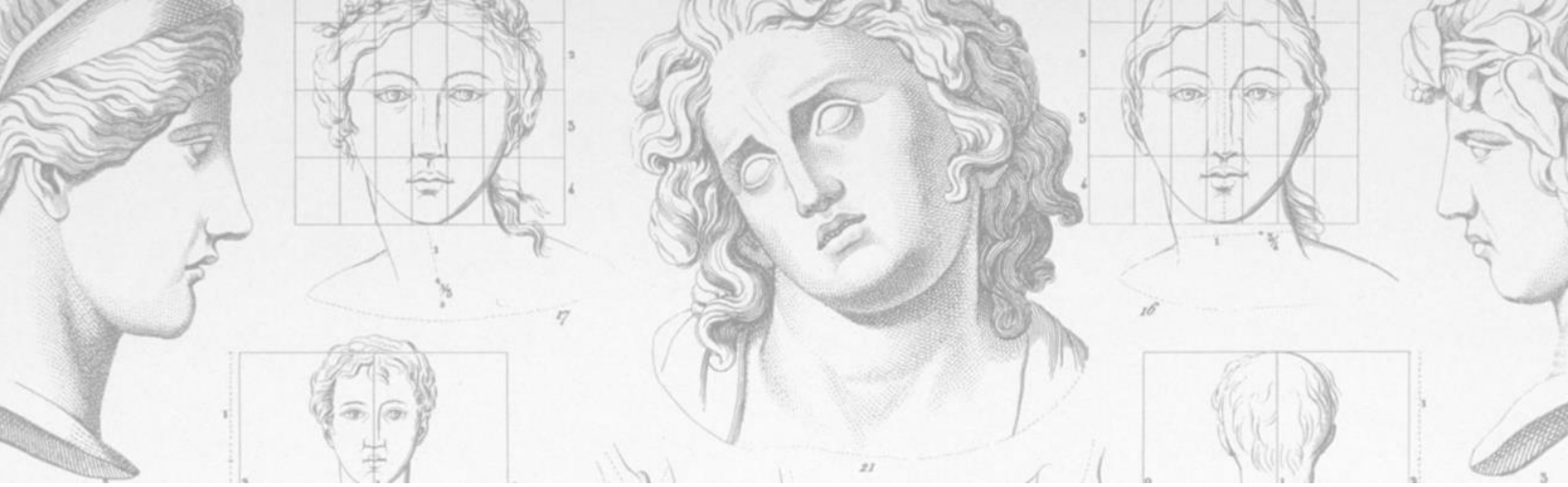

The History of Neuroscience in Autobiography
Volume 4

Edited by Larry R. Squire
Published by Society for Neuroscience
ISBN: 0-12-660246-8

Richard F. Thompson

pp. 520–550

https://doi.org/10.1016/S1874-6055(04)80026-4

Richard F. Thompson

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Portland, Oregon
September 6, 1930

EDUCATION:

Reed College, B.A. (Psychology, 1952)
University of Wisconsin, M.S. (Psychology, 1953)
University of Wisconsin, Ph.D. (Psychology, 1956)
University of Wisconsin, Postdoctoral Fellow
(Neurophysiology, 1956–1959)

APPOINTMENTS:

University of Oregon Medial School (1959)
University of California, Irvine (1967)
Harvard University (1973)
Stanford University (1980)
University of Southern California (1987)

HONORS AND AWARDS (SELECTED):

Councilor, Society for Neuroscience (1972–1976)
Society of Experimental Psychologists (1973)
Warren Medal, Society of Experimental Psychologists (1989)
President, Division 6, American Psychological Association (1972)
Distinguished Scientific Contribution Award,
American Psychological Association (1977)
National Academy of Sciences, USA (1977)
American Academy of Arts and Sciences (1989)
William James Fellow, American Psychological Society (1989)
President, American Psychological Society (1995–1996)
President, Western Psychological Association (1994–1995)
John P. McGovern Award (1999)
American Philosophical Society (1999)

Richard F. Thompson pioneered the use of simplified neural and behavioral systems in mammals to study basic processes of learning and memory. With William Alden Spencer, he showed that spinal flexion reflexes exhibited the properties of behavioral habituation and sensitization and analyzed putative mechanisms. Using classical conditioning of discrete responses (e.g., eyeblink) in mammals, he and his associates identified the cerebellum and its associated circuitry as the essential neural system for this form of learning; identified the CS, US, and CR pathways; localized the "basic" memory trace to the interpositus nucleus; and elucidated the role of the cerebellar cortex.

