



Vernon B. Mountcastle

BORN:

Shelbyville, Kentucky
July 15, 1918

EDUCATION:

Public Schools Roanoke, Virginia (1924–1935)
Roanoke College, B.S. (1938)
Johns Hopkins University, M.D. (1942)

APPOINTMENTS:

House officer, Johns Hopkins Hospital (1942–1943)
Fellow, (1946–1948); Assistant Professor–Professor, Department
of Physiology (1948–1980)
Director, Department of Physiology (1964–1980), Johns Hopkins
University School of Medicine
University Professor of Neuroscience, School of Medicine (1980)

HONORS AND AWARDS (SELECTED):

Lashley Prize, American Philosophical Society (1974)
Schmitt Prize and Medal, MIT (1975)
Sherrington Gold Medal, The Royal Society of Great Britain
(1977)
Horowitz Prize, Columbia University (1978)
Gerard Prize, Society for Neuroscience (1980)
Helmholtz Medal, Cognitive Science Institute (1980)
Flyssen Foundation Prize, Paris (1983)
Lasker Award (1983)
National Medal of Science, USA (1986)
Zotterman Medal Swedish Physiological Society (1990)
Fidia-Georgetown Medal and Prize, AAAS (1990)
The Australia Prize (1993)
Prize in Neuroscience, National Academy of Sciences, USA (1998)
Cajal Prize (2000)

Vernon Mountcastle discovered the columnar organization of cerebral cortex. He pioneered the neurophysiological study of primary sensory cortex with single-cell recordings in anesthetized and awake monkeys and inaugurated the neurophysiological study of attention and action in parietal cortex.

Vernon B. Mountcastle

Ancestry and Background

I am of Scottish descent on both sides. My family name arose in Scotland in the fifteenth century, a part of the Hamilton Clan. My mother's family names are Waugh and Robertson. How or when these ancestors migrated to the United States is unknown to me, but they appear in Virginia from early colonial times. The first census of the United States, made in 1790, is published in a large book of maps, one for each state, with the name of each landholder given, and beneath it the number of "black souls." Three Mountcastle farms are shown in eastern Virginia, and beneath each name is the notation "no black souls." I attribute their abstinence to their Presbyterianism. This meant that while comfortable they could not be wealthy, for they competed in the large plantation economy of Virginia in the pre-Revolutionary period. A Robertson ancestor was clerk to the Royal Governor of Virginia in Williamsburg, and it is through him that I am descended from Pocahontas, and thus from the Indian emperor Powhatan. I calculate that given 12 to 13 generations since then about half a million Virginians could claim (or disown!) that descent.

My paternal grandfather was born in 1841 in Charles City County in Virginia. He and his three older brothers rode in the 3rd Virginian Cavalry of Stuart's command throughout the Civil War. My grandfather sustained a gunshot wound to his arm in the battle of the Wilderness, survived amateur surgery for bullet removal by his brothers, and thus avoided the military hospitals, where amputation was routine, and death probable. The four brothers were demobilized at Appomattox and returned to Charles City County to find their homes destroyed, and their farms overgrown, for this county had been a part of the battlefield of the Peninsula campaign of 1862. The Civil War generation of 1865–1890 worked indefatigably in the postwar period of reconstruction to re-create a decent life. This generation of Virginians was called by Gerald Johnson "The Boys of New Market." My ancestors were not at New Market, but the description fits. My grandfather did not marry until 1889, which accounts for the generation gap in my family. No member of my family earlier than my own generation had a university education: they were all farmers, industrial entrepreneurs, or builders of railroads.

Childhood and Education

Our family moved to Roanoke, Virginia, in 1921, when I was 3 years old. The home office of the railroad construction firm in which my father was a partner

was in Roanoke, and the move must have been impelling for that reason. Another was to provide access to the fine public schools of Roanoke for my two older sisters and myself, and eventually for my brother and a younger sister who joined us later.

We moved into a pleasant house on a street lined with maple trees, only two blocks from open country. The community was almost ideal for me. The elementary and the junior high schools were within easy walking distance, as was a branch of the public library. There were three tennis courts in the neighborhood; I began playing at 8 years and continued my favorite sport until I was forced to stop at 80. Beyond that, 12 boys all aged within 2 years of each other lived within a radius of two blocks. This led to team sports of football and baseball, with organized games with teams from other neighborhoods. This dozen remained my friends for many years, but only three now survive. I was an enthusiastic Boy Scout and found earning merit badges another education. Summer scout camp high in the Alleghenies was a thrill. It cost only \$12 for 2 weeks; it must have been heavily subsidized.

My mother had been a professional teacher before marriage, and she taught me to read and write by the time I was 4 years old. Thus when I entered the public school system I was immediately moved ahead two grades. I remember many of my teachers with respect and affection, particularly my Latin teacher, Miss Sally Lovelace, who taught us the history of Rome and Greece, as well as 4 years of Latin. This accounts for my enduring interest in ancient history, of which I still read a great deal. The high school courses in the humanities and civics were excellent; I know now that those in the sciences were poor.

I graduated from high school at 16, and in September 1935 I entered Roanoke College, located in a nearby town, Salem, Virginia. I lived at home and commuted. It was the midst of the Depression, and I was lucky to go to college at all. This small college of about 300 students had a fine faculty of 14 professors, all devoted to teaching. I majored in chemistry and finished in 3 years. When I set about applying for medical school I had no schools in mind except the two in Virginia. However, my teacher of chemistry had been trained at Hopkins and suggested I apply there. I did so with no hope of acceptance. The acceptance letter arrived on Christmas Eve of 1937; my mother immediately declared that I should not go to school with "all those Yankees!" But go I did, and save for World War II I have remained all my life in that extraordinary place.

I arrived in Baltimore on October 1, 1938, and went by taxi to the School of Medicine, in East Baltimore; seeing that city was itself a depressing experience. I opened an iron gate and entered the Medical School square; except for the Welch Library, the square was formed by a number of dilapidated buildings, some undoubtedly condemned by the fire department, but exempted by special dispensation. In the center were several large cages filled with macaque monkeys, which I had never seen before. I approached the school

entrance (it led to the basement, alongside the men's latrine) and observed just outside a large hand-printed sign saying, "Watch out for falling snow"—the temperature was in the 90s! I concluded that an institution with a sense of humor like that was just for me; I entered and I never left.

What mattered were the people in those buildings.

Johns Hopkins: Medical School and Internship

The first-year class I entered contained 75 students, many graduates of Ivy League universities, with much better educations than my own. We were taught by an equal number of faculty members of the basic science departments, all active in their own fields of research. Teaching was direct and personal, largely in laboratories and discussion groups. The first year was arranged in the block system in which we took only one course at a time—full-time. The anatomy sequence occupied the first two 8-week quarters, followed by a quarter of physiology and then one of biochemistry. There were no tests or examinations at all until the final week of the year, and we were never given any grades. Failure was signaled by a private letter, and only two members of my class failed to reach the M.D.

The Department of Anatomy was an active research institute in which investigations ranged from histochemistry to physical anthropology. It was directed by Lewis Weed, known for his studies on the circulation of the cerebrospinal fluid, and staffed by Straus, Shultz, Hines, Tower, Streeter, Flexner, Howe, and half a dozen others of equal distinction. I remember well my first-year examination in Anatomy. I entered the room to find Drs. Weed and Hines standing to receive me. I was not asked to sit down, nor did they. There was long table covered with dissected specimens, and several microscopes and many slides. The questions began, for example, "Show us the branches of the brachial plexus and tell us the muscles innervated by each"; "Look at this section, identify the tissue and tell us its organization, innervation, and blood supply." And so on, for nearly an hour. I staggered out feeling like a boxer taking a standing eight count and convinced that my days at Hopkins were over. Somehow I survived.

The course in physiology consisted largely of laboratory and small-group sessions, with the fewest possible lectures—in my year about 40. The laboratory teaching was done by the most senior faculty, with no teaching assistants. I remember a cardiovascular laboratory exercise in which Philip Bard stood for 2 hours at our table, teaching us to observe for ourselves, and to make independent interpretations of what we saw. The course in Biochemistry was equally intensive, taught by William Mansfield Clark and his staff. We all feared this course because it demanded a background in physical chemistry, which I and many of my classmates had never had. I learned later that Mansfield Clark was an amusing companion, but in the spring of 1939 he was a threat to my remaining in medical school.

