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Clinton Woolsey: Functional Brain Mapping Pioneer

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Abstract

Dr. Clinton Woolsey was a leading twentieth century neuroscientist for almost four decades. His most significant achievements were the novel use and refinement of evoked potential techniques to functionally map mammalian brains, the discovery of secondary cortical areas, and a wide repertoire of comparative neurofunctional studies across many species. We discuss his life and work through a historical context with contemporaries, highlight the primitive state of brain mapping before Woolsey, and his involvement in advancing its rapid development through work at both Johns Hopkins University and University of Wisconsin in Madison. Dr. Woolsey's lasting impact on basic and clinical neuroscience, neurosurgery, and neurology and his important roles as a scientific mentor and leader are also described.

Keywords

neuroanatomy; brain mapping; Clinton Woolsey; history

Introduction

In April 2013, President Barack Obama announced a \$100 million initiative called “BRAIN: Brain Research through Advancing Innovative Neurotechnologies.” This project's goal is to “get a dynamic picture of the brain in action and better understand how we think⁹.” This entails mapping neural connections to uncover important brain circuitry and functional pathways. Understanding the mysteries of the human brain's functional anatomy and physiology is fundamental to advance the treatment of neurological disorders. However, the quest to “map” the brain is not a novel one.

Early clinical neuroscientists deduced linkage between the brain's organization and its function primarily through observing humans with traumatic brain injuries or via stimulating animal cortices with electrical impulses⁶. The early nineteenth century saw many innovative experiments and theories attempting to assign functions to specific brain, such as Franz Joseph Gall correlating personality traits to skull shape²² and Luigi Rolando's electrical cortex stimulation experiments⁶. Dr. Clinton Woolsey's research greatly advanced prior work, and spanned brain evolution, anatomy, physiology, behavior, and sensation, and

related disciplines. His research, in conjunction with contemporaries such as Wilder Penfield, provided essential foundations for modern neuroscience.

Electrophysiology and the Cerebral Cortex: Historical Origins

Though Woolsey employed innovative approaches to study functional neuroanatomy, his research stems from a research tradition that blossomed in the 19th century. In 1870, German physiologists Gustav Fritsch and Eduard Hitzig provided early evidence for functional localization within brain cortex. Prior to their experiments, such functional organization was inferred from observing patients with specific areas of the brain damage. However, experiments aimed at discerning functional cortical regions were unsuccessful. In their 1870 study “Electric excitability of the cerebellum,” Fritsch and Hitzig demonstrated a specific dog brain region that, when excited with electrical current, produced muscle movements in the animal⁴. These findings provided important evidence for localizing neuronal function and electric excitability of the cortex – laying the foundation for future work in electrophysiology and functional neuroanatomy.

Scottish neurologist David Ferrier was intrigued by the German findings, and received a grant to further study cortical organization¹². Ferrier recognized a connection between Fritsch and Hitzig’s work and John Hughlings-Jackson’s clinical observations that related convulsions to specific areas of the brain¹². Ferrier conducted electric stimulation experiments on several mammalian species, and provided compelling evidence for functional localization in the brain¹² by producing crude “maps” that illustrated such localization. In the first half of the 20th century, stimulation and ablation experiments continued to characterize motor cortex organization, while the idea of a sensory cortex was being developed⁸. After these early European scientists first created a crude framework for brain “maps,” in the mid-twentieth century Clinton Woolsey set out to chart unknown territory.

Throughout his scientific career, Woolsey advanced and elaborated the science of localizing cortical functions, and did so in detail and across numerous mammalian species. The early work of Fritzig, Hitsch, and Ferrier started revealing motor function localization in the motor cortex, Woolsey helped functionally map the auditory, motor, somatosensory, and visual cortices. In addition, in attempting to elaborate an evolutionary framework for his findings, Woolsey analyzed and reported detailed studies of localizing cortical functions in many mammalian species.

Woolsey’s work was performed during a time of flourishing neuroscience research. While Woolsey was mapping various mammalian cortices at Johns Hopkins, Wilder Penfield was also seeking insights into cortical localization. Penfield focused on human neuroanatomy and made significant contributions to neuroscience - notably creating the somatosensory “homunculus,” a visual representation of the cortex distribution devoted to the body’s sensory reception¹⁰. The study establishing the homunculus was published one year after Woolsey’s chimpanzee brain mapping experiments began, although Woolsey’s findings would not be published for another decade⁵. To qualitatively keep track of his data, Woolsey

produced the ape analog of Penfield's homunculus, referred to by Woolsey as a "simiunculus."