Richard F. Thompson

I was born September 6, 1930, in Portland, OR. My father, Frederick Albert Thompson, Jr., worked for the International Harvester Co., initially in Southern California. He was transferred to the Portland branch of the company in 1928 as office manager and later as branch manager. My mother, Margaret St. Claire Marr, and he were married in 1922 in San Francisco and lived initially in Southern California. Although they tried for years to have children, I was the only issue.

A few words about my family history. My father's father, Frederick Albert Thompson, was a career army man, a captain, and was for a time stationed in the Philippines, where my father spent part of his childhood. My grandfather apparently played a role in the development of Army Camp Kearney in Southern California. My father returned to the Oakland, CA, area for high school and then attended the University of California at Berkeley for one year; he then enlisted in the army at the U.S. entry into World War I. He was a lieutenant and sharp shooter instructor and did not serve overseas. After the war he farmed for a while, and then after marriage became an accountant, eventually with the Harvestor Co. (My mother, having grown up on a farm, gave him the choice of marrying her or farming.) My father was a very good and gentle man.

My mother had a remarkable career for a woman of that era. She was the youngest of nine children born and raised on a farm in New Brunswick, Canada. Her family name was Marr—the family came originally from Scotland before the revolution and settled in the colonies. Apparently, they were loyalists because they moved to New Brunswick before the revolution. An ancestor Marr fought on the British side in the revolution. It is likely that a Thompson of the time fought on the U.S. side.

My mother attended normal school to train as a teacher and taught school in New Brunswick. She saved enough money to train as a nurse at the Peter Bent Brigham Hospital in Boston, MA. When World War I began, she enlisted in the British army nurses corps, spent time in the front line hospitals in France, and was awarded a citation by King George V. She returned to Boston and when the United States entered the war, she joined the U.S. army nurses corps and went to France again. She kept a diary of her experiences in France, which I treasure.

The Early Years

In retrospect, growing up in Portland before World War II was about as idyllic as one could hope, although I of course did not realize it at the time. We lived in a modest house near Grant High School, which had a large public playground, swimming pools, and tennis courts. In my early years my mother and I would go there every day in the summer if the weather was nice. I learned to swim there at an early age.

There was a street car stop only a few blocks from our house, and my friends and I (grade school age) would take it downtown regularly on weekends and in the summer. Portland seemed a very safe place then. The stop where I got on and off was at Thompson Street. The conductor got to know us, and when we came to my stop he would call out "Thompson street for Dick Thompson!" Growing up, I had several very close friends in the neighborhood.

In grade school we were thoroughly drilled in the basics, although I somehow never mastered penmanship. One remarkable teacher stands out in my memory: Miss Crawford. She was an Irish lady who wore dark wool suits and button top shoes. She taught natural history and a good deal about life and morality. She kept us enthralled with her stories of how the British would mow down innocent Irish people. But more important, she taught us literature, an episode at a time. I think it took her at least a semester to read us the full novel *Les Miserables*.

I had learned to read before I entered first grade (no kindergarten in those days) and early on read voraciously everything from Peter Rabbit to Viking legends. Perhaps it was Miss Crawford who introduced me to good literature. Later and into the high school years, I would take the street car downtown to Portland's main library on 10th Avenue and check out a pile of books each week. I started at the A's in novels and read all the way to the Z's.

