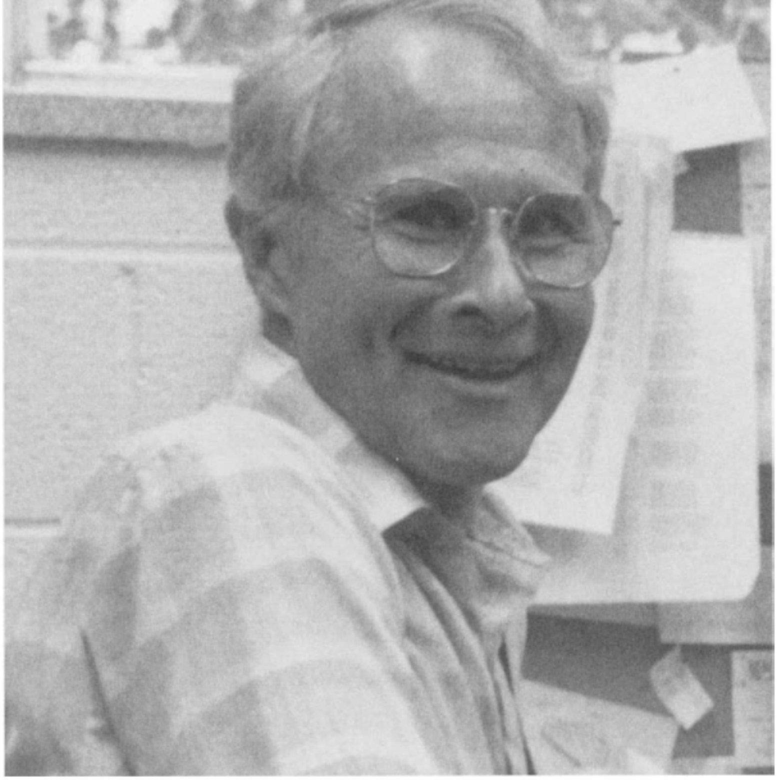
The History of Neuroscience in Autobiography
Volume 3

Edited by Larry R. Squire
Published by Society for Neuroscience
ISBN: 0-12-660305-7

Wally Welker

pp. 502–545

https://doi.org/10.1016/S1874-6055(01)80019-0



Wally Welker

BORN:

Batavia, New York
December 17, 1926

EDUCATION:

U.S. Army, 2nd Lieutenant, Officer Candidate School, Fort Benning, GA (1947)
American University, Washington, DC (1950)
University of Chicago, Ph.D. (1954)

APPOINTMENTS:

University of Wisconsin (1956)
Professor Emeritus, University of Wisconsin,(1992)

Wally Welker carried out pioneering neurophysiological and neuroanatomical studies of sensorimotor systems. Emphasizing a comparative and ethological approach, he was the first to identify the large cortical representation of the forepaw in the North American raccoon and to show in all mammals studied how cortical convolutions, fissures, and sulci are produced by the development of adjacent but distinct functional cortical areas. He also identified the unexpected patchy and fractured arrays that characterize the organization of sensory inputs to cerebellar cortex.

Wally Welker

Preamble

As a young teenager (during the late 1930s and early 1940s) I became consciously aware that natural phenomena could be described in terms of their physical features (color, size, shape, intensity, movement, hardness, etc), and that curiosity about features of the environment could be used to find answers to questions about how the environment is assembled and how its features work. In high school I became captivated by the possibility of learning about the biological bases of why animals perceive, think, emote, behave, develop, and evolve as they do. My curiosity about the natural world extended to every feature of nature. This motivational force took priority over all other features in my personal life. My enthusiasm for learning, hunger for knowledge, and search for understanding extended over a great variety of fields of human experience and knowledge. During the time that I spent in family social gatherings (family reunions and the quiet times in church and Sunday school), I came to believe that moral and ethical judgments were, appropriate topics for understanding in terms of psychological, sociological, and biological explanations. Indeed, the possibility of explaining everything seemed possible to my untrained mind. My entire career since these early days has been influenced by my faith in the fact-finding and explanatory powers of curiosity and scientific methods.

Social Background

I was born at a time of relative prosperity (1926), when Saturday bike rides in summer to the nearby town of Attica helped us to escape the drudgery and hard work on our farm. My entire childhood took place on a farm on which nature in many forms was directly underfoot and at hand. My parents, although hard taskmasters under difficult conditions, gave my sister, brother, and I relatively free permission to explore the natural world around us on the farm. World War II started to play out while I was an idealistic teenager. During this period, I was becoming more aware of worldwide social movements. Through radio, newspapers, magazines, and newsreels, we became aware of worldwide matters, social unrest, human cruelty, and widespread poverty, and it became clear to me that there was a need for cooperation in search of international peace and harmony throughout the world. These broader social events made a great impression on me and influenced how I would come to think about the brain later on.

Summary of Key Academic Experiences

The drive to explain things influenced all my career and personal choices throughout my life. These modes of inquisitive thought were expanded upon in the army during my tour of duty in the Philippines and then later in college, first while studying government and the foreign service at American University in Washington, DC, and later during my ventures into experimental psychology at the University of Chicago. In college, the course of my searches was focused initially on government and the behavior of nations. My early interest in psychological phenomena such as thinking, emotion, intelligence, personality dynamics, social behavior, and sociological phenomena grew to include the activities of governmental, ethnic, international, and religious groups. I became interested in clinical psychology during my summer job as an assistant in a private mental hospital, and after being admitted to the psychology department at the University of Chicago, I decided that training in psychotherapy would be necessary in helping me understand the human mind. While at Chicago, I was exposed to a liberal education in English literature, biology, factor analysis, experimental psychophysics, and ethology. I also expected to learn about various methods of observation, description, notation, and analysis of perception, learning, and behavior. Also at Chicago, I learned how to conduct scientific experiments, how to make careful observations of behavior and how to test for different mental, cognitive and emotional features of the human and animal mind. I was captivated by various subdisciplines of psychology, including perceptual psychophysics, behavioral analysis, and comparative and developmental psychology. I was enthralled by learning how to use libraries to conduct searches of the literature of neuroanatomy, zoology, physiology, medicine, physical anthropology, etc.

Working as an apprentice to my college mentors, I learned how to observe, describe, and analyze the phenomena in each of their fields of interest. I was encouraged to learn how to explore theoretical points of view, but my main approach to psychological subjects was empirical.

At the Yerkes Laboratories of Primate Biology in Orange Park, Florida, I carried out my Ph.D. dissertation research by observing and analyzing exploratory and play behavior of chimpanzees. The apparent similarity of the repertoires of chimps and of humans provided an understanding of the basic similarity of these phenomena in mammals. While carrying out these studies of play and exploration in the relatively unstructured and unsupervised environs at the Yerkes Laboratories, I learned how to use experimental methods to search for the biological bases of animal and human behavior. I realized that it was essential to make careful observations of natural behavior in order to understand, describe, and explain behavioral repertories in animals as well as in humans. Simple observation, description, notation, and their subsequent analysis were the basic tools that I used to study behavior. Under the guidance of neuroposychologists K. S. Lashley and K. L. Chow, I was being prepared to anticipate the next phase of my professional career as a neurophysiologist, neuroanatomist, and neurobiologist at the University of Wisconsin in Madison.

By forcing myself to carefully observe behavior in animals, I was struck early on by the spatiotemporal complexity of sequences of behavior in animals and humans. It became clear that the great complexity, contemporaneity, interdigitization, and interplay of various sequential sensory-motor events, in even the simplest of behavioral sequences, required the operation of a complex, dynamic neurological network within the brain. Behaviorists were already making it clear that those who seek for neural explanations of observable sensorimotor phenomena must study neurophysiology, neuroanatomy, and neurochemistry. It became clear to me in Florida that I would need to know extremely fine details of how the brain was constructed and functioned if I were to begin to understand the neural bases of the phenomena of behavior, perception, motivation, and cognition that interested me. It was more than a coincidence that, at that time in Wisconsin, an important new phase of brain study was well under way to discover and define the patterns of functional and structural organization of the brain in a variety of mammals by using topographical mapping, circuit tracing, and electrophysiological and neuroanatomical description as well as macroelectrode evoked potential localization methods. Opportunities to study basic research in the neurosciences were already beginning to develop everywhere.

I took the advice of the primate lab scientists at Florida and went to Wisconsin as an apprentice to C. N. Woolsey and Konrad Akert. At Wisconsin, I launched the next phase of my career by learning how to perform sterile, as well as acute, neurophysiological and neuroanatomical experiments. I have been at Wisconsin ever since, with the long-term goal of learning how the brains of mammals are put together and how they work to produce behavioral, perceptual, emotional, and cognitive phenomena. These new adventures began an exciting phase in my searches for understanding of the brain. The facilities and tutelege at Wisconsin were designed to guarantee comprehension of the basics of brain science. At Wisconsin, as at Chicago and Orange Park before, I was given considerable freedom to explore, ask questions, and design experiments for which I could provide answers. I also began to read the literature more broadly and formulate concepts, discuss neurobehavioral issues with colleagues and mentors, and present and discuss my views and ideas to professional audiences in public formats as well as in professional journals.

The Society for Neuroscience was founded during my early years of apprenticeship at Wisconsin. At that time, there was an ever-widening realization worldwide that studies of the functional localization of the brain were providing the bedrock of knowledge that would underlie the new field of neuroscience. Consequently, young postdoctoral trainees from many fields of endeavor (psychology, zoology, anthropology, sociology, physical therapy, chemistry, medicine, etc.) converged in search of understanding how the brain is constructed and how its different parts function together to produce the phenomena that we observe and experience.

Because my early academic experience in college was related primarily to behavioral and psychological phenomena in animals and humans, at Wisconsin I began to study the brain in order to learn more about the neural determinants of behavioral and psychological phenomena. However, I came to the new fields of brain science with relatively little knowledge about the nervous system. When I began my formal studies of the nervous system at Wisconsin, I was fortunate to come under the tutelage of a remarkably wise and experienced teacher and mentor, Clinton N. Woolsey. Woolsey also had a broad-scale view of interdisciplinary studies that tied together behavioral, physiological, and neuroanatomical phenomena. Woolsey had been hired in the late 1940s by the University of Wisconsin to develop a laboratory of neurophysiology as a subunit within the Department of Physiology in the medical school. I was lucky also because Woolsey's own philosophy was that learning was more successful if it occurred under an apprenticeship relationship. As a consequence, I spent much of my career in the neurosciences exploring the boundaries of existing knowledge. Because of this attitude, my fellow trainees and I were allowed the opportunity to explore a variety of relatively new phenomena. We came to the field with relatively naive, or unbiased, views about the brain and its functions. I believe that all of the discoveries listed later were made possible because we were encouraged to explore our ideas about the brain under skilled supervision but with a relatively open philosophy of exploration.

Major Discoveries and Their Relevance to the Development of Neuroscience

The following is a list of the more prominent discoveries that my colleagues and I made at Wisconsin. Most of our research was simply descriptive and involved observing and recording details of the phenomena and structures that we observed. Our approach was never based on rigorous testing of hypotheses. Rather, all our studies were carried out as simple explorations and descriptions of some part of the brain that had not

Figure 1. Behavioral specialization. Raccoon (*Procyon lotor*) feeling boiled egg fragments with forepaws while in bipedal posture. The raccoon's hypersensitive forepaws detect small details of surfaces and objects. It often dips held objects under water and vigorously rubs the object between its hands. In water, the hands are ever more sensitive and discriminating.

yet been explored. Our overall aim was to define the location of peripheral projections to different central neural regions.

1. For my Ph.D. research at the University of Chicago, I carried out the first modern experimental descriptive study of play and exploratory behavior of chimpanzees. These studies used observational methods for describing and analyzing naturally occuring behavioral sequences (Welker, 1956a,b,c).

2. During my early posdoctoral research at Wisconsin, we discovered that an animal such as the North American raccoon, which is noted for the prominent behavioral use of its hands in exploring objects and surfaces (Fig. 1), has a differentially enlarged somatic sensory cerebral cortex which receives inputs from its hands (Fig. 2; Welker and Seidenstein, 1959). In addition, the raccoon's forepaw cortex is larger in absolute size than is that of the cortical hand area in humans.

3. In the raccoon, the cortical representation of digits of its hand are topographically organized (as is the hand) on separate and distinct cerebral cortical gyri. Moreover, sulci and fissures separate the different cortical representations of each of the five hand digits (Fig. 2; Welker and Seidenstein, 1959; Welker and Campos, 1963). This was the first study to show such a high degree of precise topographical organization of sensory projections from the periphery.