From Aspiring Surgeon to Dedicated Scientist

Clinton Nathan Woolsey was born in Brooklyn, New York on November 30, 1904. He excelled academically at Olean High School. While attending Union College, Woolsey was first attracted to psychology and planned for a medical career. He entered medical school at Johns Hopkins University in 1928, with aspirations of becoming a neurosurgeon. His histology professor, Dr. Marion Hines, recommended that Woolsey work in a neuroanatomy lab to test his hands, develop surgical skills, and gain a deeper understanding of the brain before diving into the difficult field of neurosurgery. Woolsey was so enthusiastic and excited that he "didn't sleep a wink all that night"¹⁶ after Hines's colleague, Dr. Sarah Tower, accepted him into her lab. After a year in Tower's lab, Woolsey moved to the Hines lab to study cortical localization in dog brains.

Despite these promising opportunities, Woolsey never realized his aspirations for neurosurgery. His tuberculosis infection in 1932 prevented a surgical internship. Instead, Woolsey chose to remain in lab an additional year, thereby postponing his medical internship and the \$1000 Halsted surgical award he won. Despite this setback, Woolsey's tenacity caught the attention of his next major mentor, Dr. Phillip Bard. Dr. Bard provided Woolsey with more physiology research experience, an opportunity to further refine his neurosurgical techniques, and a stipend that exceeded the Halsted award. Dr. Woolsey continued working with Bard for four years, while his neurosurgical ambitions slowly faded and yielded to a lifelong passion in neurophysiology and scientific research.

Early Work on Neurophysiology and the Advent of Electrophysiology

The focus of Woolsey and Bard's early experiments was the cerebral cortex – the part of the brain most involved in sensory perception and other advanced functions. Woolsey and Bard set up experiments to analyze relationships between different parts of the body and the cortical region controlling their motor function. At first, the experiments were less than ideal. The duo relied on ablation to study cortical function, which involved creating cortical lesions in animals and observing which body parts lost motor function¹⁵. The ablation technique was useful for studying functional localization, and was then the accepted method for studying motor cortex, but did not provide quantifiable data. The arrival of Wade Marshall in Baltimore brought new techniques that advanced Woolsey and Bard's research on the cortex to an unprecedented level of detail.

While Woolsey and Bard were performing ablation studies, Wade Marshall and Ralph Gerard at the University of Chicago were attempting to use electrodes to study electrical potentials in cat brains resulting from various sensory inputs. After leaving Chicago, Marshall came to the Johns Hopkins Physiology department and agreed to bring equipment to set up an electrophysiology lab. Woolsey was intrigued when he saw Marshall's methods and conceived a different application for the new technology. He postulated that the same equipment could be used to map cortical representations of body regions by recording cortical potentials that were evoked in response to stimulating specific areas of the body,

rather than using the conventional method for brain mapping, which involved either electrostimulation or lesion of cortical areas. Woolsey's innovative use of electrodes to record evoked potentials thereby avoided cortical overstimulation or damage. His reverse strategy of stimulating the body rather than stimulating or damaging cortex yielded more precise, accurate functional mapping information of the associated sensory areas.

It was an uphill battle to start these cortical organization studies, as Marshall was resistant to the idea, since he was more interested in cellular physiology. Eventually, Marshall allowed Woolsey to use the equipment one time, on the condition that if the experiment failed Woolsey could never ask to use the equipment again. The moment of truth arrived – a rhesus macaque was prepped, the equipment readied, and electrical pulses were sent through the animal. After the trial was over, they were amazed at the results; as Woolsey recalls in an interview, “we did the first monkey and we pretty nearly mapped the whole postcentral gyrus.”¹⁶ This was the first mapping of an animal's sensory cortex carried out with substantial detail, and then the group proceeded to map the majority of the somatosensory cortex⁷. Their mapping required stimulating the body millimeter by millimeter and detailed recording of the induced cortical potentials; the average animal study took about 39 consecutive hours to complete (figure one)¹⁶. Through Woolsey's ingenuity and characteristic hard work, the team achieved a new, previously unachieved standard for detailed mapping of localized brain functions.