We were also scheduled in this year for a course called "Psychobiology." The major task was to write a personal life history. This was submitted to a senior member of the staff of the Department of Psychiatry, followed by an hour-long conference with a faculty member. Mine was with the Director of the Department, Adolf Meyer. He had read every word I wrote and remembered them all. He probed at some spots and left me with the message that to deal with patients one must first know and understand oneself, a lesson I never forgot. The first three quarters of the second year passed in intensive study in pathology and bacteriology, under the direction of Arnold Rich, a brilliant and somewhat eccentric man. In his first lecture he challenged us to "define what is living." He demolished all our ideas. During the fourth quarter we were scheduled for a course labeled "Introduction to Psychiatry" for eight Friday afternoons. There was no course description, we had only to report. And we did, climbing to that ancient and dusty lecture room in the Phipps Clinic building, each seeking a seat in the back row. Before us we saw Adolf Meyer, seated at a deal table: huge head, bearded, his feet not quite reaching the floor beneath the table. He made a few introductory comments, of which we understood nothing. Then the bombshell: we were to be shown a patient—for the first time, a patient! White suits opened a door at the rear of the stage, and there bounded into the room a wild-haired man who dashed around the room shouting, "I am the king of Siam." White suits calmed him into the chair by Dr. Meyer. The latter spoke, over cathedralized hands, "Who are you?" The patient made another trip around the room and went back to the chair. Meyer had not moved a muscle, and now he asked, "Who am I?" The quick reply from the manic patient: "You're a little bastard with a red tie on." We, the students, burst into laughter. White suits removed the patient, and Meyer gave us a lecture on how to behave in the presence of a patient. I have often wondered whether Meyer laid the whole thing on, but my friend Jerome Frank assured me that Dr. Meyer would never have been so duplicitous. But, having known many Hopkins professors, I remain skeptical. I left that session knowing I had been exposed to a first-class intellect, and I have never forgotten that searing question, who am I?

I spent the summer after my second year working in the Department of Pathology at the Philadelphia General Hospital, the old city hospital where Osier had spent several of his early years in the United States. There were several autopsies each day, and what we learned was mainly gross pathology. The safety precautions were primitive, and I had a great fear of infection with the tubercle bacillus, for we frequently dealt with tuberculous empyema. In fact, my classmate and companion there, Giles Filley, did later come down with the disease.

The third year was consumed in being taught with patients and instructors in the outpatient clinics. The most memorable of these were our visits to what was called "City Hospital," now the greatly elaborated and modern Bayview Medical Center of Johns Hopkins. That hospital in 1940–1941 was

filled with chronically ill patients, and seeing them was an important part of our education. Almost every chronic disease was demonstrated to us, particularly those of the nervous system. I remember a clinic with John T. King, a distinguished Baltimore physician. He showed us a patient, just off a ship from South America, with signs of Kaposi's disease—blood-filled subcutaneous tumors over his entire body. I have since wondered, could that have been an unrecognized case of AIDS, in 1941?

The fourth-year quarter in internal medicine was the most intensive learning experience of my life. Imagine a ward of 25 patients, 5 students, 2 interns, assistant resident Philip Tumulty, and Maxwell Wintrobe as faculty (he was then preparing for his position as Head of Medicine in the new school in Utah), and a laboratory where the students did the lab work. It was total immersion, day and night. Ward rounds were made daily by Wintrobe, and weekly by Professor Warfield Longcope, the Director of the Department of Medicine, to whom we presented our cases. He questioned us closely, remembered every detail of each patient from week to week, and insisted we follow each patient daily by direct observation. The final week of that year brought oral and written examinations in all the clinical disciplines, a period of considerable stress. It was wartime, and there was no graduation ceremony; we received our diplomas by mail.

During my time in medical school I had no objective other than to become a surgeon, and preferably a neurosurgeon. In fact I never did an experiment until my 28th year. I applied for and was appointed House Officer in surgery in the Johns Hopkins Hospital for the year 1942–1943. I had already done a good bit of interning, for the approach of the war had depleted the house staff, opening many opportunities for third- and fourth-year students to “substitute” as interns. This almost led to my dismissal from medical school, as I explain below.

The course in obstetrics was the only abysmally taught course I encountered at Hopkins—filled with interminable lists of statistics. I simply cut the course and interned in surgery. After a few days, a call: report to the Office of the Director of the Department of Obstetrics, Professor Nicholas J. Eastman. He had discovered my absence, and although attendance at lectures was always voluntary, he had taken great offense at my absence. He was furious and at once proposed to take me to the Dean's office for dismissal from the school. I knew this was an idle threat and remained silent. Finally, he dismissed me with the warning that the final exam in obstetrics was only 2 weeks away. I immediately quit interning, bought *Williams Obstetrics*, moved into a third-floor bedroom on North Broadway, and memorized the book. When the exam was over, I returned to interning. Then, another call came to visit the Professor of Obstetrics. He was even more furious, his little mustache quivering on his upper lip. He had my paper on his desk. “Mountcastle, we do not give hundreds, you made ninety-eight: goodbye.” Of course, I forgot most of it rapidly.

I spent the summer of 1942 working as the intern on Dandy's brain team. An internship at Hopkins was in those times total immersion; one was on duty 24 hours a day and there was no official time off. I spent several of the months of my intern year working in the Hopkins accident room, and there could have been no better training for my later experience in the Naval Amphibious Force. I had been a member of the Naval V-12 corps for medical students since January 1942, which allowed me to finish medical school and internship.

U.S. Naval Amphibious Force

In June of 1943 I received orders to report to the Naval Operating Base in Norfolk, Virginia, and early in July several of my classmates from Hopkins and I arrived there together: Edward Novak, George Mitchell, William Higgins, John Classen, Stuart Christhilf, and myself. Novak, Mitchell, and I were directed to the noon conference of the Chief of Surgery. We marched in and were ordered to stand at attention before him. We did so but certainly must have looked a bit sloppy, for we had never stood at attention before. He was Commander Deaver, the son of the man who devised the Deaver abdominal retractors that tortured the hands of generations of surgical interns. His first comment, delivered with a sneer, was, "So you're from Hopkins." We confessed we were. However, he could do us little harm, for we were in Norfolk "awaiting further orders." Mine arrived in mid-August: report to the 3rd Naval District in New York for duty with "Glen-57"—no news of the nature of Glen-57. I went to New York and, after a 5-day delay, was sent to Bayonne, New Jersey, to board a refrigerator ship converted to a troop transport. Once at sea I learned we were headed for North Africa. After three days at sea a loudspeaker announcement ordered all Glen-57 personnel to report to the officer's wardroom; in Navyspeak, the order was, "Lay up to the wardroom," where as a junior officer I had not previously been allowed. There I discovered that Glen-57 was to be a shore-based general hospital, not yet constructed, near Oran, Algeria. I joined a group of physicians all one or two decades older than myself. The commander was a kindly and able regular Naval physician. It seemed a fortunate assignment. Upon arrival in Oran on September 1, 1943, I saw the hulks of the French Navy, sunk by the British to prevent their falling into German hands. I also saw a line of U.S. soldiers marching along the pier and embarking for the Salerno invasion; they were bronzed, athletic, and confident and filled me with pride. They were part of the 3rd division which, together with the 36th and 45th, bore the brunt of the fighting in the Italian campaign.

We were sent for temporary billeting to a group of French vacation huts on the sea at Arzew, 50 miles east of Oran. It was like a summer vacation at the beach, with the prospect of 2 months before the hospital was completed. This vacation in wartime disquieted me. After a few days I requested transfer

for temporary duty with the Army and was sent to an Army general hospital in a French hotel in the Atlas Mountains, 50 miles south of Oran. There I served for 2 months in charge of an orthopedic ward filled with casualties from the earlier Tunisian campaign. I then returned to our completed hospital for a few weeks, but in January 1944 I was ordered to sea aboard LST 378. I served on four LSTs in the Anzio and Normandy invasions (described later) until I was ordered back to the amphibious training base in November 1944. That training was of course for the planned invasion of Japan.

The Anzio Invasion

During my time in the med I survived three life threats. The first was a typhoon in the Tyrrhenian Sea with 65-mile-per-hour winds. The second was the Anzio invasion, at first a cake walk, but later a disaster. During our daily round trips from Naples to Anzio we encountered only occasional shelling, and airborne bombs launched from high-flying German planes. Here I dealt with the bravest man I ever knew. An LST (Landing Ship Tank) carries six small boats, called LCVPs; in an invasion these are lowered to the sea and carry soldiers to the hostile shore. The six are commanded by a "small boat officer," an ensign from the LST crew. At about 3 AM on invasion day we anchored 3 miles off Anzio. Immediately the order, "Lower small boats" rang out, but no one could find our small boat officer! During the search I saw in a corner of the bridge a pile of kapok life jackets and heard emitting from the pile the beautiful sound of an Irish flute playing the "Blue Island Blues." There the small boat officer was hidden, trembling with fear, playing his flute. I was told later that he had performed magnificently at an earlier invasion at Licata, in Sicily. A few moments of encouragement, and my promise that I would be waiting for him on his return, and this trembling young boy went over the side and led his boats onto that hostile shore.

The third was more serious. For several weeks we made daily round trips between Naples and Anzio. Upon return from one of those we were lashed out board another LST in the port of Pozzuoli, on the southern shore of the bay of Baia, where Caligula had built his bridge of ships. A sudden violent storm parted the lines from the inboard LST to the dock, and we two, bound together, were swept across the bay to land on its northern, rocky shore, we inboard. The outboard LST parted the lines and got away, but we were marooned on the rocks, our ship's bottom torn out, with no power and nothing to do but await rescue; meanwhile, we ate all the steaks.