4. Cortical sulci and fissures separate the representations of different body parts in a variety of other mammals. These comparative studies led to clarification of the concept that there is a correlation of perceptually

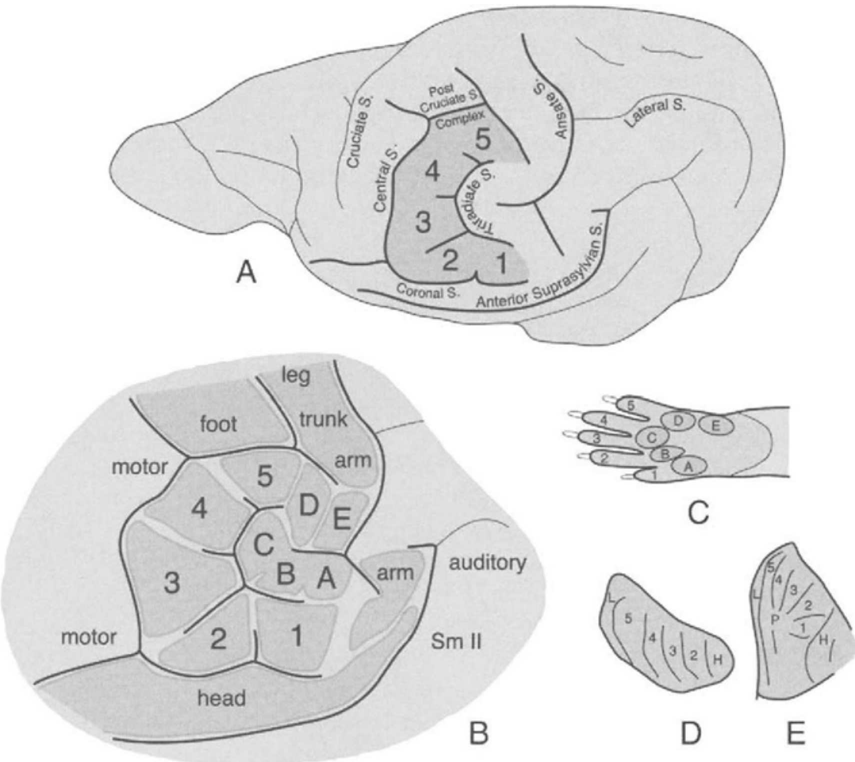


Figure 2. Neuroanatomical correlates of behavior. Somatosensory (touch) areas of raccoon's cerebral cortex (A and B) and thalamus (D, coronal plane; E, horizontal plane) from different body parts (e.g., hand: C). The studies which prompted these figures revealed that the raccoons forepaw touch circuits (in medulla, thalamus, and cortex) are differentially enlarged in the hand representations.

prominent behaviors with gyral subdivisions of the cerebral cortex. (i.e., form reflects function) (Welker, 1989).

5. There exists a similar differential development of cortex associated with behavioral specialization in a variety of mammals, leading to the generalization that cortical sulci separate functionally different cortical gyral areas in all mammals (Welker, 1989, 1990, Welker and Campos, 1963).

6. We discovered that somatic sensory nuclei and subnuclei of the thalamus and medulla are also associated with behaviorally significant (but functionally different) peripheral inputs in a variety of different mammals (Fig. 2; (Welker and Johnson, 1965). In essense, we demonstrated that fissures, sulci, dimples, and gyri are functionally significant in that they reveal the relative location and significance of the sensory projections involved.

7. In the course of all these comparative studies we demonstrated the importance of micromapping in exploring peripheral projections in order to better assess and describe the locations, patterns, and arrangements of fine details (as well as the overall pattern) of peripheral (or central) projections of portions of a sensory circuit (Welker, 1987a).

8. We developed refinements in micromapping methods for both cerebral cortex and deep sensory nuclei using electrodes of smaller size (microelectodes), lower impedance, in-depth recording methods, and multiple-unit evoked-response methods (Parker *et al.*, 1973) in defining the sensory areas or nuclei of cerebral cortex, thalamus, medulla, and cerebellum (Welker, 1987b; Krishnamurti *et al.*, 1976). These micromapping methods also utilized high-density microelectrode mapping locations, as well as strategic placement of electrode recording locations, and angle of cortical entry with respect to fissural and sulcal landmarks, taking into account the curved and folded character of both cerebral and cerebellar cortex. In conjunction with micromapping, we developed a methodology for producing tungsten ball-tipped microelectrodes of relatively low impedance, which allowed us to map multiple units using multiple-unit response (acoustic hash) criteria (Parker *et al.*, 1973). Using these methods we found that it was possible to identify relatively fine details of somatic sensory and auditory (Lende and Welker, 1972) projections and of homologous nuclei in different species than previously had been known.

9. We traced the circuits of somatic sensory systems by means of micromapping of homologous nuclei at medullary, cerebellar, thalamic, neocortical, and midbrain levels of the brain.

10. We defined the projections from individual muscles of the forelimb to the cellular clusters that comprise the external cuneate nuclear complex of the ipsilateral medulla. This was the first study to define fine details of muscle inputs to this nuclear complex. It revealed that individual neurons of this nucleus received inputs from only a single forelimb muscle (Campbell *et al.*, 1974).

11. In the course of these mapping studies we put ever greater emphasis on the use of graphic representations to clarify details and arrangements of neural circuits. Carol Dizack was the medical illustrator in the Department of Neurophysiology who made a great variety of illustrations and diagrams of neural circuits and neural functions to represent important features of localization of functions for the many researchers in our department.

12. We attempted to clarify concepts of basic functional neural entities such as nuclei, junctional thickets, neuronal assemblies, components, simple circuits, systems, and system complexes or networks, in conceptual studies of functional circuits.

13. We analyzed behavioral sequences using cinematographic methods. We explored the significance and relevance of the timing of rapid

behavioral sequences. Specifically, we quantified temporal organization of behavioral sequences, such as the cyclic whisking and sniffing behaviors in albino rats (Welker, 1964). This research formed a basis for an extended series of studies in other laboratories of vibrissae "barrel" cerebral cortex in mice and rats. We also analyzed movement dynamics of forepaw manipulative behaviors in raccoons, proboscal probing behaviors of coatimundis, and the development of locomotor and brachiating behaviors of an infant gibbon (Welt and Welker, 1963).

14. We demonstrated the importance of developmental studies in revealing the temporal sequences of ontogenetic development of neural correlates of behavioral maturation in rats, raccoons, and gibbons.

15. We provided data that enhanced arguments for comparative studies in understanding the courses, causes, and outcomes of brain evolution (including the relevance of comparative neuroscience to the field of paleoneurology).

16. We demonstrated correlations between morphological brain features and ecological preferences and niches (Welker and Campos, 1963).

17. We discovered (using micromapping procedures) novel features of the functional organization of cerebellar somatosensory cortex. These studies revealed previously unrecognized kinds of peripheral projections to the folia of the cerebellum (Fig. 3). For example, somatic sensory projections to the cerebellar granule cell cortex exhibit a fractured patchy pattern. Several interrelated studies (by my colleagues) of cerebellar circuits have prompted reevaluation of how the cerebellum is organized and functions (Shambes *et al.*, 1978a; Bower *et al.*, 1981; Bower and Woolston, 1983, Kassel *et al.*, 1984).

18. We clarified conceptions regarding the functional significance of anatomical gyration, foliation, and fissuration of cortex and of lobulation and subnucleation of deep cellular groups (Welker, 1989; Welker and Johnson, 1965). We believe that our studies have demonstrated that the physical size, shape, and orientation of gyral and sulcal structures are directly determined by active differential growth, and development of different cortical features (inputs, outputs, and intracortical circuits) is determined by the differential growth and elaboration of afferent, efferent, and intracortical cell assemblies (Welker, 1990).

19. Over the years we assembled a Comparative Mammalian Brain Collection at the University of Wisconsin (Fig. 4). The types of species of mammal selected for this collection were chosen on the basis of several criteria. For example, mammals were chosen that exhibited specialized exploratory behavior with respect to sensory objects and surfaces. We chose pigs and coatis that probe the ground with their snouts, spider monkeys that have a specialized grasping tail, raccoons that have specialized hand-feeling behavior, etc. We also decided to collect brains from mammals that are members (or representatives) of different orders, fami-

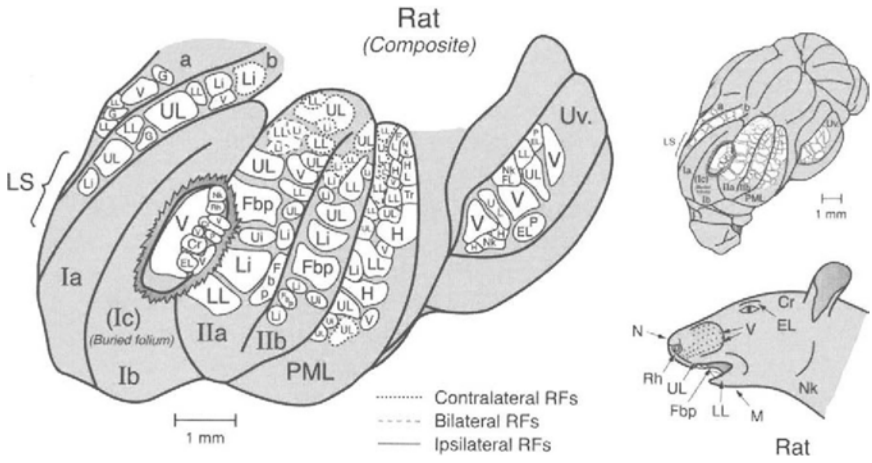


Figure 3. Fractured somatotopy of somatosensory projections of different body parts of albino rats to patchy mosaics on folia of rat's cerebellar cortex. Our new discoveries of a novel form of representation in the tactile areas of cerebellar cortex require reinterpretation of standard views of function of the cerebellum.

lies, genera, etc. (e.g., elephants, porpoises, seals, manatees, anteaters, and llamas). Animals of the same species but of different breeds having different features (e.g., different dog breeds) were also added to the collection. We also selected brains of closely related species or of genera that differ in body (and brain) size, such as the largest living rodent (the capybara) and its small relative (guinea pig) or the African lion and domestic cat. Animals were also chosen on the basis of species differences in subtle details of their behavioral repertories or on the basis of features of their anatomy.

20. Together with my long-time colleague, John I. Johnson, Jr., we have devoted our later professional years to promoting the stabilization of our brain collections by planning for their eventual transfer to the National Museum of Health and Medicine in Washington, DC, with the hope of providing a home for properly curated and preserved mammal brain sections. When our collections are finally fully moved to the National Museum, they will be made available to students, scholars, and researchers worldwide for study far into the future. In order to promote public awareness of these valuable mammal brain collections, we have established web sites where students (K–12), teachers, and researchers, as well as the interested public, can browse and download images and information about any of our nearly 200 mammal brains. To do this, John I. Johnson, Adrianne Noe, and I created and are maintaining and developing three major Web Sites on the Internet that are informative regarding brains of different mammals:

http://www.brainmuseum.org,http://www.manateebrain.org, (both being maintained by Welker at Wisconsin), and: *http://www.brains.rad.msu.edu* (being maintained by Johnson at Michigan State University). When browsing these web sites, users worldwide can access images and information about the Comparative Mammalian Brain Collections (including human brains) at the University of Wisconsin and Michigan State University. Human and other mammalian brains can be viewed from the web site of the National Museum of Health and Medicine *(http://www.natmedmuse.afip.org/collections/collections.html)* (maintained by Adrianne Noe, director of the museum).

21. We (Johnson, Reep, and Welker) also have launched a series of studies of the brain of the Florida manatee, with the collection of 10 manatee brains that have been sectioned and stained. These specimens were captured and perfused by Dr. Roger Reep, with the help of the U.S. Fish and Wildlife Service. Our web site summarizes many of our findings to date (*http://www.manateebrain.org*).

22. In all the research ventures mentioned previously, we placed great emphasis on visual and graphic representation of our experimental findings. Photographic techniques by our photographer, Terrill P. Stewart, have generated a large library of realistic images of brains. Similarly, we accumulated large collections of photographs, illustrations, and drawings of our brain specimens, research findings, and equipment, which were prepared by our medical illustrator, Carol Dizack. Carol is my wife, and we have worked together as a team for over 25 years to produce a large library of representations of complex sets of information and results from our experimental and conceptual findings of a variety of mammal brains.

Background

Early Life on the Farm

My interest in science and research began in the last 2 years of high school. However, an intense and focused curiosity developed during my life on our family's farm. These early experiences must have determined many directions and features of my scientific career, during which I expected to explain how the brain does what it does.