While in Baltimore, Woolsey mapped and analyzed with the cortices of many other mammals, including humans¹⁸. The goal of these numerous studies was to identify differences in physiology or localization between various species, and the deviations he discovered in this organization between species provided insights into how evolving brains accommodate newly developed physical traits¹⁶.

Woolsey also helped uncover an important feature of cortical organization during his early electrophysiological studies. Before starting primate experiments, it was assumed by neuroscientists that there was “a single pathway into the sensory cortex, a single pathway into the auditory, and another into the visual cortex¹⁶.” In other words, the reigning paradigm was that a single brain area managed all aspects of a given sensory function. However, in 1940, the renowned physiologist Lord Edgar Adrian claimed to have discovered a secondary sensory cortical area in cats after observing an induced electrical potential when the hairs between a cat's claws were stimulated. After failing to identify such a region in other species, Adrian concluded that this feature was unique and necessary for the cat's claw mechanism¹. However, Woolsey analyzed his own data in light of Adrian's findings, and noticed that these secondary areas were not only in the feline cortex, but also present in the cortices of many other species²¹. Further, Woolsey and his collaborators at Hopkins noticed “secondary” cortical regions for visual and auditory inputs as well. As Woolsey noted, “all of a sudden, within a period of about a year, somatosensory, visual, and auditory systems all had two areas in the cortex instead of just one.”¹⁶

Establishing and Leading Wisconsin's Laboratory of Neurophysiology

In 1947, only fourteen years after his first paper of dog cortex studies published in 1933, Woolsey's impressive body of pioneering studies on brain organization in a variety of mammalian species led to his being invited to give a special lecture at the annual meeting of the *Federation of American Societies for Experimental Biology* in Chicago; Woolsey chose to talk about "Patterns of sensory representation in the cerebral cortex."²⁰ In the audience that day was Dr. Walter Meek, director of the Physiology Department at University of Wisconsin in Madison (UW), and co-founder of the University of Wisconsin Medical School. Like Woolsey, Meek was a physiologist who was extremely interested in the nervous system. More importantly, he was a member of the committee charged with the task of recruiting a physiologist for a soon-to-be-created UW professorship. This position was offered to and accepted by Dr. Woolsey in 1948.

Initially, accommodated in Madison's antiquated Science Hall and provided with only "mediocre space and equipment"¹⁶, Woolsey's laboratory of neurophysiology was forced to return to the ablation technique that he originally utilized in his early studies with Dr. Bard, while waiting two years for the electrophysiology equipment to be built¹⁴. Despite this setback, Woolsey maintained his momentum, continuing to collaborate and innovate in his work at Wisconsin. Woolsey initially focused his research on the motor cortex, before using his new electrophysiology equipment to return to studying other cortical areas. Additionally, in 1958, Dr. Jerzy Rose moved to Madison to continue working with Woolsey and brought a microelectrode that Rose himself had helped develop³. This new piece of equipment enabled a hundred-fold amplification of detail in cortical mapping experiments. The dawn of this technology suited Woolsey's precision and he was able to conduct more novel studies to create maps of ever greater detail. This technology also formed the fundamental underpinnings of modern clinical neurophysiological monitoring.

Throughout the 1950's, Woolsey published many comparative studies examining the sensory and motor cortices of a wide range of species, using the same mapping method. While his laboratory developed, Woolsey continued to focus on studying the comparative mammalian neuroanatomy of the auditory, motor, visual, and somatic cortices. While these studies had essentially the same goals as earlier ones, they were mapped the brains of certain species for the first time, as well as discovering and exploring new cortical and cerebral regions. This work helped reveal key differences in the cortices of a wide range of species, providing insights for the evolution of the nervous system. For example, Woolsey and his team highlighted varying levels of complexity between the organization of the rat and monkey cortices, the former being organized more linearly (with respect to corresponding motor areas) and the latter possessing broken patterns of higher-order cortical areas².