But doctors were not allowed to be idle for long. I was lifted off and transferred to another LST, and later back to my base in Oran. We all knew that the Normandy invasion was coming soon, and I maneuvered to be in it by getting myself ordered to another LST, the 539, which I knew was headed for Great Britain. (Those in charge were always a bit surprised but happy when a physician requested sea duty!). The skipper of the 539 was a giant of

a man, in prewar times the chief boatswain's mate on the battleship *North Carolina*, and heavyweight boxing champion of the Pacific fleet. His officer corps consisted of six ensigns fresh from a brief period of training, and all on their first sea voyage! We set out for Great Britain, in the usual zigzag convoy. The skipper had so little confidence in his officers that he never left the bridge during the 13-day voyage to Cardiff, Wales. He knew very well that his career as an officer depended on avoiding any disaster, such as ship collision while in convoy, always a risk. I sustained him by thrice-daily deliveries of the most atrocious drink every concocted: three ounces of Lejon brandy, a large supply of which I found in the medical stores, labeled for "resuscitation." It worked.

The Normandy Invasion

It is difficult to describe the high state of morale and adventure that pervaded the Allied soldiers and sailors as we set out from England on the early evening of June 5, 1944. We felt we were on a noble crusade! We were garbed in heavy clothing impregnated with something said to neutralize poison gas, but no gas attack occurred.

We disrobed as soon as possible. The scene in the Channel is embedded in my memory: ships of all sorts, as far as the eye could see. The sight of this massive armada must have demoralized the German defenders when they viewed it at first light on June 6. We carried soldiers of a U.S. division slated for Utah beach. My LST had been designated a medical emergency ship and flew a special signal flag to that effect. I had been joined by two middle-aged Army physicians, one an obstetrician, the second a urologist. Neither had any previous experience in emergency surgery, but they performed magnificently in the emergency I describe below. I also had a group of Navy medical corpsmen, to whom I wish to pay tribute for their skill and dedication to the tasks we encountered. We were loaded with medical and surgical supplies, together with, for the first time, typed blood for transfusion.

Our approach to and landing on Utah beach was hindered only by occasional gunfire, and no air attack; we unloaded and withdrew without casualties. On the second day a destroyer hit two mines and blew up, near us, producing in her crew a large number of compound fractures and associated head injuries. These men were cast overboard as the crew abandoned ship. Many of them were rescued by a PT boat, which quickly drew alongside my LST. I swung by rope to the deck of the PT boat and began loading the injured into stretchers for hoisting to the deck of the LST. Summary: 39 compound fractures—in two limbs in many, and of three limbs in one (we saved him!). We stabilized the fractures as best we could, gave morphine and intravenous transfusion, and saved almost all from early death from vascular shock, which I knew well as a student of Alfred Blalock. We were then ordered to the beach to receive 200 walking wounded; many of them were,

however, severely wounded and brought aboard in stretchers. We lashed the stretchers to the walls of the tank deck of the LST, three high, and began a survey of wounds. We found many of these soldiers in extremis and gave emergency treatment to those threatened by immediate death. Our 48 hours of continuous work with these wounded men saved many. However, as the death rate began to mount I became desperate. I knew there was a superb British emergency hospital in Southampton, only 5 hours sail away at flank speed. I persuaded our captain to make requests that we leave at once for Southampton. All requests were denied by the British commodore in command of our flotilla. He feared German submarine action in the channel, and perhaps correctly so, but no such attack ever occurred. We sat for 5 days as the death rate among our casualties rose. Finally we sailed to Southampton and off-loaded all surviving wounded to the hospital. I expressed some criticism of the British commodore's refusal to allow our departure, though of course he was right, in military terms. My criticisms apparently became known and were passed up channels, for Eisenhower had commanded that no American officer utter any criticism of a British colleague! His order was the first thing I saw posted on the bulletin board when I arrived in North Africa. As a result I barely escaped being cashiered from the Navy, as I recount below.

During the months from June to November, 1944, we worked continually on the supply run between England and the French coast, and later to Cherbourg. We frequently worked out of the Tilbury docks in London, and I observed the destruction imposed on the British by the German air offensive. I was impressed by the grit and determination of the Londoners, who worked continuously through a host of continuing air attacks.

In November of 1944 I received orders to return to the United States and report to the amphibious base at Camp Bradford, Virginia. While awaiting transport I was sent to a camp in the beautiful apple country of South Devon. One day a commander came on a visit from London, and in the washroom next morning he said that they (meaning those in London) had heard of my criticisms of the actions of a British officer during the Normandy invasion. "Won't you come up to London and tell us about it." I knew what was up. I declined, saying that I had orders to go home, and he had no orders to force me to go to London. I escaped what could have been a disaster for me.

Shortly thereafter I went by troop train to Gurock, Scotland, and boarded the *Queen Elizabeth I* for Boston. I remember well the arrival in Boston. The shore was filled with cheering people—not for me but for the soldiers aboard. I soon carried out my orders to go to Camp Bradford, in Virginia. While there I was able to spend several weekends at home in Roanoke and reawaken an old but until then distant acquaintance with a charming and beautiful lady. Nancy Clayton Pierpont and I were married on September 6, 1975, and began a blissful marriage that has now (in 2007) lasted

62 years and produced three children, six grandchildren, and one great-grandchild; we hope of more of the latter to come!

However, on August 15 the war ended. I heard the news of the Japanese surrender by loudspeaker as I walked across the parade ground at Camp Bradford. One could almost hear the weights dropping from shoulders: we would not have to invade Japan! As luck would have it, I received insufficient points for discharge from the Navy because we were married after the end of the war. That cost me an extra year in the Navy.

My Postwar Year in the Navy

I was then sent to the Norfolk Naval Hospital and given charge of a medical ward filled with 150 chronically ill sailors. That I was given this responsibility shows how thin the Naval Medical Corps was in the immediate postwar year. Some of these patients had regional ileitis and had been treated disastrously by successive resections of lengths of small bowel. The disease always recurred. Many others were survivors of severe hepatitis and had compromised liver function. Several of these chronically ill men weighed little more than 100 pounds. I worked hard to improve their nutritional states. I gave my first ever medical paper on these two conditions at a Naval medical congress held at the hospital. I cited the ileitis case histories as evidence that in the absence of perforation or obstruction, surgery is not a proper treatment for regional ileitis.

But then, sea orders again. I was named the medical officer on a new ship of the train then under construction in Tampa, Florida, the *Cadmus*. I was sent first to the Brooklyn Naval Supply Yard to check the medical supplies for the ship; then to Newport, Rhode Island, to care for the crew then in training there; and then for precommissioning work in Tampa. The ship was magnificent and included what was virtually a hospital: 26 beds, isolation ward, operating rooms, special rooms for treatment of venereal disease, etc. The *Cadmus* was a huge repair ship, designed to repair war vessels at sea. The commissioning work completed, the crew aboard and training, we departed on the shake-down cruise, from Tampa around Florida, and then north into the Chesapeake Bay. There, just as the *Cadmus* was to leave for extended ocean duty, I received orders to proceed to Washington for discharge from the Navy. They were the happiest orders I ever received.

Transition to Physiology: Fellowship Years

I left the Navy in July 1946 and immediately sought a residency in neurosurgery, my long-term goal in medicine. Dr. Walter Dandy had died in April 1946. I learned upon returning to Hopkins that Dr. Blalock would make no house staff appointments in Neurosurgery until Dr. Dandy's successor was

named. I immediately went to Duke University in Durham, North Carolina, for an interview with their Professor of Neurosurgery, Dr. Barnes Woodhall, a Hopkins graduate, former resident surgeon in the Hopkins Hospital, and a distinguished neurosurgeon. He was very glum, saying there were a half-dozen candidates ahead of me. I then on impulse asked him how he would regard me if I spent an intervening year working with Philip Bard at Hopkins. Woodhall jumped from his chair, tapped me on the chest, and declared that if Bard would have me around for a year, I could have his residency. I returned to Baltimore for an interview with Dr. Bard. He came in to see me in typical Baltimore August weather. He recounted his wartime experience, off Nova Scotia, in LSTs with Denny-Brown, testing candidate preventive drugs for motion sickness. Then:

BARD: Do you think there is a psychological factor in motion sickness?

VBM: NO.

BARD: Come in September.

I was astonished and suggested that he might wish to reconsider, and then asked him to write to me in Roanoke. That tore it: there was no letter, just a request to come in September. I arrived September 1 to learn by telephone that he was writing at home. He obviously did not know what to do with me. I suggested a month's reading in the Welch Library. He was delighted, and so was I. Thus I conjecture that I am perhaps one of the few neurophysiologists of my generation who has read (almost) all of Sherrington. I also read Cannon, Bard, Woolsey, Forbes, Adrian, and a good deal of clinical neurology, and I studied neuroanatomy intensely in preparation for the coming year.