I was the older of two boys, and we were required to learn and perform many duties in the barn, fields, maple woods, yards, gardens, and house that were part of growing up, on a dairy farm in western New York State. We had a 120-acre farm on the outskirts of the town of Darien Center, in eastern Genesee County just east of Buffalo. We maintained 15–20 milking cows, flocks of laying hens, and young poultry, including turkeys for sale and pigs for market. Before we used tractors, our horses performed the heavy duties of plowing, cultivating, cutting, and hauling hay; binding wheat and oats; harvesting potatoes; pulling stoneboats to remove frost-heaved rocks from the fields in spring; etc. In later years horses were replaced with tractors and hand-milking with milking machines. Although we managed a dairy farm, we also raised additional "cash" crops such as wheat, oats, cabbages, potatoes, beans, eggs, and maple syrup. My father was a rigorous taskmaster, and he required my brother and I to be intimately involved in all these work activities from an early age; this instilled a disciplined work ethic that required knowledge of machinery, seasonal schedules and activities adjusted to the maturation of the different crops, as well as knowledge of animal husbandry. Cows required early milking (from 4:30 to 7:00 AM). To prepare the day's milk, it had to be cooled and transported by hand cart to the highway (U.S. Route 20) and from there trucked 25 miles west to dairy plants in Buffalo. House chores were also required and my mother was also a strict disciplinarian.

There was much to do on a farm, requiring long hours of work, 7 days a week, although Sunday was a day of rest from field activities (except as dictated by seasonal pressures for field and crop care and harvesting). There was much work to do, much of it physically difficult and routine. In February and March, we tapped sugar maple trees and boiled maple sap to produce up to 200 gallons of maple syrup in the maple woods at the back of our farm. Fall, winter, and early spring activities included maintenance and lubrication of machinery as well as fixing fences, painting barns, etc.

My older sister (Arlene Coccari, now retired, living with her husband in Babylon, NY), my younger brother (Neil, now a professor of biochemistry at Northwestern University in Evanston, IL), and I were raised in a small wooden frame house constructed in the 1830s. We lived there from the early 1920s to 1938, when my father and my grandfather (a retired carpenter) built a new larger house on an adjacent lot. We had an older brother who died of rheumatic fever when he was 9 years old. This small, old house was heated in the cold western New York climate by a cellar furnace, by a single floor vent in the living room, and by an iron wood-burning kitchen stove and oven. Soft water was pumped from a rainwater cistern in the basement. Except for the early years, we had plumbing, a toilet, and hot and cold water. Our small house had four bedrooms upstairs. Downstairs, there was a living room, dining room, kitchen, and a toilet (with bathtub) as well as a small guest bedroom. A woodshed was attached to the rear of the house, and a full-length veranda (porch) faced the front of the house. We also had vegetable and flower gardens, shrubs, an extensive orchard, a vineyard, freshwater spring, a creek, etc. A large barn contained a basement for 20 cows and four horses, as well as two cattle pens and an attached ceramic corn sileage silo. We also had two or three chicken houses, tool sheds, pastures, several fields for crops, a large sandpit, and a huge trash pit behind the barn. A pasture and a fenced lane led to a pasture and to a large sugar maple forest at the back of the property.

The Glory of Play and Exploration

Every day when chores were finished, we children were given freedom to play in the house, the barn, outdoors in a sand pit, or along the creek. We explored everywhere on the farm. We roamed at will the farm fields, orchards, gardens, woods, pastures, and swamps. As youngsters, these activities were accompanied by the thrill of adventure and discovery and of imaginative play. In these environments we learned much about nature, the seasons, wildlife, both animal and plant life, as well as the determinants of phenomena in the natural world. Hard work was balanced by a wonderful life of play and exploration.

In these environs I experienced the development of a conscious, rational curiosity. As an early adolescent, I learned to systematically explore the natural environment. I developed curiosity about the causes of the natural features of plants and animals that I encountered. It was an unusual thrill and excitement when I learned that it was possible to ask questions about why things are as they are and why different plants and animals have the different forms, shapes, colors, and behaviors that they do. I trace my lifelong curiosity about the phenomena of nature to these early adolescent yearnings. Having the freedom to ask questions, daydream, play act, imagine, and think about possible answers to the many questions that life poses—this philosophy of open enquiry began in these early years and has persisted throughout my life.

Out in nature, I observed the spatiotemporal dynamic effects of blowing wind that produced waves in the grass, the spring leafing, and the fall shedding of leaves; the turmoil and eddy currents of swirling wind and water; the complex behavioral repertoires of birds, amphibians, lizards, snakes, cows, cats, dogs, and people; and the birth, development, sickness, and aging and death of all living forms. In the course of my play, I became aware of the intensity of my visual observational capacities, the interesting vagaries of thought that take place in both day dreaming and introspection. I also became aware that I was not adept at dialogue in social settings and tended to be quite shy and embarrassed when put on the spot socially.

During these years on the farm, I developed many mechanical skills. I learned how to repair equipment, sharpen blades, construct cabinets, repair door hinges, and to work on many types of small equipment. I enjoyed creating electric circuits to control buzzers or activate switches. I also learned how to garden as well as how to plant, grow, cultivate, and harvest various farm crops as well as all the common garden vegetables and flowers. My father took pleasure in landscaping our property. He arranged and planted shrubs, small trees, flower beds, lawns, a fruit orchard, and grape vineyards. We had a great variety of fruits available, including plum and cherry trees and currant bushes. Starting with the first thaws in February, we mounted great efforts in harvesting maple syrup in our maple woods. The entire family (including the hired man and neighbor kids) would ride a horse-drawn sled back to the woods, tap the larger trees, hang buckets on the spigots, haul tanks of maple sap from emptied tree buckets up to the sugar bush, and empty the sap into two large rectangular tanks. The sugar bush shed contained a large boiling wood-fired furnace with boiling pans. A chimney at the rear of the boiler carried heat, smoke, and sparks into the air.

The boiling sap was routinely routed forward as it thickened and darkened, and periodically it was drained off into a 10-gallon milk can through a heavy felt filter. The boiling sap required constant tending, day and night. Only when "just right" could the fresh, hot syrup be drawn off at the front pan of the stove and new sap be drawn in at the rear pan of the stove from the two holding tanks outdoors. It was a special treat when I was old and smart enough to tend the sugar bush by myself overnight. After everyone else had gone back to the house for dinner and to the barn, to conduct the evening's and next morning's chores, it was a special time to be tending the hot steaming vats through the silent twilight hours and on through the night, periodically drawing off the dark golden syrup. These solitary times were special times for reflection on life, on nature, on my role in the family and the farm economy, and on the future.

As kids, we had early experience in sacrificing farm animals for food (cattle, pigs, chickens, and turkeys) and in disposing of aged or sick animals (horses and cats) or pests (rats, mice, snakes, woodchucks, etc). These early experiences habituated us to the fact and to the necessity for such destruction. It is likely that in my professional life the use of animals in experiments, including their initial capture, anesthetization, the surgical procedures used (acute and sterile), their eventual sacrifice by overdose of anesthetics and perfusion with saline and fixatives, and subsequent dissection and removal of portions of the nervous system for eventual photography, measurement, and histological processing and microscopic study, in time became tolerable and somewhat acceptable because of these early experiences on the farm. Of course, all these experimental uses were important and essential to achieve the objectives of the project goals in the neurosciences.

Other activities I engaged in on the farm that fostered thoughtful examination of mind and matter included driving horses or tractor in plowing, cultivating, and harvesting, and driving the cows along a narrow lane to a grazing pasture at the rear of the farm. Other creative activities that involved active curiosity and playful adventures included the use of commercial fireworks, rockets, and manufacture of my own recipe of gunpowder to which I added smoke ingredients that created interesting and alarming effects. I also experimented with electrical circuits, manufacture of homemade cannons, and the use of an air rifle.

My father was a bandleader and he required us all to learn to play a musical instrument. I learned how to read music and to play the trumpet, later (in high school) the trombone, and finally the B-flat-bass horn. I also had early experience with competitive sports, bands, choirs, etc.

Being taught to play and read music by my father introduced me to the fierce emotion and difficult drives ncessary to overcome a difficult cluster of cognitive emotional and mathematical skills as well as the special language of musical notation. It taught me about the dynamic spatiotemporal activities involved in musical activities. These experiences gave me an appreciation of the marvelous mathematical, emotional, and sensorimotor capabilities that the human brain has evolved to express.

Personality: Self-Expression, Rebellion, Biological Urges, and Alcoholism

Although I have emphasized the importance of my yearning for solitude, quietude, of the calming effect of my youthful curiosity and play with nature, and the honest intellectual pursuit of knowledge and truth in all its forms, my life also manifested a kind of shy brooding that made me vulnerable to social forces and that made me unfit for leadership of more than a small informal, task-oriented group of colleagues on specific projects. I avoided formal teaching as in standing before a group of students, chairmanship of committees or a department, or leadership of professional societies.

I was fortunate to have two beautiful, interesting, and creative daughters, Mara and Nila, now in their 40s and 30s, have brightened and enriched my life in numerous and varied ways, despite that fact that they have lived most of their lives 2000 miles or more away.

Early on, at the University of Chicago, work was obviously stressful despite its fascination. I always bit off more than I could chew. I began to use alcohol and cigarettes in ways that seemed to allow me to distract myself from the burden of my ambitious work horizons. Booze helped me to lighten the load and intensely pursue multiple facets of science. It seemed to allow me to explore many research dimensions simultaneously, to attain a tolerance for ambiguity, and it oddly it seemed to give a kind of perspective to all of life's other claims on my time. In retrospect, I realized that I was predestined to becoming an alcoholic, when, in telling about my alcoholic experiences to fellow recovering addicts in meetings of Alcoholics Anonymous (AA) during the first week of 1972, I realised that I drank alcoholically the first time I drank mixed drinks in a social situation while at the University of Chicago. Monthly parties were set-ups for developing alcoholic behaviors in graduate school. Throughout graduate school I found that drinking was the only way that I could manage social settings.

Despite the sudden and clear-cut attraction to alcohol, I was not aware that I was heading down a one-way trail. In the beginning, alcoholic behavior was sporadic and interpolated amidst my professional activities and duties. The self-induced stress in my professional activities was not clear to me, and denial of my addiction was strong and convincing until the standard signs of alcoholism became apparent to me: family life (divorce, remarriage, etc.), financial distress, work impact, inability to write and think and carry out tasks to completion, physical problems (hospital admissions), suicidal adventures, etc.

Recovering from an active alcoholic lifestyle began on the second day of January 1972, the last day of drinking. I owe my recovery to AA, within the fold of which I learned to live one day at a time and gradually restore balance to my life. Then I met my last wife, Carol Dizack, who has been my abiding and best friend and companion ever since.

The School Years

Grade School.

Grade School was a time during which learning social skills was my main interest. I learned how to make friends, appreciate the existence of different personality types, and how to get along without conflict and controversy. I learned the essentials of becoming a responsible, cooperative citizen, and how to collaborate and cooperate with my fellow students and teachers to reach our common goals. Also, I learned social skills of how to make casual friends. All these experiences affected the style of my research and mentoring activities. I also learned the sweet experience of females.

My sister, brother, and I were required by our parents to receive religious training in a Methodist church and Sunday school. My curiosity about history in the Middle East began at this time, but it was here too where I first clearly became aware of bigotry and was exposed to strong religious beliefs and the emotional fervor about origins of everything, which included concepts of God and the universe. My exposure to science and learning about prehistory, and about evolution of animal and plant life, began at about this time. I became aware of systems of belief, including atheism and agnosticism, and the fact that there were so many different views on such broad issues.

Middle and High School.

During high school I learned much about biology, about how scientific experiments should be conducted in chemistry and physics, and of the value of mathematics in characterizing different features of nature. I also learned how ideas can be best expressed and about the importance of editing and writing for accuracy, mood, and communication.

In the last 2 years of high school I made an almost conscious decision to become socially responsible and a citizen of the school community. I developed a strong interest in people and children and in history and geography. I learned how to type, study, and how to play different sports (particularly basketball and tumbling), and I became a member of the band, choir, drama club, public speaking team, etc. I believed that I was becoming broadly civilized as I was exploring diverse capacities of human personality.

In my junior year in high school I published a small pamphlet with a variety of observations, which I called the *Weekly Foo*. In my senior year I became involved as editor of the class yearbook. We were faced with production, securing advertisements, arranging formats, obtaining and integrating text segments with illustrations, and photographing of class activities, school facilities, sports groups, and individual student portraits. This was my first experience in learning how to edit, organize and administrate the activities of several people to achieve common publishing goals of presenting concepts and ideas in informative and interesting ways. I was the class clown.

In my senior year in high school, it became clear to me that my interests were in the natural sciences and that I wanted to become a scientist engaged in research. In response to a senior year book question that asked what I expected to do in the future, I said "basic research."

Early Reading and Use of the Library

Our parents read very little to us kids. What little reading we did, we did on our own. We had a variety of reading material at home. I became an avid reader of the magazines that we had in our living room bookshelf: *Popular Science*, *Popular Mechanics*, *National Geographic*, *Life* magazine, and *Reader's Digest*. Available books included Grimm's fairy tales. I spent a considerable amount of time reading in the school library. After graduation, during which I was rewarded with the state of New York recognition of my scholarly potential, I spent the summer hanging around the halls of the school, painting railings and doing odd jobs. In my senior year, I also read selected writings of Sigmund Freud and other psychoanalysts.

