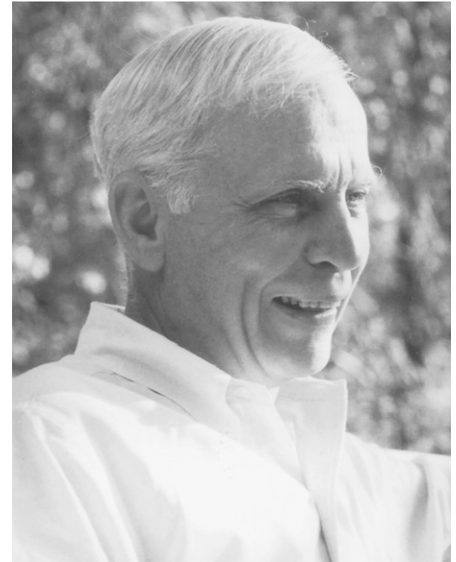
Mountcastle and his students traced touch and flutter signals through the thalamus and into the cerebral cortex, where he described in 1957, for the first time, the columnar organization within the layers of the cortex: in a vertical penetration of the cortex, successive neurons responded to the same patch of the

skin and had similar response properties. It is difficult for us to appreciate what a radical hypothesis this was at the time. Neuroanatomists, armed with the Nissl stain, saw different cell types of cells in the different cortical layers and attributed different functions to them. Although Mountcastle was not yet 40, cortical columns were considered "the musings of an old man" (1). Similar observations by David Hubel and Torsten Wiesel in the visual cortex subsequently confirmed his discovery.

Cortical areas are arranged in a hierarchy and the sensory areas feed into the association cortex. The great expansion of the cerebral cortex in humans is largely in these associational regions, which are multimodal and contain higher-order representations of the world and our intentions. Mountcastle and his students extensively explored one of these associational areas, the posterior parietal cortex in awake and behaving monkeys. He was undaunted by the difficulty in interpreting the complex properties of these neurons, which responded to a bewildering range of eye movements, hand movements, and other visually guided behaviors. The title of his pioneering paper (2) announced the discovery of "command functions for operations within extrapersonal space," which transform integrated sensory inputs into motor outputs. How to interpret these responses in the posterior parietal cortex is still debated today, although there can be no doubt that they constitute our internal representation of extrapersonal space.

Mountcastle once described his service to a physiology study section at the NIH, in which he and Theodore Bullock were the only neurophysiologists. Bullock believed that all biological systems were of equal value for research projects, whereas Mountcastle took seriously the mission of the NIH to solve human diseases, and favored mammalian research in general and primate studies in particular. "Ted usually won," he reported (1). The tension between these two approaches to biomedical research continues to this day.

Mountcastle set high standards for himself and his colleagues, whose research was elevated by his insistence on worthy goals and attention to detail. At a meeting in 1988,



Vernon Mountcastle. Image courtesy of the Society for Neuroscience.

Steven Muller, then president of The Johns Hopkins University, asked for advice from his faculty on the founding of the first Mind Brain Institute. Mountcastle responded that the time was right to undertake this ambitious goal and that he was prepared to lead the effort to establish the new Institute. Mountcastle was indefatigable in launching the Mind Brain Institute with Guy McKhann as the founding director, and he eventually joined the Institute faculty. Mountcastle devoted the final phase of his career to exploring and writing about the challenges that remained toward understanding how brains generate and govern behavior.

Vernon Mountcastle had a vision for the future of neuroscience that foreshadowed the national BRAIN Initiative announced in 2013, which he lived to witness. Some of his thoughts along these lines were expressed in a 1998 interview in *The Gazette Online*, the newspaper of the Johns Hopkins University (3), where Mountcastle states: "There is virtually no science that's not relevant to the study of the brain"; "Brain science is extremely important, independently from its importance in medicine. It provides the opportunity to understand ourselves, to

Author contributions: T.J.S. wrote the paper.

¹Email: terry@salk.edu.