In 1946 the Department of Physiology contained five faculty members: Philip Bard, its director; Chandler Brooks, that year on leave with Eccles in New Zealand; Clinton Woolsey; Evelyn Howard, an endocrinologist; a newly arrived neuroanatomist, Jerzy Rose; and a superannuated graduate student, Reginald Bromley, just returned from six years in the Canadian Army. Bard had appointed six postdoctoral fellows in that first postwar year: H. T. Chang, from China; LeMessurier, from Australia; Evelyn Anderson, an endocrinologist; Leonard Jarcho; Elwood Henneman; and myself. The department contained a library, one telephone line, an animal room, an operating room, and an ancient electrophysiological rig Woolsey had brought back from the Johnson Foundation in the mid-1930s. That was it.

That sounds dreary, but exactly the opposite was true, for the department was pervaded with an electric excitement about research on the physiology of the brain. That atmosphere was cultivated by Philip Bard himself. He exhibited in a powerful way what was then the prevailing atmosphere at Hopkins, which I term "the expectation of excellence." He simply assumed that we were all skilled investigators, which we were not (and he knew it);

that we were all well-informed neuroscientists, which we were not (and he knew it); and that we were all in the process of making important discoveries about the function of the brain, even though we were beginners (and he knew it!). I experienced this strong pull from above from the dean, from my revered teachers of medical school years, including my Chief of Surgery, Dr. Blalock. They all seemed to think that I was better than I thought I was! This was a strong and sustaining influence on me during my early years in neurophysiological research.

I abandoned my career goal of neurosurgery and stayed a second year as a fellow. During that time I assisted Bard in a number of investigations. The first was to determine whether the visceral afferents played any role in producing motion sickness. He prepared and I nursed and tested five dogs with high spinal transections, vagotomies, and total sympathectomies. The result: no change in swinging time to salivation, the prodromal sign of motion sickness. The second was aimed to determine if any particular forebrain structure was critical in the control of rage, which he had shown in his doctoral work at Harvard to follow decortications. We studied cats with a variety of forebrain removals. The result was that removal of the neocortex alone, leaving all limbic structures intact, produced placid animals who did not display the violent rage reaction of wholly decorticated cats. Subsequent removal of the surviving limbic structures uncovered the classical rage reaction (Bard and Mountcastle, 1947). In the third study we sought to determine if the removal of any part of the temporal lobe or subjacent structures of the forebrain would convert the wild and unmanageable macaque monkey into the placid and easily handled animal produced by large temporal lobe removals. We found that bilateral removal of the amygdaloid complex produced the placidity described by others. This work was never published.

During these years I began electrophysiological experiments with Elwood Henneman, later Professor of Physiology and Chair of the Department at Harvard. We mapped with gross electrode recording the patterns of representation of the body in the thalamus of cats and monkeys (Mountcastle and Henneman, 1949, 1952).

At the end of my fellowship years I became a member of the department and abandoned my career goal in neurosurgery. I was encouraged by Bard to begin my own research program. I was given total freedom to do as I wished and allowed 6 years of daily laboratory work with no press to publish, no requests that I ask for external support, and only 9 to 10 weeks of teaching in each year. However, even though most of the departmental members were neurophysiologists, we were obligated to teach the general course in physiology for students of medicine. My first assignment was five lectures in gastrointestinal physiology. They took me a month to prepare.

During those years I taught myself neurophysiology by repeating many of the classical experiments—for example, the spinal cord preparation used by Lloyd and Eccles. This proved useful when I began a study of the central

projections of deep afferents with two of Dr. Bard's postdoctoral fellows: Miguel Covian, later Professor of Physiology at Ribeirao Preto in Brazil, and Clinton Harrison, later a prominent neurosurgeon in Baltimore. We stimulated the nerves to deep structures and monitored the composition of the afferent volleys by recording the ventral root reflex discharges they evoked. We confirmed the well-known projection of muscle afferents to the cerebellum and sought to determine which components projected to the cerebral cortex, with indifferent success. We also observed a hitherto unknown form of somatic sensibility, that light mechanical stimulation of the periosteum evokes an input to both somatic sensory areas of the cerebral cortex. The periosteal afferents are so sensitive that they respond to even a light mechanical stimulus to the overlying skin, and I believe they must play a role in tactile sensibility (Mountcastle, Covian, and Harrison, 1950).

My first postdoctoral fellow, Edward R. Perl, arrived in 1950 and expressed an interest in the small afferent fibers and the neural mechanisms in pain. Perl was already a much more experienced investigator than I; while a medical student at Illinois he had devised a method of measuring cardiac output by recording changes in impedance across the chest wall. He devised a sensitive pressure clamp, and with it he was able to block the A-fiber component of a dorsal root volley and observe the reflex discharges produced by a pure C-fiber input. He observed the widespread ventral root discharge pattern predicted by what was known of the flexion-crossed extension reflex evoked by nociceptive input. This work was left unfinished when Perl was called away in the doctor draft. Edward Perl continued his interest in the central neural mechanisms in pain throughout his distinguished career, first at Utah, and then as the long-time Chair of the Department of Physiology at the University of North Carolina, a pattern of discovery he continues to this day.

I interrupt recounting this story to express my great admiration for and gratitude to the individuals who came to work with me in CNS physiology in following years. Many of these individuals were already sophisticated investigators when they came and contributed ideas and techniques I would not otherwise have had. They number 48, of whom 33 at this writing (2007) have become professors in their own institutions. Thirteen were graduate students. I name them in alphabetical, not temporal, order.

Carlos Acuna
Richard Andersen
Sven Anderson
Pradep Atluri
Frank Baker
Alvin Berman
James Campbell
Giancarlo Carii

Mirko Carreras
Ian Darian-Smith
John Downer
Charles Duffy
Robert Dykes
Solomon Erulkar
Apostolos Georgopoulos
Edward Glaser
Gundez Gucer
Thomas Harrington
Clinton Harrison
Juhani Hyvarinen
Kenneth Johnson
Cecil Kidd
Hans Kornhuber
Robert LaMotte
James Lane
Randall Long
James Lynch
Michael Merzenich
Mark Molliver
Brad Motter
Hiroshi Nakahama
Edwardo Oswaldo-Cruz
Edward Peri
Gian Poggio
Thomas Powell
Barbara Renkin
Rodolfo Romo
Sten Skoglund
Michael Steinmetz
Tadaaki Sumi
William Talbot
James Taylor
Thomas Yin

With the progress of central nervous system (CNS) physiology over the years, the experiments became increasingly complex, particularly in the era of the waking monkey experiment, and could only be executed by the collaborative effort of individuals with different skills. William H. Talbot assumed control of our computer operations and wrote all the training and collection programs, at first on the original LINC and then with PDP 11s. Edward H. Ramey designed much of the specialized electronic equipment needed and manufactured it in our shops, with the help of Victor Meinhardt.

We were fortunate to have the collaboration of a skilled engineer from our Applied Physics Laboratory, John Chubbuck, who designed and had manufactured our complex stimulating apparatus. Belan Fortune, a skilled histologist, provided serial sections of all our experimental brains. These individuals contributed magnificently to the success of our research programs, which grew to occupy four recording laboratories.

Single-Neuron Studies of the Somatic Afferent System

By the year 1948–1949, Adrian’s method of single-neuron analysis had become the dominant mode of research in CNS physiology. It is worth noting that virtually no one in the field was entranced by the study of single neurons *per se*, but all sought to reconstruct population events by studying neurons one by one. This of course lost what may be of critical importance: the time relations between the impulse discharges of elements of the population, now under intensive study in the new century. Jerzy Rose and I began a program using this method in study of the somatic afferent system, beginning in the cat ventrobasal complex. We made a quantitative study of the response properties of thalamic neurons but at this level of the system saw little other than a tenacious replication of the first-order input, and little sign of what we had hoped to find—some aspect of neuronal processing suggestive of perceptual operations (Rose and Mountcastle, 1954). During those long days and nights I learned a great deal about the history of Poland, and he something of Stonewall Jackson’s genius in the Valley Campaign.

We then set about separate studies of the cerebral cortex, he in the auditory cortex together with Philip Davies and a graduate student, Solomon Erulkar, later a professor of pharmacology at the University of Pennsylvania, and I in the somatic sensory cortex, together with Davies and Alvin Berman, a graduate student, later a Professor of Neuroscience at the University of Wisconsin. The technical problem of stability was solved by Davies, who devised a closed recording chamber that stabilized the cortical surface within the chamber; he then worked with both of us in the separate studies.