I lamented having to leave the newfound socially and intellectually stimulating atmosphere of high school during my senior year to go forth into an uncertain future in the world at-large. Reading and spending quiet time in the hush of the library felt like being in a sanctuary. I came to worship books, writing, and the intellectual atmosphere surrounding the written word in all its forms. I had not yet come to realize that exploring the larger world outside my familiar haunts in western New York State had many facets that were yet to feed my curiosity.

Cowboy films (the *Lone Ranger* and *Tom Mix*) adventure films, and later romantic films provided additional avenues for flights of fancy into novel environments.

Interruption of the Safe Academic Life by Joining the Army

For some time during my youth, my father had suggested that I might benefit by going to a military school. My own view was undecided, but I felt sure that my father felt that I needed the personal discipline that military exposure could provide. It had been clear to me for some time that I preferred to be engaged in idle curiosity and playful imaginative activities rather than the hard work on the farm. My father suggested that I apply for an appointment to West Point, the officer-training military academy for the army. To obtain an appointment at West Point, it was necessary to be recommended by the congressman from our district. Consequently, I wrote to Representative Wadsworth requesting that he appoint me. I drove to the congressman's estate in the Finger Lake region of New York and met with him one afternoon in the summer of 1944. As a result of this interview, together with letters of recommendation from two businessmen and a minister from our town, I was appointed as a first alternate and would be accepted at West Point if the designated principal appointee could not accept the appointment. While awaiting news of the choice of the appointee from my district, I enrolled at Cornell University in Ithaca to begin my college training. At the end of the first quarter, I joined the army at the age of 18. I went to Fort Dix, New Jersey, for induction into the army, and after basic training (much discipline, hard work, and KP duty) I was sent back to Cornell University, where I and other new recruits took basic courses in mathematics, chemistry, biology, and literature. After the end of the first quarter of college at Cornell, the army gave all of us potential West Pointers the opportunity to enter Officer Candidate Training for Infantry at Fort Benning, Georgia. Near the end of this officer training tour of duty, I learned in June 1945 that, because the principal appointee from my congressional district had accepted the appointment, I was therefore ineligible. In this circumstance, I was given the choice of going to any officer candidate school (OCS) of my choice. I chose to continue training at the infantry OCS at Fort Benning. As a consequence, I went through the entire officer training routines for a second time. At the age of 19, I graduated as a second lieutenant in February 1946. World War II had come to an end during the previous few months, and I was sent to Fort Ord, California, to prepare to ship to the Philippine Islands to replace those troops stationed there who were slated to return stateside.

I boarded a troop ship at the docks in San Francisco with several thousand infantry troops. We sailed under the Golden Gate Bridge and out across the Pacific Ocean with stops at Honolulu and Midway Island, and we docked finally in the bay of bombed-out Manila in April 1946. I was shipped to Clark Field, the air base north of Manila, to take up administrative duties in the quartermaster unit at the infantry command post. This was my first administrative post.

While crossing the Pacific Ocean, one of my duties was to stand guard on the decks of the troop ship. It was at these times that I became aware of the vastness and beauty of the Pacific Ocean. I was also aware that I was part of an operation far greater than any that I had previously been involved in. I learned from one of my fellow officers, whose family was involved in the diplomatic corp and foreign service, of the great importance of solving some of the world's problems that had led to World Wars I and II. During the postwar period, many nations had decided that it was essential, to this end, to establish a worldwide organization, the United Nations, which might play a regulatory role in maintaining peace among nations. One of my other close companions on the long journey across the Pacific was a young man who was a Mormon, who acquainted me with the Mormon practice of public service abroad.

In the Philippines I experienced cultural shock and became aware of the cultural differences so obvious between the United States and the Phillipines. I also witnessed General MacArthur's speech in Manila attesting to the importance of containing military aggression. I stood before my company on the apron to Clark Field during a brief visit by General Eisenhower. Years later (when General Eisenhower became president), the National Institutes of Health were founded and became a major funding source for research in the neurosciences. During this entire time I became familiar with the military might of the United States and the organizational hierarchy of the military. I saw my first jet fighters over Manila and flew in the belly of a B-12 Bomber from Manila to Clarks Field.

In Manila I met my cousin, who was a nurse in the army. My father had taken ill when I was in the Philippines and my cousin arranged (through Red Cross channels that she was aware of) for me to obtain an emergency family discharge to return to the farm to aid my brother and our hired man in harvesting the crops and operating the dairy herd.

I flew back across the Pacific Ocean in a DC-3 from Manila to Ames Field in northern California. As soon as I arrived stateside, I called home to inquire about my dad's health. My sister answered the phone and she told me that dad had died. I had not known this. Strangely, I felt unmoved and confused by this loss. I flew to Washington, DC, where I walked about in the Pentagon to obtain my discharge papers, after which I returned home to help my brother and a hired man with the fall harvest. The flight back across the Pacific was as impressive, strange, and striking as was the oceanic ship ride in the westerly direction. I began to develop a more realistic conception of the appearance of planet Earth and the human inhabitants on it. Upon discharge, I was given the opportunity to reenlist in the army and was aware, for the first time, how much I disliked the regimen and discipline of military life. It was clear that I needed to have great freedom and latitude for exploration and mental play. I suspected that this was the kind of life that college could afford.

Back on the Farm

My experiences with managing the farm were equally onerous, offering little enticement for my future, and in a few weeks I realized that my major enthusiasm lay primarily in the direction of continued higher education. I applied to the American University in Washington, DC, with the intention of joining the Foreign Service as well as learning about constitutional democracy and government. I hungered to learn more about the world at large and to explore the new horizons to which I had been exposed in my military and college experiences at Cornell.

The Beginning of Serious Academic and Scholastic Experience.

As mentioned earlier, my introduction to college life occurred at Cornell University before I went into rigorous training in the army. I had taken only one-quarter of classes at Cornell, mostly the usual introductory required courses.

The American University

After my army service and a short autumn of hard work back on the farm, I was accepted for full-time enrollment at The American University. In Washington, DC, I was a serious and dedicated student. I spent all my spare time and weekends in the libraries, both on the campus and at the Library of Congress. My initial goal was to gain an understanding of government as part of my search for a life in the Foreign Service. I visited the museums of the Smithsonian Institution and the National Archives, I explored the U.S. Capitol Building, I watched Congress in session, and I explored the departments of the executive branch of government.

My readings in the Library of Congress and my courses at American University focused on biological topics, the evolution of life, as well as the size and evolution of the universe, the galaxies, and our planetary system.

I became aware that I was intensely interested in biology, and a first course in general psychology convinced me that I was interested in human and animal behaviors and mental operations. I excelled in my psychology course, which was taught by a new Harvard graduate, Dr. Dalbir Bindra. His teachings and demonstrations of the principles of perception, psychophysics, behavior, emotion, thinking, and evolution, using Munn's general survery textbook, were so logically precise and rationally presented that I became aware for the first time that human mentation, emotion, social behavior, perception, etc. could be understood by direct study, analysis, and experimentation.

During my last year of high school, I had become interested in the writings of Sigmund Freud and other early psychotherapists and psychologists. This interest was rekindled at college in Washington, and I decided to try to go into the field of psychology, despite my original motivation to learn about government and other large-scale attempts to regulate and understand human behavior.

After 2 years at American University, I applied to several universities for continued training in Psychology. The psychology department at the University of Chicago was the first to accept me. The admissions Committee at Chicago included Dr. Garth Thomas, who had been a fellow student at Harvard, with Dalbir Bindra, my professor at American University who undoubtedly recommended me since I routinely passed all his exams with top scores. During the 2 years in Washington, DC I hitchhiked several times back and forth from Washington to our farm near Buffalo. Hitchhiking was a safe and enjoyable mode of transportation in the late 1940s. It gave me many hours of solitude by the side of the road (day and night) and allowed me to talk with many different types of people in different parts of the country. I also hitchhiked to Chicago for my interview with the Admissions Committee in the psychology department.

I utilized the financial support provided by the GI Bill to attend American University. During the summer before I left Washington for Chicago, I worked as an aid in a private psychiatric hospital near Rockford, Maryland. This was an important learning experience because it gave me intimate experience with psychotics, paranoid schizophrenics, hysterics, and catatonics. It was here that I learned an important lesson about the many capacities of the human brain. I also worked for two semesters as a lab assistant to the zoology professor. I was accepted at the University of Chicago, probably based on recommendations from Dr. Bindra. I was told later that the fact that I was motivated enough to hitchhike to Chicago to have my interview also may have been influential in my being accepted.

At the end of my first year at American University, I married a fellow student, and we went to Chicago after I had been accepted at the university there. At the University of Chicago, neither a bachelor's or master's degree was required if it was clear that a student was going on directly to graduate school and a Ph.D. I finished all my required courses at the University of Chicago (except for my doctoral research) between 1949 and 1952. I could afford to go to college because of financial support from the GI Bill. In addition, I worked 20 hours a week in the psychology department shop. During my second summer in Chicago, I was a door-to-door salesman for the *Encyclopedia Brittanica, Junior*.

I enjoyed my exposure to the city of Chicago. It was my first exposure to a large metropolitan region. In conjunction with my courses in social psychology and sociology, I explored the city by riding the elevated trains, surface trolleys, and subways. I also wandered around the Loop, nearby steel mills, the poor neighborhoods, and the downtown skyscrapers. I felt that I was enlarging my understanding of human civilization. I also expanded my knowledge of major features of animal behavior, anatomy, ecology, evolution, and paleontology by visits to the Field Museum, Adler Planetarium, the Shedd Aquarium, the Museum of Science and Industry, and the Brookfield and Jackson Park Zoos.

The University of Chicago

The educational philosophy at the University of Chicago was to provide a fertile environment for learning and discovery. Emphasis was given to basic research, the development of new knowledge, and the search for basic truths and laws of nature.

I was naturally adapted to this approach to learning. I was exposed to several fields of experimental study:

Psychophysical studies: Garth Thomas was conducting a series of experiments in visual perception using a tachistoscope apparatus designed to analyze critical flicker/fusion thresholds. Garth was a kind and intelligent mentor. He taught the importance of introspection, with attention to subtle and fine perceptual details and thresholds. Working with him, I became aware of the complexity, subtlety, and accuracy of human perception.

Ethological Studies: Ekhardt Hess was an advocate of thoughtful and piercing analysis and identification of an animal's natural behavioral repertoire. He placed major emphasis on careful observation, the importance of naturally occurring behaviors, clarification and identification of stimulus and response parameters as determinants of behavior, as well as attention to quantification of behavioral features. He showed us how to identify individual components of behavioral repertories. Hess emphasized the importance and complexity of spatiotemporal sequences, reviewing the literature on how to describe and quantify behavioral sequences and identifying the stimulus features that trigger them. He emphasized that there are a variety of experimental methods that are available to conduct field studies of an animal's natural behaviors and the importance of viewing an animal's behavior within the context of its entire environment and natural history. He made it clear that a common problem in attempting to assess the features of any natural phenomenon is that attempts to quantify and analyze the phenomena can possibly interfere with, or bias, the outcomes of the analysis. Thus, attempts to quantify specific features of natural behavioral sequences can "force" or "skew" the experimental outcomes in ways that can influence the results of the experiment in unnatural or unexpected ways. (Thompson and Welker, 1964).

Developmental Psychology: At Chicago, in a course on developmental psychology, I was given the opportunity to carry out observational studies of young children in one of our country's first nursery schools. In this course, great emphasis was placed on observation, description of behavioral sequences, and quiet notation of human subjects without disturbing the children's expression of their natural behaviors.

Experimental behavior study: I carried out my first experimental study of "innate" sensory preferences of newly hatched chicks. In the psychology department at the University of Chicago, we were exposed to all branches of psychology and biology—experimental, cognitive, theoretical, statistical, factor analytical, and quantitative, clinical, educational, social, and group dynamics, as well as comparative and embryological aspects of development. We participated in pilot experiments in each of these subdisciplines. This broad exposure to the many fields of psychobiology provided us with expanded perspectives that were topically diverse. Such diversity had powerful influences on my later studies of neural bases of behavior, emotion, perception, etc.

Another important aspect of my experiences at the University of Chicago was being exposed to some of the giants in the psychobiological sciences. These included the psychotherapist Carl Rogers, the naturalists Wolfgang Kohler and Karl von Frisch, the experimental embryologist Roger Sperry, the neurobiologist Heinrich Klüver, and the famed expert in factor analysis, L. L. Thurstone.

After I had finished my formal coursework and passed my prelims, I needed to carry out my dissertation research. However, I did not have much enthusiasm for the research projects of my professors. It was suggested that I spend the summer at the primate labs at the University of Wisconsin, with the hope that a dissertation project might become obvious to me there. I also asked for advice about a possible Ph.D. dissertation from Dr. Austin Riesen, a well-known primatologist who had a history of research with chimpanzees at the Yerkes Laboratories of Primate Biology in Florida. Dr. Riesen also knew of an upcoming vacancy for a project assistant at Orange Park and was willing to recommend me for that position.