After Woolsey had been in Madison and performed over a decade of inventive research, a new dean (Dean Bowers) was elected at the University of Wisconsin School of Medicine, and expanded the clinical and experimental facilities of the school. From Woolsey's arrival at UW in 1948 to this expansion project in 1960, Woolsey's neurophysiology lab had grown large enough to rival the entire Department of Physiology in terms of both research activity and staff. By constructing a new Medical Sciences Building, Bowers provided Woolsey's

lab with the means to expand. When the new facilities opened in 1960, Woolsey moved in with his “Laboratory of Neurophysiology,” now one of the most significant research groups within the Department of Physiology.

In 1973, two years before Woolsey reached retirement age, the new Waisman Center on Mental Retardation and Human Development was established on the UW campus. Woolsey, an expert on the nervous system and a valuable resource for the university, was a key member of the committee charged with designing and implementing the new Waisman facilities. With his retirement and the future of his employees in mind, Woolsey secured and moved his neurophysiology lab into a section of the new building in 1973. Only two years later, Clinton Woolsey retired from his position as the head of the Laboratory of Neurophysiology. Before doing so, he established his group as a separate Department of Neurophysiology – the first of its kind at any university. Woolsey’s motivation for creating the department was to enable his highly interdisciplinary team, comprised of scholars and scientists from many departments, to stay together and continue their research. Following retirement in 1975, Woolsey remained active in the UW and national scientific community.

Contributions to Neurosurgery and Neurology

Although Woolsey ended up choosing a life of scientific research rather than clinical neurosurgery, the results of his expertise and research studies in cortical organization are valuable in the diagnosis and treatment of neurological diseases.. Woolsey’s research on both humans and non-human primates was directly helpful to contemporaneous neurologists and neurosurgeons. In fact, during a visit to Montreal, he met another pioneer in neuroscience – Wilder Penfield – and was able to contribute to the advancement of clinical practice.

In 1947 – the same year as his FASEB lecture in Chicago, Woolsey was also invited to give several lectures in Montreal on the cortical organization of the motor and sensory areas¹⁷. One of Woolsey’s lectures was focused on his recent discovery of a second somatosensory area on the ‘upper bank of the Sylvian fissure’ in monkeys²¹. Wilder Penfield was in the audience. Penfield was focused on treating epilepsy, and his research was independent but remarkably synchronized with Woolsey’s studies. Following Woolsey’s lecture, Penfield got on stage to describe similar observations when stimulating the same region of the upper bank of the Sylvian fissure. However, based on the knowledge at that time about cortical organization, Penfield and his colleagues dismissed the possibility of a second sensory area and instead concluded that the current must have been too strong, spreading to the internal capsule to elicit leg sensation. Still, Woolsey was confident and reviewed his findings of evoked potential data recorded from the cortex after peripheral stimulation. Woolsey concluded that the data could not have resulted from direct cortical overstimulation. The data were convincing enough that Penfield decided his lab should look again and, in 1950, Penfield published “The cerebral cortex of man; a clinical study of localization of function,” confirming the presence of such an area in the cortex¹¹.

Based on Woolsey’s elucidation of the secondary sensory area on the parietal operculum along the Sylvian fissure, clinicians were soon able to diagnose epileptic foci in this area

that was previously ignored due to poor understanding of function and relative inaccessibility during operations. Once Woolsey and Penfield demonstrated sensory function in this cortical region, neurosurgeons were better able to identify epileptic foci in patients by including intraoperative implantation of electrodes in this area along the Sylvian fissure. Thus, Woolsey's research discovery of a novel cortical organization also directly benefited patient care.

After Woolsey's lecture caught Penfield's attention, Woolsey was invited on clinical rounds with Penfield at Montreal Neurological Institute the very next day. One of the day's epilepsy patients was being planned for therapeutic lesioning of his 'epileptic focus' - the cortical region thought to be responsible for seizures. At that time, Penfield's strategy to localize epileptic foci was to electrically stimulate motor and sensory cortices until he came upon an area that induced a seizure. When proceeding with this particular patient, Woolsey recalled, the surgeons were surprised when the patient reported facial sensation after stimulation of the upper postcentral gyrus near a region previously felt to be associated with the trunk. They returned to stimulate this area – not commonly thought to be associated with facial sensation – several times throughout the operation with similar results, and eventually asked Woolsey if he might have explain this anomaly. Woolsey explained that in macaque monkey studies, he had mapped an area in the same cortical region that was associated with sensory perception in the head.