My own studies are described in two papers of 1957, in which I described the columnar organization of the cerebral cortex (Mountcastle, 1957; Mountcastle, Davies, and Berman, 1957), Evidence for columnar organization is simple and convincing and can be demonstrated on any experimental day. To wit: in a microelectrode penetration made vertically to the cortical surface, one encounters at each succession of depths neurons with similar functional properties, which we called “modalities,” with overlapping peripheral receptive fields. In contrast, when penetrations are made slanting across the vertical dimension of the cortex, one encounters successive blocks of tissue containing neurons with different properties. Many friends have inquired why the description of this general principle is contained in the paper authored by me alone. The answer is: by request! My two colleagues

were so apprehensive over my proposal of such a radical hypothesis that they sought to disavow themselves from it! Indeed, it is not possible to exaggerate the calumny I was subjected to over this proposition, and with the most vigor by my colleague Jerzy Rose. He and most other anatomists had been trained in the schools of Nissl cytoarchitecture, Rose by the Vogts themselves, and the idea of layered cytoarchitecture dominated the scene; some even designated different layers for different functions! All this was before the revival of Cajal-type studies of the cortex. One critic said that the idea was just the “musings of an old man,” and I was only 39! Columnar organization was confirmed in a few years for the visual cortex by Hubel and Wiesel, and then by many others for the homotypical cortex as well, and it is now part of the cortical zeitgeist.

In earlier studies of the thalamus I had observed neurons in the posterior nuclear group that responded specifically to noxious stimuli. I then took up this study with my long-term colleague and friend, Gian F. Poggio, from Genoa, using the method of single-neuron analysis. We defined the posterior nuclear group as one receiving a powerful nociceptive input, and this has now been confirmed as one of the relay nuclei for the pain system in primates, including humans (Poggio and Mountcastle, 1960). Poggio remained for many years as a professor in the department, devoting his independent efforts to study of the visual cortex, with original and important results.

The Primary Sensory Cortex in the Primate

I then took up the study of the monkey postcentral gyrus in the anesthetized macaque monkey. One day, as I was laboring to clean up the lab after a long experiment, the fifth in the series, a young man wandered in and introduced himself as Tom Powell, adding that he had come from Oxford to work with me. I had no prior knowledge of his coming; I think it must have been arranged between Bard and LeGros Clark, then Head of Anatomy at Oxford. What luck for me! We began an intensive, productive, and pleasant collaboration in experiments on more than 50 monkeys, and a warm friendship that lasted until his death. We obtained convincing evidence for the specificity for place and modality from the periphery to the postcentral cortex, documented extensively the columnar organization of the cortex, showed the gradient of modality representation from area 3 to 1 to 2, and made attempts to study the temporal patterns of neuronal activity. The results are described in four papers in the *Hopkins Medical Bulletin* (Mountcastle and Powell, 1959a, 1959b; Powell and Mountcastle, 1959a, 1959b). This pleasant relation was sustained in several following years, in each of which Powell returned to Hopkins for a period of 2 months to join us in teaching our combined course in neuroscience for students of medicine.

However, there remained the problem of the anesthetized state, which we surmised affected powerfully the dynamic activity in the nervous system,

just what we wished to study. We had long dreamed of studying the somatic system as an animal worked in a somesthetic task. It would be a decade before we reached that level.

Before that, an important event: one day a slightly built, partially bald man of early middle age appeared in my office. He declared, "I have come to become a neurophysiologist." He was Gerhard Werner, who became a valued colleague in research, and a lifelong friend. He was subsequently Professor of Pharmacology and later for a time Dean of the Medical School of the University of Pittsburgh.

Studies in the Unanesthetized State: Position Sensibility

I made a denervated head preparation by intracranial, retrogasserian transection of the trigeminal nerves and transaction of the upper cervical dorsal roots. These animals required intensive postoperative nursing to treat the keratitis that followed and tube feeding for the first week. We devised a way of positioning the head in the Horsley-Clarke coordinate system by holders touching only denervated regions of the head. Electroencephalogram (EEG) recordings during the experiments showed that these animals varied from full wakefulness to light sleep, from which they were readily aroused by sensory stimulation, at least for the first few hours. Successful experiments with single neuron recording in the ventrobasal complex were made in 35 monkeys prepared in this way, with neuromuscular blockade and artificial respiration. We observed that the static properties of place and modality were as specific as they had previously been observed to be with deep anesthesia. However, there was a remarkable difference in the dynamic properties of the system. The recovery cycles of thalamic neurons virtually matched those of first-order fibers, and the system followed stimulus frequency to high levels (Poggio and Mountcastle, 1963).

We then planned the study of position sensibility, recording first in the monkey's ventrobasal complex. This required a device with which we could rotate the joints of the monkey's limbs, painlessly, at different speeds to different angles. Previous studies had shown that the first-order afferents innervating the joints and the central cells to which they are linked at successive stages of the system are sensitive indicators of the rotation of the joints. It is this relation we set out to study quantitatively. Such an experimental objective raised difficult problems. The first was what measure to use for the neural activity. We settled on frequency in each successive short interval of time, usually 200 milliseconds. The second is the ubiquitous variability of the spontaneous and evoked activity of central neurons; we studied this separately (Werner and Mountcastle, 1963).

We paid particular attention to whether the "deep" neurons we studied were true joint neurons or were activated from muscle afferents. We devised a number of controls that we applied to each neuron before designating it as

one activated by joint rotation and not from muscle stretch afferents. We studied more than 1000 neurons and identified 410 as “joint” neurons. We observed a clear sign of integrative action in the system. Whereas the receptive angles of first-order joint afferents are narrow and double-ended, those of thalamic neurons are very wide and smooth, and always maximal at full extension or flexion; they respond to movement in only one direction. Thus the thalamic neuron expresses in its receptive angle and discharge pattern a running integral of the inputs from a number of first-order afferents with narrow excitatory angles scattered along the path of movement. We found the relation between joint angle and neuronal discharge to be best fitted by a power function with an exponent of 0.6 to 0.7. This finding was of interest in relation to Steven’s psychological law defining power functions for a wide variety of stimulus-intensive continua in human subjects (Mountcastle, Poggio, and Werner, 1963, 1964).

Study of First-Order Afferents

We found it relatively easy to dissect free and record from the large mechanoreceptive afferents in monkey peripheral nerves. Werner and I did this for those innervating the hairy skin of the arm (Werner and Mountcastle, 1965), and then in studies over a number of years we defined the static and dynamic response properties of each of the large mechanoreceptive sets innervating the glabrous skin of the monkey hand (LaMotte and Mountcastle, 1975; Mountcastle, LaMotte and Carii, 1972; Mountcastle, Talbot and Kornhuber, 1966; Talbot, Darian-Smith, Kornhuber and Mountcastle, 1968; Werner and Mountcastle, 1968). We used this information to determine the integrative action within the system by comparing it with recordings made at thalamic and cortical levels, and for comparison with psychophysical measures of the several modalities in monkeys and humans. The results of these studies support the general conclusion that the relation of the primate to the external world, as detailed by the somatic afferent system, is determined by the nature and transducer properties of the first-order fibers. These transduced images of peripheral stimuli are transmitted with fidelity through the system to the postcentral somatic sensory cortex. We also observed that fibers of a given modality class, with overlapping peripheral receptive fields, were segregated into bundles in peripheral nerves, a peripheral precursor of the columnar organization of the sensory area of the cerebral cortex.

Changing Responsibilities

Toward the end of the 1950s I began to receive invitations to lecture, both at home and abroad. I do not lecture easily and consider myself poor at it, but I always sought to include in each lecture original research results not previously published, and this seemed to arouse interest. In my career I

gave many named lectures in the United States and foreign countries. I found these visits of great value to me because they gave me the chance to meet other neuroscientists and to see their laboratories. During the early years of the development of systems neuroscience there were so many problems evident to all that a sense of competition seldom arose; there were always new problems over the horizon. I also felt obliged to entertain requests that I serve the National Institutes of Health (NIH), and for 3 years in the late 1950s I was first a member of and then Chairman of the study section on physiology. We judged grant applications over the entire field of physiology, including neurophysiology. Ted Bullock and I were the only neurophysiologists on this committee, so decisions on grant applications in this area commonly fell to us. We had many serious but friendly confrontations, largely because Ted, as the superior biologist he was, believed that all biological structures were of equal value as research objects, while I, following the NIH charge to solve the problems of human disease, pled for research in mammals, and in primates if possible. Ted usually won. When NIH began to fund training grants, I also served on that study section, and I served a term on the Advisory Council of the National Eye Institute.

I step ahead of my story to say that in 1964 I succeeded Philip Bard as Director of the Department of Physiology. I devoted considerable effort to enlarging the purview of the department by persuading superior scientists and teachers such as William Milnor and Kenneth Zierler to join us, and I obtained sufficient resources to support a number of young physiologists in fields outside my own. The heaviest duty was participating in decisions important for the future of the Medical School. I served on seven committees to nominate new directors of departments. This involved study in fields outside my own, reading the publications and interviewing candidates, and sometimes visiting them on their home ground. At Hopkins at that time these decisions were kept in the hands of faculty committees; we passed to the Dean one name at a time. If his recruitment efforts failed, we passed him a second name. We declined occasional requests to provide the dean with a list from which he would choose.

I found the duties of Director of a department very light, particularly with the help of a talented secretary-administrator, whom I describe below, and I was able to continue my research program with sustained vigor. I usually finished all office work by 9:00 AM and then departed for the laboratory.