Primate Labs at the University of Wisconsin (The Beginning of a Research Project)

I spent the summer of 1952 at the University of Wisconsin, where I took a course on comparative studies of behavior with visiting Professor Frank Beach, who was a well-known comparative psychologist. While at Wisconsin I acted as a laboratory assistant at the primate lab under direction of Harry Harlow, where I trained in the use of the Wisconsin General Test Apparatus (WGTA), which Harlow developed to study learning in rhesus monkeys. These experiences helped me to clarify the distinction between the use of observational methods and formal testing methods in studying behavioral phenomena. This was my first exposure to the behavioral repertoire of primates. Here I became experienced with experimental testing methods, but I also developed a basic methodology for testing discrimination learning using curiosity drives rather than food reward as a motivation for performance of a learning task. In my first test construction, which was attached to the inside of the monkey's cage, the animal had access to pairs of screw eyes (protruding from the face of the test board), one of which (of the correct color) was detachable merely by being grasped and pulled from the board. The incorrect (differently colored) screw was fixed and nonremovable. Monkeys learned this paradigm in fewer than four trials. This was further evidence to me that the classical methods of assessing learning in animals interfered with the demonstration of such learning because they did not take into account the animals inherent perceptual and motivational capabilities. Here was another example of a human-centered testing technique that biased animals' responses and prevented the easy revelation of their natural talents.

Having discovered that I might be competent now to conduct my own research on primate behavior, I began to prepare to depart Wisconsin for the primate laboratory in Florida. It was ironic that, while at Wisconsin, I had not become aware that after my experiences at Orange Park I would return to the Laboratory of Neurophysiology at Wisconsin to begin serious study of the nervous system, for which I had been preparing all this time. The Laboratory of Neurophysiology had been started by Dr. Clinton N. Woolsey in the medical school 5 years earlier. Nearly 3 years later, Dr. Woolsey would give me the encouragement and assistance that I would need to become a real neuroscientist in Wisconsin.

Yerkes Laboratories of Primate Biology (and University of Chicago Ph.D.)

The outcome of all these experiences at the University of Chicago and the Wisconsin primate laboratory was that I decided to move in the direction of allowing the animals to tell me what was important to them rather than my imposing some experimental paradigm on them. It became apparent that animal perceptual curiosity is so strong, and was so poorly understood or investigated, that deciding to examine curiosity and play behaviors seemed to be a perfect solution to my search for a dissertation project.

After my summer experience at Wisconsin I drove to Orange Park, Florida, to begin my assistantship with Keith and Cathy Hayes. They had raised a captive-born female chimpanzee, Vicki, in their home for over 3 years in an attempt to teach this animal to "speak" using gestural and vocal behavioral signs. My main assignment, in addition to baby-sitting Vicki, was to evaluate Vicki's play behavior and construct play devices that would highlight her sensorimotor talents. I also spent a few hours per week testing older laboratory chimpanzees in the main animal compounds using food rewards in the standard WGTA to test certain hypotheses about learning being developed by Keith Hayes. This was a part-time job, and the rest of my time I spent learning about the Yerkes labs chimpanzees (about 50) under the tutelage of Henry Nissen, who was the associate director of the laboratories.

This was my first experience with these larger, more complex primates. I set about to devise objects and surfaces that would allow me to assess the stimulus determinants of the natural curiosity and play behaviors of young chimps as well as to devise ways to describe and take note of their play-action sequences. All these studies were done out doors, in the open-cage portion of each animal's living quarters. During my 2 years at the Yerkes labs, I spent many hours observing and testing the behavioral capacities of chimpanzees. These solitary times with these remarkable animals were crucial in allowing me to inquire more thoughtfully and deeply into the mental capacities of chimpanzees as well as other animals and myself. The similarities between chimpanzees and humans were striking. My thesis research specifically described playful and exploratory behaviors of young chimps using stimulus objects that varied in size, shape, color, surface texture, and complexity.

This was a formative time. I was introduced to the thinking and writing of many well-known scholars who had been studying animal behavior, perception, emotional expression, and learning. Others at Orange Park were doing brain ablation studies in search of brain correlates of various aspects of behavior, learning, cognitive, and emotional behaviors. These were some of the earliest studies of the roles of the brain in behavior, learning, development, and perception. Karl Lashley was one of the few early great thinkers and experimental psychobiologists using brain ablation techniques in rats, cats, and monkeys. Being at Orange Park in the early 1950s was a great intellectual bonus since Karl Lashley was the director of these labs and he was one of the greatest thinkers of the time. The neurosciences were picking up steam around the world. However, at this stage, neuroelectric studies of the nervous system were still very primitive. Microelectrodes were not being used, nor had the electron microscope been employed to study the nervous system. Neurohistochemical methods were still rather primitive.

The formal tests that I used to study learning and perception gave me insight into the limitations of these testing methods in assessing the behavioral repertoire of animals. Important in this regard were the daily luncheons participated in by all the staff and researchers at the Yerkes labs. These lunches took place among a cluster of small palm trees in front of the administration building of the Yerkes labs, where there was a collection of wooden chairs and a table. It was at these luncheon meetings that I became familiar with the intellectual stimulation that was possible among scientists. It was here that important concepts were discussed, research progress was reviewed, and good humor was expressed. Karl Lashley, the laboratory's director, was always present at these lunch discussions, as were Henry Nissen (the assistant director), K. L. Chow, Jack Orbach, Keith Hayes, and a physical anthropologist, James Gavin. Mr. and Mrs. Yerkes visited from time to time. A variety of well-known psychobiologists occasionally visited to take tours of the labs. These included Alfred Kinsey and Karl Pribram (with whom I assisted in my first sterile neurosurgery, in this case with monkeys).

While at Orange Park, I raised a gray squirrel and a nestling blue jay from infancy. These experiences prompted a lifelong interest in the ontogeny of behavioral repertoires, and they also kindled my strong interest in the correlated development of both the behavioral repertoire and the nervous system. It became clear that watching the maturation and first occurrence of different elements of the behavioral repertoire of an animal was like watching the outward expressions of the developing nervous system.

While exploring the capabilities of chimpanzees for natural exploration and play with objects, I realized that I had discovered my dissertation research project that was required by the University of Chicago to receive my Ph.D. The university had approved of my going to Florida (upon Dr. Riesen's recommendation) to do my research. I returned to Chicago a couple of times to write up my thesis and have it bound and distributed to my dissertation committee. My final trip north was to meet with my committee and to present my research results. My committee approved of my dissertation, and I received my Ph.D. degree in the early summer of 1954.

The Transition from Florida to Wisconsin

On the recommendations of Karl Lashley, Austin Riesen (my adviser), Henry Nissen, and K. L. Chow, I conducted my postdoctoral research at the University of Wisconsin under the supervision of Dr. Clinton N. Woolsey (the new director of the laboratory of neurophysiology in the department. of Physiology). Since I was also strongly interested in behavioral analysis, I obtained the permission of Dr. Harry Harlow to do a behavioral research project in his laboratory that we might mutually agree upon. During the summer of 1954, I also applied for, and was awarded, an a National Institutes of Health (NIH) postdoctoral fellowship to carry out brain and behavioral research at Wisconsin.

Before leaving for Wisconsin, I spent a month at the marine laboratory on the island of Bimini in the Bahamas, that was operated by the American Museum of Natural History (AMNH). I wrote the head of the icthyology Department at the museum and was given permission to use their facilities at Bimini for the months of July and August (just before hurricane season). I was approved to go there on the basis of a proposed experiment to study the responses of fish to novel stimuli. The experience at Bimini was remarkable. I gained a broadened perspective about marine life and about the evolution of vertebrates. I read as much as I could find about marine life and spent a considerable amount of time snorkling among the fantastic floral and faunal life on the coral and coastal sea beds. The proposed experiment was carried out and was published (Welker and Welker, 1958). These experiences broadened my comparative perspective and introduced me to concepts of evolution in marine environments.

The University of Wisconsin and Postdoctoral Experiences

Clinton Woolsey was one of the first early neurophysiologists in the United States with a broad interest in experimentally defining various kinds of functional and structural organization in the brains of a variety of mammals. Woolsey pioneered the electrophysiological mapping of cerebral cortex. After receiving his M.D. at the Johns Hopkins University School of Medicine, he became a research physiologist in the Department of Physiology as an assistant to Dr. Philip Bard (who wrote the major textbook of Physiology used by Medical Schools in the United States at the time). Woolsey was recruited by the University of Wisconsin to set up a laboratory of neurophysiology. This was one of the few basic research laboratories devoted to training in neurophysiology that existed in the late 1940s.

Apprenticeship.

I arrived at the University of Wisconsin on September 1, 1954, to begin my postdoctoral fellowship under the tutelage of Dr. Woolsey. I joined Dr. Woolsey's experimental group, together with two other new postdoctoral students, Dr. Robert Benjamin and Dr. Joseph E. Hind. Dr. Woolsey trained us initially in both recording and electrical stimulation studies of the cerebral cortex in different mammals: rats, marmosets, squirrel monkeys, and chimpanzees. By the time Benjamin, Hind, and I arrived at Wisconsin, Woolsey had already developed an international reputation for the broad scope of his work and interests in comparative neurophysiology and neuroanatomy. He was one of the first neuroscientists to systematically map sensory and motor areas of the cerebral cortex from a comparative standpoint. Woolsey developed methods for data portrayal (e.g., figurine maps) that easily allowed the reader to see how different sensory surfaces (skin, retina, and cochlea) projected topographically to central brain regions. He was an accomplished neurosurgeon, a generous teacher, a wise mentor, an outstanding human being, and a great friend. He was skilled in the application for, and administration of, federal grants for conducting basic research, As an accomplished laboratory organizer and manager, he possessed the administrative intelligence required to obtain what was needed to carry out a program in basic research but was unencumbered by university administrative and teaching duties. His neurophysiological recording lab was set up with the latest equipment (e.g., oscilloscopes) for electrophysiological recording, and stimulating equipment for providing precisely calibrated mechanical, visual, and acoustic stimulation, and electrode manipulating and animal immobilizing equipment that allowed researchers to use mapping methods for sampling extensive regions of the brain (particularly cerebral cortex). We also were provided with photographic, neurosurgical, and neurohistological facilities. Administrative office support was separate from that of the physiology department.

Woolsey encouraged many enthusiastic and curious young scientists to join one or another of his research groups. He gave generously of his time and attention to helping his apprentices build their careers. It turns out that this period (when research funding was becoming readily available) was ideal for curious young men and women to enter the field of neuroscience. In Woolsey's labs at Wisconsin, inquiring students were given freedom and encouragement to conduct basic research projects under his guidance and to work with Woolsey on experiments of his interest. Woolsey supervised his pupils closely and helped them learn how to perform experiments with care and precision. He taught us all how carefully to handle animals, perform acute and sterile neurosurgery, operate a photographic laboratory, learn histological procedures, as well as how to use the microscope to analyze stained brain sections in order to identify those specific regions from which we were recording. Woolsey also encouraged us to perform literature searches, read the literature broadly, write up scientific reports, and present our research results at scientific meetings and, thereafter, publish our results in scientific journals.

Woolsey's major electrophysiological tools involved recording evoked potentials by surface macroelectrodes activated by focal stimulation of somatosensory, visual, or auditory receptors.

After our early training, Woolsey set Benjamin and I to work on our own by assigning us the task of mapping the cortical sensory and motor areas first in albino rats and then in small primates such as the squirrel monkey. We were the first to publish anything about the brain of these unique small primates. The aim of these mapping studies was to describe and define the projection patterns of sensory (tactile, auditory, and visual) stimuli to cerebral cortex. A crucial aspect of these experiments was to identify the anatomical location of physiological recording loci in order to correlate the structural–functional sets of data in search of the neuroanatomical substrates of the recording data. Functional localization was a major thrust of Woolsey's life's work. He and all his students made it their life's work to discover major principles by which the brains of mammals are organized into nuclei, simple circuits, systems, and networks. He made the entire brain his field of study. The breadth of Woolsey's interests was surely a major character that attracted so many of us from nonneural fields to become neuroscientists in search of the neural mechanisms of behavior and perception.

Woolsey had been engaged in such studies for many years before he moved to Wisconsin. He began these mapping studies at the The Johns Hopkins University School of Medicine in the Department of Physiology under the tutelage of Philip Bard. Woolsey's favored teaching philosophy was that of a mentor–apprentice relationship with his trainees. Over a period of four decades, Woolsey's laboratory became world famous for successfully training people in the neurophysiological and neuroanatomical sciences. Woolsey's apprenticeship program expanded to include as many as 20 students at any one time and up to 150 over a four-decade time frame. He secured funding for training predoctoral as well as postdoctoral students. Over this period the neurophysiology facilities expanded to include laboratories headed by senior scientists, who had initially trained with Woolsey and subsequently became competent principal investigators on their own merit. In addition to Joe Hind, Bob Benjamin, and myself, other such early mentor/trainees included Jon Kaas, John Allman, John Brugge, Bill Rhode, Jay Goldberg, Don Greenberg, and Mike Merzenich. Woolsey's initial focus on mapping visual, auditory, and somatic sensory projections to cerebral neocortex expanded to include recording studies of these types of sensory projections to brain stem, thalamus, and cerebellum, as well as electrical stimulation studies of cerebral cortex. Separate laboratories were set up for studying somatosensory, visual, and auditory systems.