During the years from about 10 to 15, I developed interests in chemistry and electricity. Early on I had a chemistry set that I expanded. I began with color change assays, but found this rather dull and branched out. In those days in Portland kids could buy almost any chemical, including very dangerous ones. We discovered sodium. We could buy a pound of the metal for about a dollar. Sodium, of course, catches fire and explodes when it comes in contact with water, which led to all sorts of possibilities. Our greatest achievement was a sodium cannon—an iron pipe with an inside diameter a little larger than a marble and sealed at one end. We filled it half full of water and dropped in some sodium and a marble. We set it up in my backyard and aimed it at our garage wall. Our first trial was our last. There was an incredible explosion that blew the marble entirely through the garage wall. Several neighbors came running, thinking our furnace had exploded.

My fascination with electricity stemmed, in part, from a biography of Nikola Tesla. A friend and I constructed a Tesla coil to generate very high frequency, high voltage in my room. We made a spark gap out of two nails; our condenser was a milk bottle half full of salt water and wrapped in tinfoil; the power source was a 15,000-V transformer we obtained from a neon sign shop. I gave "shows" for my long-suffering parents and their friends. Holding a metal rod, I would draw a large continuous spark from the coil, and it would light up a light bulb I held in my other hand. (I also put on magic shows, but I fear my talents did not lie in that direction.)

When activated, our Tesla coil system broadcast a wide band electrical signal that caused very loud static in radios in a several mile radius. My friend had a Tesla setup as well, and we would send signals to each other via radios. Of course, everyone in that part of town also received our loud static signals on their radios. Given that this occurred in the war years, it is surprising no authorities ever investigated us.

I was also generally very interested in science and the "big" questions—the nature of the universe and the mind. It wasn't until I was in Grant High School that I realized education had anything at all to do with my interests. I took all the math and science courses, Latin, and extra literature. The most remarkable teacher I had was Miss Curie (no relation to the Nobel Laureate), who taught physics. She had worked as a graduate student with the physicist Robert Milliken and told us many stories. For extra credit, I made heavy water, only to have the janitor dump it down the drain.

Reed College, 1948–1952

I entered Reed College in 1948 with the intention of majoring in theoretical physics. Reed was (and is) remarkable—the course work was intense, and we read several full volumes a week in the humanities course. For the first time I really had to work at my studies. In my sophomore year in physics, I attempted to repeat Milliken's measurement of the charge on the electron and failed. More important, several of my classmates had an intuitive grasp of math and physics that I did not. I was good at math, enjoyed it and could work through the problems, but with no intuition. I began to have second thoughts about my major.

I became very interested in philosophy and read widely, particularly in epistemology. Writers such as Bertrand Russell, Ludwig Wittgenstein, and others convinced me, at least, that science, as imperfect as it is, was the only way to learn about "reality." At about that time I took Introductory Psychology from Monty Griffith, a Welshman who was an early admirer of John Watson and behaviorism. He was a realist, some would say cynic, and cut through much of the mystique in the field. He was also intellectually brilliant and entertaining. The other key faculty member in the Psychology

Department was Fred Courts, an excellent behavioral scientist who had done research on human factors. Thanks in part to Monty and Fred, I changed my major to psychology.

At Reed, all seniors had to complete a comprehensive thesis. I attempted to solve the continuity–non-continuity controversy—do we learn to see new perceptions by building on details (continuity) or do so *de novo* (non-continuity) as gestalts? Karl Lashley argued the latter. I built a Lashley jumping stand: rats had to jump from a platform against one of two cards. The correct card would fall back and the rat could enter and obtain food. The incorrect card would not move and the rat would fall onto a hammock. I had planned the experiment carefully, but had not counted on the rats. No self-respecting rat would jump against a wall; instead, if they jumped at all, most jumped all the way down to the floor. I did manage to get some data, but my results were inconclusive. However, I learned a good bit about rat psychology.