The Department of Neurology

I was chairman of a succession of committees working to create a Department of Neurology, which Hopkins had never had. Neurology had for nearly a century been a small unit in the department of medicine. When I made the proposal to the Advisory Board of the Medical Faculty that we establish a Department of Clinical Neurology, the most persuasive argument I could use

was that of the 10 classes of Hopkins students of the 1950s, not a single student had gone into the specialty of clinical neurology! It was also possible to persuade our Professor of Medicine, A. M. Harvey, that clinical neurology went beyond the treatment of disease to the area of brain and behavior. He immediately became a strong advocate. My colleagues on the Advisory Board were persuaded by these and other arguments and quickly passed the resolution establishing the department. Our Dean, Thomas B. Turner, had just at that time obtained funds for two endowed chairs, and he assigned them to the new department; this itself contributed greatly to its success. Guy McKhann and Richard Johnson accepted our invitation to occupy those chairs, and over the years they and their successors have built a world-class department.

Earl Walker, our Professor of Neurosurgery, had worked vigorously with me on this proposition but remained doubtful that we would obtain approval of the board. In fact, we bet a bottle of champagne on the outcome. Within 20 minutes after my phone call telling him of the successful vote, he came walking down the hall to my office, a bottle in his hand! In my time at Hopkins, Earl Walker had the widest and deepest knowledge across the neurological disciplines of anyone; I admired him greatly. I learned a good lesson from this enterprise: when making a proposition that involves space and lots of money, for which every department director is necessarily hungry, it is first necessary to show your colleagues that none of the resources you ask for will rebound to yourself. This leaves the proposer in a good position, for then his arguments are perceived as genuine.

The Society for Neuroscience

One day in late 1969 I received a telephone call from Ed Perl: would I agree to stand for election as the first President of the newly forming Society for Neuroscience? I asked the identity of my opponent. He replied, "Seymour Kety." I was so certain that Kety would win, I agreed. I was elected and have often suspected that my friend Seymour campaigned for me! It is important to note here that the creation of this society is largely due to the efforts of Ed Perl. He had worked for 2 years gathering support, in both people and funds, and in persuading the neuroscience community that one overarching society was preferable to alternatives. Ed Perl himself wrote the constitution and bylaws of the society, by which it is run to this day. He has given a description of the formation of the society in his autobiographical chapter in Volume 3 of this series.

My immediate task was the planning for the first general meeting of the society. It was held in 1971, when the society already had more than 1000 members. The meeting was a great success, marked by the obvious joy that scientists from different disciplines of neuroscience felt at being together. More than 300 papers were presented. When I went to the podium to give the

first presidential address, I looked into the audience to see Ragnar Granit and John C. Eccles sitting in the front row. These then already famous neuroscientists had traveled from distant places to attend our meeting. I knew we were home.

The society has grown enormously since then, and more than 30,000 attend its annual meetings. Many of these young men and women are attracted by the problems of brain function and wish to devote their lives to solutions. That raises a problem, for it is unlikely that there will be sufficient resources to provide positions and independent laboratories for each of them. There is an increasing tendency for them to serve many years as post-doctoral fellows, often in teams clustered around a senior neuroscientist. Obviously they have not been able to initiate their own, independent programs. There is no clear solution to this problem, absent unlimited funding.

I now return to the description of my own research program.

Study of the Postcentral Cortex in Unanesthetized but Immobilized Monkeys: Choice of Flutter-Vibration as Model for Study

We first established in psychophysical experiments that monkeys and humans have similar capacities to discriminate between the frequencies and amplitudes of mechanical stimuli delivered to the glabrous skin of their hands. We had previously defined the response properties of the large mechanoreceptive afferent fibers innervating the glabrous skin of the monkey's hand in terms of their thresholds to oscillating mechanical stimuli. We found the Meissner afferents (QA) to be most sensitive in the low-frequency range of 10 to 80 Hz, and the Pacinian afferents (PC) to be most sensitive in the high-frequency range of 80 to 300 Hz. The slowly adapting Merkel afferents (SA) entrained at very low frequencies, far below human thresholds. This was later confirmed for the SA neurons in the postcentral cortex, thus providing an example of a beautiful neural code that is not used for sensation/perception—at least not for those we could test. The overlapping threshold curves for the QA and PC fibers blanketed the detection threshold curves for monkeys and humans. We termed this the dual sense of “flutter-vibration” and found that it depended critically upon the postcentral somatic sensory areas (LaMotte and Mountcastle, 1979). We then began to study the neural events in the postcentral somatic sensory cortex activated by oscillating mechanical stimuli delivered to the hands of monkeys. We again chose to work in unanesthetized animals, free of nociceptive input. We fixed the heads by grasping a knob previously implanted on the skull, maintained the animal under neuromuscular blockade, and held end-tidal CO₂ and body temperature within normal limits. These animals oscillated between sleep and wakefulness, as monitored by EEG recording, but after some hours passed into a state of

“coma” from which they could not be aroused; we then terminated the experiment.

We found that each of the three classes of large mechanoreceptive afferents innervating the glabrous skin of the monkey hand sends projections over relatively isolated channels of the somatic system, to and through the post-central somatic, and that each has a privileged access to perception. We confirmed in this state all the static and dynamic properties of postcentral neurons we had observed in a series of studies dating back to 1959 (Mountcastle, Steinmetz, and Romo, 1990b; Mountcastle, Talbot, Sakata, and Hwarinen, 1969). However, I concluded that the unanesthetized, neuromuscularly blocked animal was in an abnormal state, and that progress depended upon work in the waking, behaving animal. That opportunity soon arose.

The Waking Monkey Preparation

A revolution in the mode of research in CNS physiology occurred early in the decade of the 1960s. That was the introduction of the “waking monkey experiment,” which has now become the standard method of research in both human and nonhuman subjects. The principle is simple: record some aspect of behavior while observing simultaneously the brain activity thought relevant to it, in the monkey case with the method of single-neuron analysis. Simple as it sounds, the execution is complex and difficult. This was the legacy of Berger and had been pursued for many years after 1932 using EEG recording in humans. The result had been the important clinical discipline of electroencephalography. Many attempts had been made to correlate EEG patterns with behavior; significant success had followed studies of sleep and wakefulness. However, attempts to correlate EEG patterns with activity in specific cortical areas had met with only moderate success. For us, this new method allowed recording the sensory-perceptual performance of monkeys, while studying the activity of cortical neurons thought relevant to it. This major contribution was made by the late Herbert Jasper and his colleagues Ricci and Doane (Jasper et al., 1960). Jasper published a photograph of a monkey in such an experiment in the volume of the Moscow colloquium. CNS physiology has never been the same since, and one can scarcely exaggerate the thrill it was for those of us who had spent years working with anesthetized or reduced preparations to see and to work with the brain in action! The method was taken up and elaborated by the late Edward Evarts in his studies of the motor cortical mechanisms controlling movement.

In the midst of all this I visited Evarts in his laboratory to see his experiment. I left Bethesda that Friday somewhat despondent, for it was not at once obvious to me how we could immobilize the hand of the waking monkey to deliver somatic sensory stimuli controlled at the micron level. (We later achieved this by prolonged training.) The next Monday morning I glanced down the hall from my laboratory to see that same Edward Evarts

striding toward me, with that great smile on his face, and carrying a large box on his shoulder. He had brought me all the gadgets—head holding and so on—for the waking monkey experiment. I used them for a year, and our adventure into this new world began.

This combination of behavioral control and electrophysiological recording in waking monkeys allows one to observe the activity of hundreds of cortical neurons, one by one, in repeated microelectrode penetrations made into a chosen area of the neocortex day after day for several weeks, in the same animal, and thus reconstruct post hoc population events. The monkeys were trained to emit the chosen item of behavior, repeated in hundreds of trials in each day's recording session. It is of course another large step to suggest a causal relation between the two, even if they covary in a predictable way. Some other neural activity not recorded may be the critical neural event for the behavior observed! This method proved to be complex and difficult, and to depend upon the conjoined effort of several investigators with different skills. It proved so productive that I never did any other type of experiment.

The Posterior Parietal Cortex

I began the waking monkey experiments with Giancarlo Carri and Robert LaMotte, recording once again in the postcentral gyrus. We observed the specific static and dynamic properties of postcentral neurons predictable from earlier experiments, and a precise columnar organization. We also saw a direct correlation between behavioral frequency discrimination and differences in cycle lengths of the neural activity evoked by the two frequencies discriminated. This cyclic entrainment depends upon a sequential order code, for it is destroyed by a random shuffle of the temporal order of impulse intervals. We also observed in both monkeys and humans an "atonal interval," a narrow range of stimulus amplitudes within which subjects can detect the presence of oscillating stimuli but cannot make a frequency discrimination.