To assist him in localizing neuroanatomical structures that had been surgically removed, or recorded from, Woolsey invited Dr. Konrad Akert from Switzerland to join the laboratory of neurophysiology and become the neuroanatomist in charge. Later, Woolsey recruited Dr. Jerzy E. Rose to join this expanding laboratory when he had secured funding to design and build two floors in the new medical sciences building which was being built as an adjunct to the existing medical school training facilities. One of the experimental rooms in this new building was designed for my own somatosensory studies.

Jerzy Rose played a major role in developing and promoting the use of microelectrodes, which could then be used to carry out sophisticated and precise analyses of responses of single neurons. In addition, under the guidance of Dr. Joseph E. Hind, a variety of more complex recording and stimulating equipment led to greater refinements and control of sensory stimuli: soundproof rooms, stabilized recording tables, and the development of more sophisticated animal care and respiratory equipment. Operating microscopes were introduced to allow greater control of electrode placement as well as to facilitate more precise neurosurgical maneuvers.

During this explosive development of neuroscientific studies throughout the country, equipment companies were developing a variety of more sophisticated apparatus to accommodate the needs of the growing neuroscience community worldwide. In addition, improved animal facilities, animal care, and veterinary supervision were developing into a single specialty.

Woolsey's neurophysiology labs expanded in size and diversity as students from around the world desired to train with him. The senior neuroscientists, who had apprenticed with Woolsey and desired to expand their experience to include exposure to the remarkable facilities available at Wisconsin, established several different laboratories devoted to other neurophysiological studies. I, and the students who worked with me, specialized in defining somatic sensory circuits in a variety of different mammals. Dr. Robert Benjamin and his students specialized in studying taste and chemoreceptors in several mammals. Drs. Allman and Kaas worked together on comprehensive comparative studies of visual cortex, thalamus, and midbrain nuclei. Drs. Joseph E. Hind, Bill Rhode, and Jerzy Rose focused on defining auditory circuits of the medulla, midbrain, thalamus, and cerebral cortex. This auditory group became the largest research program, occupying the greatest number and variety of laboratories and conducting the most sophisticated analytical studies of stimulus–response relationships in the auditory system of mammals then in existence. Other students were allowed to carry out independent studies of their own design, although they were given assistance and supervision as required.

The great variety of research activities being carried out in the Wisconsin Laboratory of Neurophysiology (and, after 1973, the Department of Neurophysiology) provided one of the most attractive postdoctoral research training facilities in the country. Woolsey's neurophysiology group at Wisconsin became world famous for the free atmosphere of conducting pure apprenticeship-type research. We were all very fortunate to be part of this group effort, apparently at the forefront of research into mapping the sensory and motor projections within the brain. These studies developed the foundation for the ever-more precise neuroelectric, neurochemical, and neurocytological researches that have been emerging at the forefront of the microneurosciences from the 1960s into the new millenium.

Guiding My Own Research Program at Wisconsin

As I became more experienced in neurophysiological and neuroanatomical studies, I focused my own work on a variety of microelectrode recording studies of somatic sensory circuits within different parts of the brain in a variety of different mammals (Lende and Welker, 1972; Carlson and Welker, 1976; Campos and Welker, 1976; Welker *et al.* 1976; Krishnamurti *et al.*, 1976). I concentrated on exploring parts of the brain not yet explored, on animals that exhibited specialized neuroanatomical features, or on sensory or behavioral capacities that were unusual in some way. I continued to use descriptive micromapping methods to provide broader overviews of somatosensory projections. I preferred to examine the forest and leave the exploration of the trees, twigs, and leaves (i.e., intracellular recording, studies of neuroreceptors, and channels) to those more competent, more inclined, and better trained to work at this more precise level of neural function and structure.

Thus, my own research emphasized somatic sensory systems, tracing such circuits at several different levels within a given brain. We also used comparative studies to examine homologous nuclei and circuits in different species in order to explore unique specializations of particular somatic sensory circuits.

One of our first studies of the first-order somatosensory receptive fields (dorsal root fibers in the cervical region) was a comparative study of receptive field size and density in raccoons, coatimundis, and domestic cats. This study, when published, contained the greatest number of single neurons (over 2000) ever presented in a single experimental report. (Pubols *et al.*, 1965)

Our study of the first-order vibrissae receptive fields, recorded within the trigeminal sensory ganglion in albino rats, demonstrated that every trigeminal ganglion neuron subserved a single vibrissae, which indicated the great degree of sensory specificity of which the rat's sensory vibrissae are capable (Zucker and Welker, 1969).

A third set of experiments, also of the trigeminal ganglion neurons but in coatimundis and raccoons, revealed how extremely small were the sizes of the receptive fields of single neurons that innervate the glabrous skin papillae of their snouts. This unique somatic sensory study was made possible by our development and use of von Frey wires calibrated to deliver extremely small pressures. This approach allowed us to define, for the first time, receptive fields that were at the threshold of the animal's detection (Barker and Welker, 1969). This standardized approach made it possible to compare the threshold receptive field sizes in different animals.

In our study of the vibrissae receptive fields of rats, we also explored the quantitative features of the stimulus–response profiles by employing precisely driven stimulus probes for which stimulus amplitude, velocity, acceleration, and frequency could be independently controlled (Gibson and Welker, 1982, 1983a, 1983b; Gibson, 1987).

Study of Behavioral Specialization in Raccoons: Developmental Studies

Throughout my career at Wisconsin I conducted several developmental studies of behavioral repertoires of raccoons, African lion, a gibbon, puppies, kittens, and rats.

In the case of raccoons, I was curious to examine details of behavioral development postnatally. After a litter of four raccoons were born, I took daily movie sequences of the newborn animals until they could be removed from their mother and fed by bottle. For 6 weeks thereafter, I placed each of the four raccoon kits in its own observation box, with overhead lights suitable for movie making. I described the development of the behavioral repertoire of each of these four infants, focusing on the ontogenetic development of their exploratory and play behavior (Welker, 1959c).

As a corollary to behavioral development, I began to collect the brains of different animals at different ages, with the intent of following the neuroanatomical development of brain shape, size, fissural pattern, and nuclear formations.

Coincidently, I developed a keen awareness of species differences in lifestyles as they relate to specific environments and habitats, e.g., beavers, least weasel, guinea pig, capybara (the latter two emphasized differences in brain sizes and body sizes). Careful observations were noted and written, and photographic and movie notations were included.

I carried out several informal studies of behavior in different mammals in which I obtained a large reservoir of knowledge about the behavioral repertoire of a wide variety of mammals. I learned how to work with, handle, and develop rapport with a variety of animals of different ages and species. I studied the ontogeny of infant raccoons. I home-raised an African lion from birth to 9 months, coatimundis, coyotes, a two-toed sloth, kittens, an infant gibbon (from birth until 11 months of age; Welt and Welker, 1963), a flying squirrel, an armadillo, a slow loris, a gray squirrel, a blue jay, a young chimpanzee, a litter of raccoons, and a litter of puppies. All these experiences enhanced my understanding and perspective of how different brains are differentially organized.

Neurophysiological Mapping (Which Revealed the Functional Significance of Cortical Enlargement and of Cortical Gyration and Fissuration).

Since I had access to the raccoon breeding colony of the Wisconsin Fish and Game Deparement at the Poynette Animal Game Farm, I was able to obtain pregnant females from them as well as other adults for mapping studies of their somatic sensory cerebral cortex.

It was a surprise to find that the hand area of the cerebral cortex of raccoons was very large–larger than that of humans. The evoked potentials in raccoons were of enormous amplitude. Moreover, we discovered that when the slow waves were filtered out with low frequency filters, there were large high-frequency "hash" evoked responses induced by delicate touch to the raccoon's contralateral glabrous forepaw. Later, we attempted to use smaller diameter electrodes, and we discovered that the somatotopic resolution of peripheral projections to the cortex was increased markedly when we used more delicate peripheral stimuli, finer microelectrodes, as well as more precise neuroelectric evoked potential criteria. In addition, if the forepaw skin was moistened (as would occur when the animals were feeling objects under water), the size of the receptive fields that activated a single peripheral axon (or a single microelectrode locus within cortex) was considerably smaller than when the skin was kept dry.

I then decided to map the somatosensory cortex of several other members of the raccoon family: coatimundi, kinkajou, ring-tailed cat, and lesser panda (Welker and Campos, 1963). Each of these different species exhibited different gyral and fissural patterns of their cerebrum. In each of these species, the cortical sulci, dimples, and fissures separated adjacent gyri, but with different somatic sensory peripheral projections. The coatimundi was unique in that its face projections were unusually large, particularly that part that receives projections from the glabrous snout, which the coati uses to palpate and dig about in the forest litter.

We carried out several other mapping studies of cerebral cortex in search of something unusual, that might suggest how evolutionary forces may have shaped relative size, shape, and organization of somatosensory projections to the cerebral cortex. We mapped the cerebral cortex of the slow loris and found, for the first time, that there were several different modality-specific subareas within the slow loris's somatic sensory areas. In this animal too, sulci demarcated different somatic sensory projections (Krishnamurti *et al.*, 1976). This study also revealed that the precision of the peripheral projections to cortex depended on the size of the microelectrode used and the fineness of the neural responses recorded (i.e., single neuron, multiple unit, or evoked potential).

We compared the somatic sensory, visual, and auditory projections to cerebral cortex in the small guinea pig with those areas in the larger brain of the related rodent, the capybara (Campos and Welker, 1976). It was known that larger animals have larger brains when closely related species are compared. Thus, lion brains are larger than domestic cat brains. However, we did not find a simple explanation of why larger specimens have larger brains since the sensory areas were merely larger. The reasons for these size differences were not revealed by our simple studies of their sensory projections to cerebral cortex.

Summary of Mapping Studies.

The purpose of all the mapping studies was to obtain overviews of sensory projections to relatively large regions of cerebral cortex. Once the overall maps were obtained, finer-grained recording studies with microelectrodes could provide more detailed information of sensory coding and information processing within the system under study (Welker, 1976a).

We performed multilevel mapping studies in some of our work on the raccoon in order to trace the pathways of information flow as well as to determine how different nuclei within a circuit or pathway processed the spatial and temporal information flow differently (Welker, *et al.*, 1964).

We carried out quantitative stimulus–response analyses in several instances [infant raccoon first-order neurons (Beitel *et al.*, 1977) and rat trigeminal first–order neurons (Zucker and Welker, 1969)] from the vibrissae and facial hairs. These studies required the construction of precise mechanical transducers to move the vibrissae hairs. They also required the construction of complex sets of recording equipment capable of measuring and recording fine features of displacement of the transducers as well as response profiles of the single neuron responses that were recorded (Gibson and Welker, 1983a,b).

We focused on somatosensory systems for reasons of economy, equipment costs, and experience.

Personnel Who Worked in Our Somatosensory Group

A variety of pre-and postdoctoral students came to work with me at different phases in our work. These included John I. Johnson, Benjamin Pubols, John Gibson, Richard Lende, Gilberto Campos, Bob Compton, A. Krishnamurti, Georgia Shambes, Jon Joseph, Tom Parker, Sue Campbell, Ralph Beitel, Dave Barker, Ellen Zucker, Mary Carlson, F. Sanides, Ken Sanderson, Jim Bower, Jeff Kassel, Don Woolston, Claudia Blair, Lillian M. Pubols and Richard Thompson.

Micromapping of Cerebellum

During the first few years after I had stopped drinking, I spent a considerable amount of time trying to determine the content and course of the next phase of my work. I searched for a novel approach, for fresh insights, for a different target of my curiosity, and for a different part of the nervous system to study. A new student arrived, Georgia Shambes, who was a physical therapy staff member who wanted to become involved in brain research. Because she was experienced in the basic facts of neuromuscular systems, she was skilled in identifying muscles involved in any movement. She was also very knowledgeable about the basic organization of the nervous system.

We decided that we would study the somatosensory projections to the cerebellum, particularly muscle spindle projections to the granule cell cortex. We both decided to read the literature about the anatomy and physiology of the cerebellum, particularly the books by John Eccles. Concomitantly, we decided to explore cerebellar cortex in the albino rat. We had previously mapped the external cuneate nuclei (Campbell *et al.*, 1974) in rats, in which we found that muscle spindle receptors projected to different neuron clusters of this medullary nuclear complex. Since it was generally assumed that the cerebellum was an integrating center for control and organization of movement sequences, we thought that searching for muscle spindle inputs to the cerebellum would be a sure bet.