Later in his career, following retirement and movement of his lab into the Waisman Center, Woolsey made further contributions to clinical neuroscience by collaborating with UW neurosurgeons. Using either electrical stimulation or the more precise and accurate evoked potential technique (depending on how much of the brain was exposed during operation), then displaying results in his signature "figurine" illustrations (figure two), Woolsey intraoperatively mapped the primary and secondary motor and sensory areas of the cortices of 20 patients¹⁹. This opportunity and the study results were significant to both neuroscience and neurosurgery, yielding a more accurate map of the human cortex – a goal that was difficult for Woolsey to achieve experimentally earlier in his career. Furthermore, two of the patients studied were experiencing phantom limb pain, and Woolsey and the UW neurosurgeons successfully determined the cortical regions connected with their phantom pain for excision. Surgical removal resulted in therapeutic 'loss' of the phantom limb sensation and pain relief.

The Impact and Legacy of Dr. Woolsey

During his time at the University of Wisconsin, Woolsey worked hard to further the research tradition of neuroscience and pursue collegial collaborations with many other scientists by conducting wide-ranging research that contributed to physiology, psychology, medicine, and evolutionary biology. Woolsey was also a leader in many of his era's scientific organizations, serving on the editorial boards of the *Journal of Neurophysiology*, *Physiological Reviews*, as an American Neurological Association representative to the National Research Council of the National Academy of Sciences, and a special consultant to the National Institute of Mental Health. These appointments reflected the respect of fellow

neuroscientists for Woolsey's expertise in multiple disciplines and his passion for advancing both basic and medical sciences.

Woolsey's lasting impact is still felt through his mentoring of many scientists and medical practitioners. While in charge of the Wisconsin Lab of Neurophysiology, Clinton Woolsey attracted graduate students from across the country and around the world. This included (at least) 100 from the United States and 43 international graduate students. Woolsey trained them in neurophysiology, but most continued in different fields – embodying the interdisciplinary scholarship of their mentor. According to Woolsey, many of his students intended to enter clinical professions and came to train with him to learn about the nervous system – much like Woolsey did in his early, post-medical school years. One notable neurosurgeon who spent time in Woolsey's Laboratory of Neurophysiology was Ron Tasker, who spent a year working on Woolsey's comparative studies of the somatosensory and motor cortices after completing fellowship in Toronto.

It is remarkable how far human understanding of the brain and nervous system advanced during Woolsey's career. But due to the brain's complexities, Dr. Woolsey recognized that despite the pioneering advances made by him and contemporaries like Penfield, there remain much to be learned about mapping brain functions. "We have learned a great deal about the brain in the half past century," remarked Dr. Woolsey upon retiring in 1975 from his position as director of the Neurophysiology Department in Madison, "but it is really only a beginning in understanding the complex and fascinating ways in which the nervous system functions¹³." Twenty years after his death, Woolsey's impact is still present in neurophysiology by virtue of the neuroscience tradition he helped start at the University of Wisconsin, and through his integral role in founding the Waisman Center on Mental Retardation and Human Development. After his retirement in 1976, the University of Wisconsin started the annual Clinton N. Woolsey Lecture series to bring leading neuroscientists to visit and speak at UW-Madison.

Clinton Woolsey passed away in 1993, but his three sons who remain involved in neuroscience today as a medical illustrator, physician, and zoologist. The work of Clinton Woolsey produced invaluable knowledge on cortical organization, comparative mammalian brain anatomy, and physiology, and contributed to many scientific fields such as clinical and basic neuroscience and evolutionary biology. Twenty years after his death, initiatives such as BRAIN will build on fundamental studies performed by Clinton Woolsey, and carry on his spirit of developing technologies and research strategies to chart the vast complexities of the brain to an even more detailed level of understanding.

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Figure one.

Woolsey performing an experiment. His cortical mapping procedures were time consuming, rigorous, and detailed. (Image courtesy of UW-Madison Archives, #S12715)

Figure two.

Dr. Woolsey with of his signature “figurine” diagrams (Image courtesy of the UW-Madison Archives, #S12716)