In the midst of these experiments, we discovered that the postcentral neural activity evoked in correct trials did not differ clearly from that evoked when the animal made a mistake. We saw no clear neural signals of the differential discrimination process itself. Then, while recording with Robert LaMotte and Carlos Acuna we more or less in frustration moved the locus of a microelectrode penetration into the posterior parietal cortex, behind the intraparietal sulcus. What we saw on that day determined my experimental life for 15 years! Neural responses to stimuli occurred only if the animal attended to them—that is, if they seemed of interest to him. Activity occurred with projection of the arm toward objects he sought, such as food, but not during casual arm movements. Other neurons were active when the animal manipulated within a small box to obtain food, but not during casual hand movements. Neurons were observed with very large mechanoreceptive fields

covering large parts of both sides of the body. Visual neurons were observed with very large and frequently bilateral receptive fields, and were sensitive to the direction of stimulus movement within those fields. Neurons defined by these functional properties are arranged in type-specific columns. All of these preliminary observations appeared as positive images of the defects we later found to follow removal of the posterior parietal cortex in monkeys (LaMotte and Mountcastle, 1979). These initial observations were confirmed and extended in the more formal studies that followed.

We then set about preparing for more extensive and better controlled studies of the posterior parietal cortex. First, I reviewed all the cases in the hospital archives labeled the “parietal lobe syndrome.” Humans with parietal lobe lesions show unusual disturbances of behavior. The most striking is a change in their perception of the body form and its relation to surrounding space, for example, in manual and visual exploration of the immediately surrounding space and a profound neglect of objects and events in that space, including their own body parts. They make errors in reaching into that space, and there are a host of other unusual signs that differ for lesions in the two hemispheres.

I made a detailed study of the cytoarchitecture of the parietal cortex and reviewed what was known of the connectivity of this region. We later found that the syndrome produced by parietal lobe lesions in the macaque monkey is a similar but somewhat fainter replica of that in humans (LaMotte and Mountcastle, 1979). John Chubbuck designed test equipment that required the animal to reach to stationary or moving targets, to fixate stationary and to track moving visual targets, to make saccadic movements between two stationary visual targets, and so on. We had already learned how to train waking monkeys to allow head fixation and to make somatic sensory detections and discriminations with stimuli delivered to immobilized hands. We now began to train them in these new tasks; it required 8 to 10 weeks of training, 2 hours daily, before monkeys were ready for recording—a major investment of time and effort for each animal. But we were ready to begin.

This experiment required the active participation of a number of investigators. Those who participated with me in the parietal lobe studies were members of successive teams: Carlos Acuna, Pradeep Atluri, Richard Andersen, Charles Duffy, Apostolous Georgopoulos, James Lynch, Robert LaMotte, Brad Motter, Hideo Sakata, Michael Steinmetz, William Talbot, and T. C. T. Yin. The two primary papers describing our initial results are Mountcastle, Lynch, Georgopoulos, Sakata, and Acuna (1975), and Lynch, Mountcastle, Talbot, and Yin (1977). Some of the papers and reviews describing the results in detail are Andersen and Mountcastle (1983); Motter and Mountcastle (1981); Mountcastle (1976, 1977b, 1978a, 1982, 1988); Mountcastle, Motter, and Andersen (1980); Mountcastle, Andersen, and Motter (1981); and Yin and Mountcastle (1977, 1979). The results of this long series of studies confirmed and extended our preliminary results given above. I will not detail

them all here. The field has since attracted a number of investigators, with the result that the functions of the parietal-transcortical-frontal systems in directing attention, and in manual and visual action within the immediately surrounding space, are now well understood, at least at the first level of analysis.

The Bard Laboratories and the Department of Neuroscience

Our group in neurophysiology grew to include four separate and independent laboratories, identified as the Bard Laboratories of Neurophysiology. They were Dr. Poggio, the visual system; Dr. Georgopoulos, the motor cortex; Dr. Johnson, the somatic afferent system; and my own, the posterior parietal cortex. Together with the associated shops we put heavy pressure on space in the Department of Physiology. A grand solution was found when the Howard Hughes Medical Institute funded an additional 10th floor to the new basic science building. I suspect that my friend Max Cowan had much to do with this decision to provide new space for the Bard Laboratories. The 10th floor also housed Dr. Mark Molliver and his colleagues working in experimental neuroanatomy. The 10 years we spent in these splendid new surroundings were the happiest and most productive of my experimental life.

There was, however, another reason. The Rockefeller University was actively recruiting one of the most productive neuroscientists ever to work at Hopkins. That is Solomon Snyder, who was then a member of the Department of Pharmacology. I proposed to Dean Ross that we execute what I termed "three-cushion pool": that we create a Department of Neuroscience, with resources sufficient to persuade Dr. Snyder to remain in Baltimore; that I step down from the directorship of the Department of Physiology, which gave the Dean freedom to develop it in other directions if he wished; and that the Bard Laboratories become a division of the new Department of Neuroscience. These proposals were executed on July 1, 1980. It seemed to be a proposal in which everyone won, and indeed, so it has evolved. I was freed from all administrative and teaching duties, and housed with all my colleagues in neurophysiology in beautiful new quarters. It was paradise! The Department of Neuroscience began in 1980 and has since established itself as a world-class center for neuroscience research, particularly in molecular neuroscience.

Study of the Motor Cortex: Output Signals of a Sensory Decision

We had never seen in all our studies of the postcentral somatic sensory cortex any neural sign of the detection or discrimination process itself. We therefore considered the hypothesis that the decision process is embedded in the multinoded, transcortical, distributed system linking the sensory area

of one hemisphere to the motor cortex of the other, driving the responding arm. Pradeep Atluri, Ranulfo Romo, and I therefore undertook a study of that motor cortex in monkeys as they made discriminations between flutter stimuli delivered to their hands (Mountcastle, Atluri, and Romo, 1992). We observed a selective signal for the upcoming correct discrimination in about 25% of neurons in the motor cortex contralateral to the critical sensory cortex. The motor cortical activity began within 200 milliseconds of stimulus onset, which blankets the intracortical time for such sensory performances derived from psychophysical experiments. The motor cortical responses were aperiodic. The most interesting observation was that in trials in which the monkey made a mistake, the output of the discrimination process reaching the motor cortex was itself in error, followed by the appropriate arm response to the incorrect target. This localized the discrimination process to the transcortical system linking the sensory to the motor cortex, the transitions from sensation to action. These systems are neither sensory nor motor, in the usual sense. These problems Dr. Romo has pursued with success since his return to Mexico. This was my last experience in laboratory research. I was nearly brokenhearted to leave it, for I found no greater thrill in life than to make an original discovery, no matter how small.

The Bristol-Myers Symposium. Neuroscience: Integrative Functions

In 1989 as my first retirement loomed (I had three!), my colleagues in the Department of Neuroscience and the Bard Laboratories persuaded the Bristol-Myers company to hold their first symposium in neuroscience research in Baltimore. The symposium went under the title given above and was given honoring me. Some 300 scientists attended, 31 from foreign lands. Many of these visitors presented scientific posters, and major lectures were given by the following, all my longtime friends: Per Anderson, W. Maxwell Cowan, John E. Dowling, Gerald M. Edelman, Michael E. Gazzaniga, Tomas Hokfelt, David H. Hubel, Edward G. Jones, Bela Julecz, Eric R. Kandel, T. P. S. Powell, Marcus E. Raichle, and Pasko M. Rakic. A gala dinner followed the first day. I treasure the memory of this affair, and regard it as the most important honor I ever received.

The Mind/Brain Institute

In 1988, Steven Muller, President of the Johns Hopkins University, called together all members of the University working in the field of neuroscience for a general powwow on what might be done to enlarge and intensify activity in the brain sciences at Hopkins. Perhaps 50 to 60 individuals attended. I proposed to them that we create an Institute of Brain Sciences focusing on how the brain generates and governs behavior, and that such an Institute

aim more toward systems neuroscience than molecular neuroscience, already blossoming in the Department of Neuroscience. Muller was enthusiastic and grasped the idea at once, and he asked me to come to his office the next Monday morning. At that time I knew Muller only casually, but over the following several years I came to recognize his superior intellect and, what was important in this case, his quick grasp of ideas foreign to his earlier experience.

Muller did not bat an eye when I said we needed \$40 million for building and \$60 million for endowment. He then took me aback by saying that the proposed Institute was a great thing, but that it must be on the Homewood undergraduate campus, or not be at all. This I foresaw as a handicap because the great strength in neuroscience was in the School of Medicine, where at least six departments had successful programs in this field. Finally, after much further discussion, approval of the Board of Trustees was obtained, and we went to work.

Guy McKhann stepped out of his directorship of Clinical Neurology (he was followed by Richard Johnson) to become the director of the new Institute, which then occupied a few rooms on the undergraduate campus. He planned a new building for 12 labs of a wide variety, together with all supporting shops and internal animal care facilities, including those for primates. A model of this building was constructed. Then, catastrophe struck. The University entered a period of financial stress. Guy McKhann did succeed in obtaining an endowment of \$7.5 million dollars from Zanvyi Krieger, \$1 million from the Merrick Foundation, and about 20,000 sq ft of space in a former physics building. The Institute began at a size reduced from that originally planned and was officially opened in 1990. Stewart Hendry, a skilled systems neuroanatomist, was the first staff appointment and has remained as an essential member of the staff since that time. The Institute was established as a part of the Department of Neuroscience of the School of Medicine, and almost all of its members have appointments in that department.