However, we found to our surprise that the only inputs to cerebellar cortex were those regions responsive to cutaneous stimulation. The cutaneous projections from gentle touch stimulation were delimited to four folia of the rat's ipsilateral hemispheres and to several folia of the posterior vermis. Moreover, these cutaneous representations were not organized in the usual somatotopic patterns. Rather, sensory projections were mostly from the head, face, and forelimbs, and they were organized in patchy, fractured, mosaical arrays (Shambes *et al.* 1978a,b). Because they were so unexpected, it took some time before we were able to define those projections that seemed most valid (Fig. 3). Ultimately, we realized that these projections were arrayed in fractured mosaics that were somatotopically disrupted. We also found that similar kinds of projections existed in cats (Kassel *et al.*, 1984), opossums, (Welker and Shambes, 1985) and Galagos (Welker *et al.*, 1988). This was a new and surprising finding. In a series of related studies our group defined the nature of circuits within cerebellar cortex as well as cerebrocerebellar circuits (Kassel, 1980; 1982; Woolston *et al.*, 1981; Woolston and Lalonde, 1983; Bower and Woolston, 1983).

All our studies have provided a new look into somatosensory circuits of the cerebellum. Our studies were the first to examine and define somatosensory inputs to the granule cell cerebellar cortex. Other studies revealed that the Purkinje cells were activated primarily by the granule cells directly beneath them (Bower & Woolston, 1983), and that parallel fibers played a different role than proposed by the classical literature on cerebellar circuitry (Welker, 1987a,b, 1989). These new findings provided motivation for an eager young group of investigators for several years. Moreover, it seems that the many tiny folia, such prominent features of the cerebellum in all mammals, are likely individuated functional units whose exact significance is as yet unclear (Welker, 1987a,b 1989).

Comparative Neuroanatomical Collection

It became clear, at the beginning of our comparative studies, that there were recognizable neuroanatomical correlates of neurophysiological as well as behavioral phenomena. We deliberately and systematically began to assemble a broad collection of mammal brains that would include a wide variety of brains that are representative of all but two of the taxonomic orders and of a large variety of most major families within the class Mammalia (Fig. 4). We also collected the brains of animals that exhibit specialized sensory and/or motor capabilities that might be reflected in the neuroanatomical arrangements of their brain structures. Thus, we collected raccoons (hand specialization) and coatis (snout specialization) within the family Procyonidae. In this case we examined the somatic sensory projections to first-order and cortical levels of these two animals. We collected

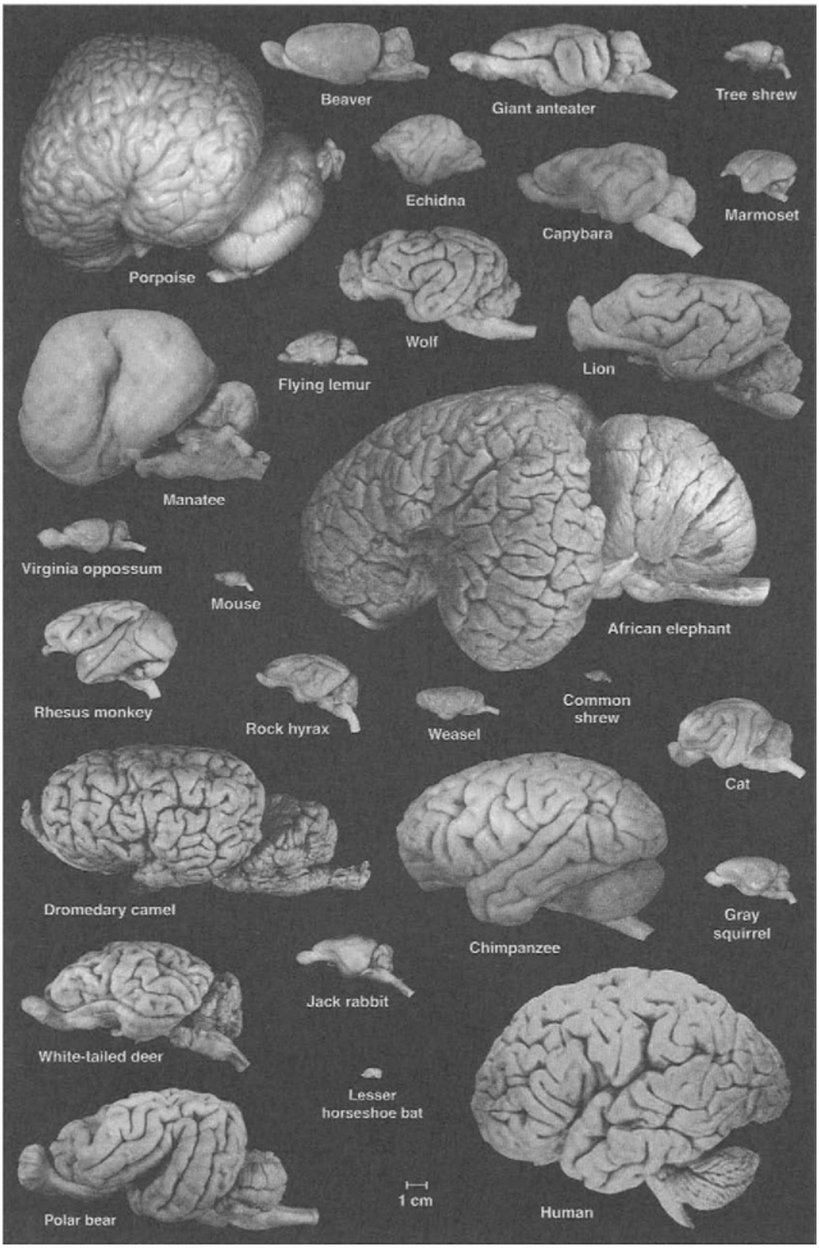


Figure 4. Comparative mammalian brain collection (Wisconsin), showing left lateral views of 27 different mammals from 14 different orders. These brain pictures show a sampling of a representative set of brains from our brain collections of over 275 specimens. Most of these have been sectioned and stained to reveal cytological details, which can be studied and analyzed microscopically from the archives.

large and small specimens within a single taxon (lion vs domestic cat; capybara vs guinea pig). We collected brains of the largest living rodent (capybara) and the smallest living carnivore (least weasel). With Roger Reep we obtained several brains of the large, but smooth, brained Florida manatee. Johnson was the main initial collaborator for our early collecting activities. Johnson continued his comparative studies after he left Wisconsin and joined the faculty at Michigan State University. While there, he expanded his comparative brain collection, specializing in a wide variety of marsupials. With Richard Lende, we collected monotremes (echidna; 1980) and the large highly foliated brain of the echolocating bottlenose dolphin (*Tursiops truncatus*) (Lende and Welker, 1972).

Assembling a brain collection at Wisconsin began with the impetus of Woolsey but was given additional guidance by Dr. Konrad Akert, who was one of the first neuroanatomists in Woolsey's laboratories. Akert revealed to us the value of fixing brains properly, i.e., by perfusion through the heart and removal of the brain after a period of 24 hours after perfusion in order to prevent fixation artifacts from developing. Akert also supervised the proper sequencing throughout histological processing. Helen Brandemuehl was the senior histologist at the beginning and supervised the training of other histologists (JoAnn Ekleberry and Joan Meister). Inge Siggelkow is now the chief histologist, and she has maintained the high standards of fixation and staining of sections, with thionin to stain cells and hematoxylin to stain myelin sheaths. These high standards of fixation, histological processing, preservation, staining, and mounting of sections have resulted in a brain collection that has endured use for microscopic study for several decades, without alteration of the quality of the stains.

Current Projects (2000)

My current work includes promoting knowledge and images about all specimens in our brain collections on two Internet sites (Fig. 5),

http://www.brainmuseum.org and http://www.manateebrain.org, and preparing our collections for their final transfer to the National Museum of Health and Medicine. When the Wisconsin Comparative Mammalian Brain Collection and the Michigan State Mammalian Brain Collection are finally located and stabilized at the National Museum, they will be available for view and use by students, researchers, and teachers for a long time to come. In Washington, these collections will be properly curated and cataloged.

Postscript

When I first began my studies of the brain at the University of Wisconsin, I believed that I had finally reached my destination in my lifelong search

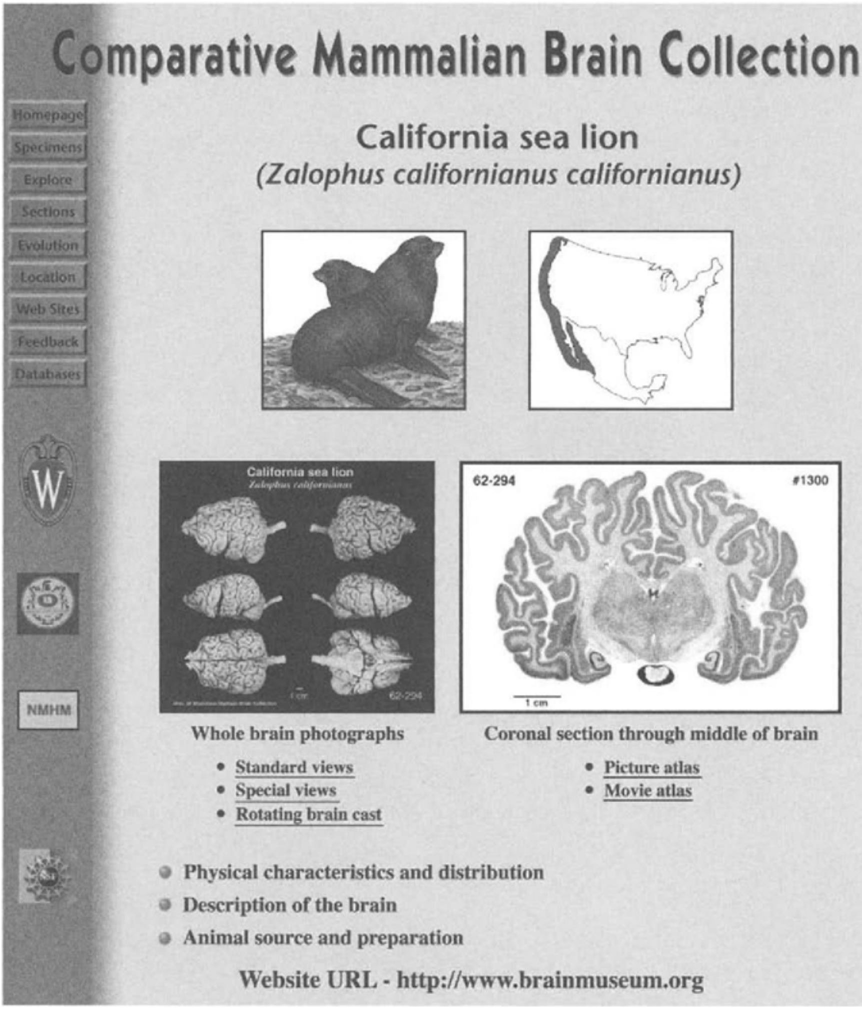


Figure 5. Sample specimen page (of California sea lion) showing features to be found on the Comparative Mammalian Brain Collection Web site: *http://www.brainmuseum.org*. Browsers can explore our entire brain collection and view whole brain photos as well as histological details and information about each specimen.

for neural mechanisms of behavior. The title of my first successful NIH grant application was simply "The Neural Mechanisms of Behavior." I was naive enough to believe that the exploratory mapping methods that we were being introduced to, as well as others then being developed to explore other brain operations, would soon provide us with a full understanding of how the brain worked to produce all the complex behavioral, emotional, cognitive, learning, and perceptual phenomena of which we are aware.

We carried out all the studies mentioned previously in search of these neural mechanisms, but 45 years later I realize that we have not achieved even a beginning in explaining how the brain works to produce the phenomena that interest us most.

Despite the "Decade of the Brain," and the enormous strides being made in the neurosciences, I believe that we are still just at the beginnings of our attempts to unravel the great "unraveled knot." We do not even know how to describe what happens in the brain when a pitcher winds up and throws a curve ball within the strike zone. Nor do we have an inkling how the brain works to enact a motion even so simple as grasping a pencil, placing its tip to the paper, and writing one's name.

The mammal brain is the most complicated object in the universe. Understanding its structure and function is the predominant intellectual challenge of our time.

Selected Bibiography

Full Experimental Reports

Barker DJ, Welker WI. Receptive fields of first-order somatic sensory neurons innervating rhinarium in coati and raccoon. *Brain Res* 1969;14:367–386.

Beitel RE. Gibson JM, Welker WI. Functional development of mechanoreceptive neurons innervating the glabrous skin in postnatal kittens. *Brain Res* 1977;129:213–226.

Benjamin RM, Welker WI. Somatic receiving areas of cerebral cortex of squirrel monkey. *J Neurophysiol* 1957;20:286–299.