Shortly afterward, the Bard Laboratories moved with all its equipment to the Zanvyl Krieger Mind/Brain Institute, providing its critical mass. The Institute now consists of six laboratories of neurophysiology, one of experimental neuroanatomy, and one theoretical unit. This Institute, somewhat reduced in size from our original plan, has been eminently successful. Seven of the eight labs have continued external funding, and research productivity continues at a high level. I had hoped originally that such a free-standing institute, reporting directly to the President of the University, would be free of all routine teaching obligations and aim at training senior research fellows for other universities. Such was not to be the case, and the members of the Institute are now burdened with (1) their own large Ph.D. training program, (2) teaching neuroscience to students of medicine, and (3) the steadily increasing program of teaching neuroscience to undergraduates.

The existence of the Mind/Brain Institute, and its brightening hopes for the future, we owe almost wholly to the energy and foresight of Guy McKhann.

Editorial Functions

I have spent an inordinate amount of time in my life in editorial functions, mostly midnight oil work. Under some silent but powerful persuasion from Philip Bard, I assumed the editorship and wrote several chapters in two editions of the textbook *Medical Physiology* (13th and 14th editions). Many friends advised me not to do this, with the prediction that it would hamper my research work. I found exactly the opposite, for with these editorial duties and those listed below I enjoyed an extensive and up-to-date education in neuroscience, one which I would not have obtained in any other way. If one has to write out a chapter on a rather large subject in neuroscience, one has to know it! And, if one has to provide a critical and helpful review to an author, one has to know the subject matter! In 1957 Professor John Fulton asked me to serve on the editorial board of the *Journal of Neurophysiology*. Upon his death in 1960 he willed the *Journal* in equal parts to Yale University and to its publisher, the CC Thomas company. The American Physiological Society purchased the property rights to the journal from Yale and Thomas and asked me to become its chief editor. I accepted and recruited a distinguished group to serve with me as its editorial board, and over a few years we were able to restore this journal to its position as the leading journal for systems neuroscience, a position it retains to this day.

An even heavier editorial duty followed, in which I agreed to join my old friend John Brookhart as a co-editor of the *Handbook of Physiology. Section I. Neurophysiology*. This grew to nine large volumes; after the onset of Brookhart's serious illness, the editorship fell to me alone. I had again the experience I described above, but here in spades: an intensive postdoctoral education in neuroscience.

A Decade in Semiretirement: Reviews and Monographs

After I stopped laboratory work, I enmeshed myself in scholarly endeavor and writing. During the following decade I was afforded an office in the Mind/Brain Institute, which allowed me access to the libraries of the University and the School of Medicine, and funds to employ part-time help for library search. During that time I published a number of reviews (Mountcastle, 1995a, 1995b, 1997, 1998b) and two books: *Perceptual Neuroscience: The Cerebral Cortex* (Harvard, 1995) and *The Sensory Hand. Neural Mechanisms in Somatic Sensation* (Harvard, 2005). I retired completely from all involvement in neuroscience or in university life in November 2005, at age 87. It was about time!

Family Life

When we arrived in Baltimore in September 1946, our first child was on the way. Vernon B. III was born in March 1947, quickly followed by his sister

Anne Clayton in 1948, and another son, George Earle Pierpont, in 1949. We found that having all our children so quickly, though not easy for Nancy and not exactly planned that way, was a great boon for family happiness. We lived in apartments in Baltimore for our first 6 years, but in 1952 we were able to buy a large, dilapidated brown shingle house in Roland Park. This turned out to be just the place to raise children. The house was very large, with five bedrooms, a screened back porch, and a sleeping porch off the second floor. There were a dozen children of the ages of our children in the immediate neighborhood, and a forested hill close by. We had moved there because the local public school was said to be of high quality. However, Nancy quickly returned to her premarital profession of teaching and found a wonderful opportunity at the famous Calvert School. Thus Nancy stabilized our financial life and provided a Calvert education for our three children. They went through the fine private schools of Roland Park and were admitted respectively to Brown, Vassar, and Harvard.

I look back on our children's early childhood and adolescence as the happiest years of our lives. Our children were excellent students; each of them became National Merit Scholars, and interacted with their mother's charm in social relations. They all participated in sports, and our youngest son was a varsity athlete at Gilman School in football, lacrosse, and wrestling. Later we all took up sailing on the Chesapeake Bay, our sons first in an International 14, and all of us later in an Alberg 30. At that time there were about 25 Albergs on the bay, mostly based in Annapolis, as we were, and there was one-design racing on every Sunday, weather permitting. After we began sailing, I took Sundays off.

Our youngest son, George, was killed in an accident in October of 1969, at age 19, while a sophomore at Harvard. We only survived this tragic period through family bonds of love and affection.

But, more about Nancy: She adapted completely to the demands of my research life. She assumed the decision-maker role in our family, saw to the education and well-being of our children, and handled with ease and charm the demands of many scientific visitors. Many of these latter were postdoctoral fellows arriving from abroad, with wives and children. Nancy housed and fed them for their first few days in Baltimore. My custom was to go to work early, come home for dinner and visits with family at 6 PM, then on many days go back to the lab and work until midnight. During those early years we made several weekend trips each year to our old homes in Roanoke and Salem, Virginia, so that our three children came to know well their four grandparents and their many first cousins.

But, more about Nancy: During her 18 years of teaching 9-year-old girls, she came to know intimately about 400 of them. Many of these are now the matrons of Baltimore. I observe a remarkable interaction whenever we go to some non-Hopkins social function in Baltimore. Nancy is quickly approached by one or more of her former students, frequently with hugs and sounds of joy.

Then I observe Nancy's remarkable performance in memory search. She first examines closely the facial features of her former student, then devolves what she sees into what that face looked like at age 9. Then the memory search begins, and within 5 to 10 seconds out comes the name, where the student went to college, whom she married, and sometimes much more. I remain the spouse in the background.

After our children finished college, Nancy and I moved to the wonderful countryside north of Baltimore and took up horseback riding, with Arabian horses. A notable event was when Nancy's mare, whom we had bred to a famous stallion, was about to deliver. Now, the vet was late, and there was nothing for it but for me to take charge. Fortunately, I had read a good bit about it, so I delivered this colt in our barn, as two grandchildren watched through the stall door. It was an experience none of us will forget. We raised that colt with the method of never punish, only reward, with the result of a splendid horse at maturity. Finally, at our advanced ages we found it prudent to stop riding and left the country for a town house just on the edge of Baltimore City.

Mary Hilda Counselman

Every man who has led a life devoted to scientific research knows that he is indebted to a number of women who have made that life possible. I have already described the essential role of my mother and my wife in my life. There is a third, Mary Hilda Counselman, who from 1969 on was, while officially my secretary, actually the executive administrator of the Department of Physiology. She is beautifully educated, knows every rule of spelling and syntax in the English language, possesses a charming and winning personality, and knew the way to get things done within the confines of University rules. She showed throughout her career a total devotion to the welfare of the department and the people in it. Some examples: On experimental days she protected me from all except the most urgent calls and visitors, passing through only those from my wife, the Dean, or the President of the University. What is important, she could do this without offense. She welcomed fellows from abroad, found them places to live, and helped them in the sometimes difficult transition to the American culture. This was brought home to me on several occasions when, while abroad, I met with former fellows. The first question they asked was not how the research was going, or how the department was, but, "How is Mary Hilda?" She now lives in comfortable and happy retirement. My gratitude to her is unbounded.

Sunny Uplands

I made a complete withdrawal from my life in neuroscience at the age of 87 and found the sudden break just the thing for me. It had become apparent

in recent years that I could no longer cope with, or enjoy, the outdoor life in our country home 25 miles north of Baltimore. In 2006 we moved to a town house just outside the city limits of Baltimore—from which the Johns Hopkins Hospital is quickly reached! I was able to fit into this new house only half the library I had accumulated (3000 volumes), but we have ready access to the University and public libraries. Here I have taken up through reading a number of old interests I had long neglected, including classical and American literature. I have been reading eagerly some of what the astrophysicists have discovered about the nature of our universe during the decades I was head down in the laboratory. What an accomplishment! I have restarted an old habit, my reading of ancient history.

The greatest delight of all is to observe the evolving lives of our six grandchildren. Our youngest granddaughter, named Nancy Pierpont Mountcastle (II), has just graduated from North Carolina State (June 2007) and is threatening to go to law school. Our next youngest granddaughter, named Julia Vemon Bainbridge, is a graduate of Boston University and has just earned a master's degree in food science (of all things), and she wants to write in this field. She is presently an apprentice at a food magazine in New York City. Our oldest granddaughter, Leslie Mountcastle Moss, has just produced the first of the next generation, named Jacqueline Mountcastle Moss. Our three grandsons have until now escaped matrimony, but I hope for not much longer!

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