Bower JM, Beermann DH, Shambes GM, Welker WI. Principles of organization of a cerebro-cerebellar circuit. *Brain Behav Evol* 1981;18:1–18.

Campbell SK, Parker TD, Welker WI. Somatotopic organization of the external cuneate nucleus in albino rats. *Brain Res* 1974;77:1–23.

Campos GB, Welker WI. Comparisons between two brains of a large and a small hystricomorph rodent: Capybara (*Hydrochoerus*) and guinea pig (*Cavia*); Neocortical projection regions and measurements of brain subdivisions. *Brain Behav Evol* 1976;13:243–266.

Carlson M, Welker W. Some morphological, physiological and behavioral specializations in North American beavers (*Castor canadensis*). *Brain Behav Evol* 1976;13:302–326.

Gibson JM, Welker WI. Stimulus-response profile analysis: A comprehensive, quantitative approach to the study of sensory coding and information processing. *J Neurosci Methods* 1982;5:349–368.

Gibson JM, Welker WI. Quantitative studies of stimulus coding in first-order vibrissa afferents of rats. 1. Receptive field properties and threshold distributions. *Somatosensory Res* 1983a;1:51–67.

Gibson JM, Welker WI. Quantitative studies of stimulus in first-order vibrissa afferents of rats. 2. Adaptation and coding of stimulus parameters. *Somatosensory Res* 1983b;1:95–117.

Gibson JM, Beitel RE, Welker WI. Diversity of coding profiles of mechanoreceptors in glabrous skin of kittens. *Brain Res* 1975;86:181–203.

Hind JE, Rose JE, Davies PW, Woolsey CN, Benjamin RM, Welker WI, Thompson RF. Unit activity in the auditory cortex. In: Rasmussen CL, Windle WF, eds. *Neural Mechanisms of the auditory and vestibular systems.* Springfield, IL Thomas: 1960.

Johnson JI, Jr, Welker WI, Pubols BH, Jr. Somatotopic organization of raccoon dorsal column nuclei. *J Comp Neurol* 1968;132:1–44.

Joseph JW, Shambes GM, Gibson JM, Welker W. Tactile projections to granule cells in the caudal vermis of the rat's cerebellum. *Brain Behav Evol* 1978;15:141–149.

Kassel J, Shambes GM, Welker W. Fractured cutaneous projections to the granule cell layer of the posterior cerebellar hemisphere of the domestic cat. *J Comp Neurol* 1984;225:458–468.

Krishnamurti A, Welker WI, Sanides F. Microelectrode mapping of modality specific somatic sensory cerebral neocortex in slow loris. *Brain Behav Evol* 1976;13:267–283.

Lende RA, Welker WI. An unusual sensory area in the cerebral cortex of the dolphin (*Tursiops truncatus*). *Brain Res* 1972;45:555–560.

Parker TD, Strachan DD, Welker WI. Tungsten ball microelectrode for extracellular single-unit recording. *Electroencephalogr Clin Neurophysiol* 1973;35(6): 647–651.

Pubols BH, Jr., Welker WI, Johnson JI, Jr. Somatic sensory representation of forelimb in dorsal foot fibers of raccoon, coatimundi and cat. *J Neurophysiol* 1965;28:312–341.

Reep RL, Johnson JI, Switzer RC, Welker WI. Manatee cerebral cortex: Cytoarchitecture of the frontal region in *Trichechus manatus latirostris*. *Brain Behav Evol*, 1990.

Sanderson KJ, Welker W, Shambes GM. Reevaluation of motor cortex and of sensorimotor overlap in cerebral cortex of albino rats. *Brain Res* 1984;292:251–260.

Shambes GM, Gibson JM, Welker W. Fractured somatotopy in granule cell tactile areas of rat cerebellar hemispheres revealed by micromapping. *Brain Behav Evol* 1978;15:94–140.

Shambes GM, Beermann DH, Welker W. Multiple tactile areas in cerebellar cortex: Another patchy cutaneous projection to granule cell columns in rats. *Brain Res* 1978;157:123–128.

Thompson RF, Welker WI. Role of auditory cortex in reflex head orientation by cat to auditory stimuli. *J Comp Physiol Psychol* 1964;57:996–1002.

Welker WI. Effects of age and experience on play and exploration of young chimpanzees. *J Comp Physiol Psychol* 1956a;49:223–226.

Welker WI. Some determinants of play and exploration in chimpanzees. *J Comp Physiol Psychol* 1956b;49:84–89.

Welker WI. Variability of play and exploratory behavior in chimpanzees. *J Comp Physiol Psychol* 1956c;49:181–184.

Welker WI. "Free" vs. "forced" exploration of a novel situation by rats. *Psychol Rep* 1957;3:95–108.
Welker WI. Persistence of sniffing after bilateral ablation of olfactory bulbs in rat. *Physiologist* 1958;1:84–85.
Welker WI. Escape, exploratory, and food-seeking responses by rats in a novel situation. *J Comp Physiol Psychol* 1959a;52:106–111.
Welker WI. Factors influencing aggregation of neonatal puppies. *J Comp Physiol Psychol* 1959b;52:376–380.
Welker WI. Genesis of exploratory and play behavior in infant raccoons. *Psychol Rep* 1959c;5:764.
Welker WI. An analysis of sniffing behavior of the albino rat. *Behaviour* 1964;22:223–224.
Welker WI. A method for preparing brain casts. *Anat Rec* 1967;158:239–244.
Welker WI. Principles of organization of the ventrobasal complex in mammals. *Brain Behav Evol* 1973;7:253–336.
Welker WI. Mapping the brain. *Brain Behav Evol* 1976;13:327–343.
Welker WI. Introduction to five neocortical mapping studies. *Brain Behav Evol* 1976b 3:241–242.
Welker W. Brain evolution in mammals: A review of concepts, problems, and methods. In Masterton RB, Bitterman ME, Campbell CBG, Hotton N, eds. *Evolution of brain and behavior in veretebrates*. New York: Erlbaum A Wiley, 1976;251–334.
Welker W. Spatial organization of somatosensory projections to granule cell cerebellar cortex: Functional and connectional implications of fractured somatotopy. In King JS, ed. *New concepts in cerebellar neurobiology*. New York: A R. Liss, 1987a;239–280.
Welker W. Comparative study of cerebellar somatosensory representations. The importance of micromapping and natural stimulation. In Glickstein M, Yeo C, Stein J, eds. *Cerebellum and behavioural plasticity*. New York: Plenum, 1987b.
Welker W. The significance of foliation and fissuration of cerebellar cortex. The cerebellar folium as a fundamental unit of sensorimotor integration. *Arch Italiennes Biol*, 1989.
Welker W. Why does cerebral cortex fissure and fold? A review of determinants of gyri and sulci. In Jones EG, Peters A, eds. *The cerebral cortex*, Vol. 8. New York:Plenum 1990.
Welker WI, Campos GB. Physiological significance of sulci in somatic sensory cerebral cortex in mammals of the family *Procyonidae*. *J Comp Neurol* 1963;130:19–36.
Welker WI, Carlson M. Somatic sensory cortex of hyrax (*Procavia*). *Brain Behav Evol* 1976;13:294–301.
Welker WI, Johnson JI, Jr. Correlation between nuclear morphology and somatotopic organization in ventrobasal complex of the raccoon's thalamus. *J Anat* 1965;99:761–790.
Welker WI, King WA. Effects of stimulus novelty on gnawing and eating by rats.
J Comp Physiol Psychol 1963;55:838–842.
Welker W, Lende RA. Thalamocortical relationships in echidna (*Tachyglossus aculeatus*). In Ebbesson SOE, and Vanegas H eds. *Comparative neurology of the telencephalon*. New York: Plenum Press, 1980.

Welker WI, Seidenstein S. Somatic sensory representation in the cerebral cortex of raccoon (*Procyon lotor*). *J Comp Neurol* 1959;111:469–501.
Welker W, Shambes GM. Tactile cutaneous representation in cerebellar granule cell layer of the opossum (*Didelphis virginiana*). *Brain Behav Evol* 1985;27:57–79.
Welker WI, Welker J. Reaction of fish (*Eucinostomus gula*) to environmental changes. *Ecology* 1958;39:283–288.
Welker WI, Benjamin RM, Miles RC, Woolsey CN. Motor effects of stimulation of cerebral cortex of squirrel monkey (*Saimirir sciureus*). *J Neurophysiol* 1957;20:347–364.
Welker WI, Johnson JI, Pubols BH, Jr. Some morphological and physiological characteristics of the somatic sensory system in raccoons. *Am Zool* 1964;4:75–64.
Welker WI, Hind JE, Campos GB, Gilmore MA. Chronic implantation of multiple macroelectrodes. A technique for mapping auditory neocortex in unanesthetized cats. *Electroencephalogr Clin Neurophysiol* 1965;19:309–312.
Welker WI, Adrian HO, Lifschitz W, Kaulen R, Caviedes E, Gutman W. Somatic sensory cortex of ama (*Lama glama*). *Brain Behav Evol* 1976;13:284–293.
Welker W, Sanderson KJ, Shambes GM. Patterns of afferent projections to transitional zones in the somatic sensorimotor cerebral cortex of albino rats. *Brain Res* 1983;292:261–267.
Welker W, Blair C, Shambes GM. Somatosensory projections to cerebellar granule cell layer of giant bushbaby (*Galalgo crassicaudatus*). *Brain Behav Evol* 1988;150–160.
Welt C, Welker WI. Posturoel and locomoton development of a gibbon (Hylobates lar). *Am J Physiol Authropul* 1963;21:425.
Zucker E, Welker WI. Coding of somatic sensory input by vibrissae neurons in the rat's trigeminal ganglion. *Brain Res* 1969;12:138–156.

Doctoral Theses of Trainees

Bower JM. Congruence of the spatial organization of tactile projections to the granule cell and Purkinje cell layers of the cerebellar hemispheres of the albino rat: The vertical organization of cerebellar cortex. Ph.D. thesis, University of Wisconsin, Madison, 1981.
Campbell SR. Somatotopic organization of the external cuneate nucleus of albino rats. Ph.D. dissertation University of Wisconsin, Madison, 1973.
Compton RW. Morphological, physiological and behavioral studies of the facial musculature of coati (*Nasua*). Ph.D. thesis, University of Wisconsin, Madison, 1967.
Hazelton DW. A quantitative investigation and a model of mechanoreceptors in the raccoon rhinarium. Ph.D. thesis, University of Wisconsin, Madison, 1970.
Pubols LM. Some behavioral, physiological and anatomical aspects of the somatic sensory nervous system of the spider monkey (*Ateles*). Ph.D. thesis, University of Wisconsin, Madison, 1966.
Sturlaughson WR. Some acoustic effects of central nervous system ablations in cats. M.S. thesis, University of Wisconsin, Madison, 1966.

Zucker EK. Coding of vibrissae stimulation in the trigeminal ganglion of the rat. Ph.D. dissertation, University of Oregon Medical School, Portland, 1968.

Supervised Publications of Trainees

Bower JM, Woolston DC. Congruence of the spatial organization of tactile projections to the granule cell and Purkinje cell layers of the cerebellar hemispheres of the albino rat: The vertical organization of cerebellar cortex. *J Neurophysiol* 1983;49:745–766.

Compton RW. Morphological, physiological and behavioral studies of the facial musculature of the coati (*Nasua*). *Brain Behav Evol* 1973;1:85–126.

Gibson JM. A quantitative comparison of stimulus-response relationships of vibrissa-activated neurons in subnuclei oralis and interpolaris of the rat's trigeminal sensory complex: receptive field properties and threshold distributions. *Somatosensory Res* 1987;5:135–155.

Kassel J. Superior colliculus projections to tactile areas of rat cerebellar hemispheres. *Brain Res* 1980;202:291–315.

Kassel J. Somatotopic organization of SI corticotectal projections in rats. *Brain Res* 1982a;231:247–255.

Krishnamurti A. Some aspects of neurological research in the understanding of the brain. *Singapore Med Jr* 1967;8:65–71.

Pubols LM. Somatic sensory representation in the thalamic ventrobasal complex of the spider monkey (*Ateles*). *Brain Behav Evol* 1968;1:305–323.

Sanides F, Krishnamurti A. Cytoarchitectonic subdivisions of sensorimotor and prefrontal regions and of bordering insular and limbic fields in slow loris (*Nycticebus coucang coucang*). *J Hirnforschung* 1967;9:225–252.

Woolston DC, La Londe JR. Corticofugal influences in the rat on responses of neurons in the trigeminal nucleus interpolaris to mechanical stimulation. *Neurosci Lett* 1983;36:43–48.

Woolston DC, Kassel J, Gibson JM. Trigeminocerebellar mossy fiber branching to granule cell layer patches in the rat cerebellum. *Brain Res* 1981;209:255–269.

Woolston DC, La Londe JR, Gibson JM. Comparison of response properties of cerebellar and thalamic projecting interpolaris neurons. *J Neurophysiol* 1982b;48:160–173.