University of Wisconsin—Graduate and Postdoctoral Years, 1952–1959

In any event, I became greatly interested in brain bases of behavior, particularly learning and memory. I applied to several graduate schools and received good offers from W.J. Brogden at the University of Wisconsin in Madison and Kenneth Spence at the University of Iowa. Fred Courts advised me to go with Brogden, who had done classic work with Culler and Gantt on brain substrates of learning. However, when I arrived in Madison, I discovered that Brogden had changed his interests to human learning and performance. So I completed several studies of target pursuit learning and learning of "mental mazes" with fellow graduate students George Briggs and James Voss. Although at the time I was unhappy about this, in retrospect it was very good experience. Brogden was a very rigorous behavioral scientist with the highest standards. I learned scientific writing by his tearing apart my drafts over and over again.

The Psychology Department at the University of Wisconsin at that time was extraordinary. A number of leading behavioral scientists were at their most productive periods—Wulf Brogden, Jack Gilchrist, David Grant, Harry Harlow, Hershel Liebowitz, Fred Mote, Donald Meyer (a visiting Professor) and Will Thurlow. Clinton Woolsey's neurophysiology laboratory at the medical school (all on the same campus) was deeply involved in brain-behavior research and encouraged psychology graduate students to participate.

The Wisconsin psychology faculty had a strong empirical orientation; it was sometimes referred to by more theoretically oriented psychology departments as the "dust bowl of empiricism." (Harry Harlow had a chamber pot so labeled in his office.) But the Wisconsin faculty were broadly interested in the issues of psychology at that time. Looking back, we, the graduate

students, felt that the 1950s were the golden years of the Department. My fellow students of that era included Norman Anderson, William Battig, Lyle Bourne, George Briggs, Gilbert French, Isidore Gormezano, Leslie Hicks, William Prokasy, Allan Schrier, Joseph Sidowski, and James Voss. The graduate program then was Darwinian. I believe more than 30 began in my graduate class and 6 received their Ph.D.

As was true of many others, my interests in brain substrates of memory were greatly stimulated by Donald Hebb's remarkable book *The Organization of Behavior* (1949). Hebb tried to reconcile Lashley's "mass action" with neuronal connectivity. Hebb's book revitalized this field, which had been somewhat dormant since Lashley's 1929 monograph. When it came to details, Hebb was rather lacking, particularly about synaptic processes. But in all fairness, John Eccles discovered synaptic inhibition only about the same time as Hebb's book.

Because of my interests, Brogden agreed to set up an animal training laboratory and Woolsey graciously allowed us to do so in his facilities. I completed several studies of *sensory preconditioning* using shock avoidance with cats. Brogden had discovered this phenomenon much earlier working in Gantt's laboratory at Johns Hopkins. I also began a series of studies on stimulus generalization and lesion studies on the role of the auditory cortex in frequency discrimination (cats) (Thompson, 1960). I obtained a three-year NIH postdoctoral fellowship to work with Woolsey.

Woolsey's laboratory was a most exciting environment. Much of the work focused on the organization of the motor cortex in a series of primates, including chimpanzees, using electrical stimulation and on the organization of sensory cortical areas using surface-evoked potentials. P.W. Davies visited the lab and described the new extracellular microelectrode technique he and Jerzy Rose had developed at Johns Hopkins. During that time (Davies taught us a seminar), I read the Hodgkin–Huxley papers with great admiration. Jerzy Rose visited one summer, and using the Davies–Rose electrode, we completed the first single-unit recording study of the tonotopic organization of the primary auditory cortex (in cat) (see Hind et al., 1960).

During my time (and of course, earlier and later, as well) there were extraordinarily talented scientists in the laboratory. Konrad Akert provided solid expertise in neuroanatomy; Joseph Hind was expert in the auditory system and all matters acoustic; and W.I. Welker and Robert Benjamin were young scientists at the height of their productivity. There were many others as well. Woolsey was a very tolerant laboratory chief. If the work we did was to some degree relevant to cortical organization and functions and was carefully done, we were free to follow our own interests. Personally, Woolsey was a gentle man. I never saw him lose his temper. He was an ideal role model in that he was totally focused on the work (and his family), was objective, and never engaged in *ad hominem*. However, if you took a particular position on cortical organization, you had better be prepared to defend it. He had very

high standards and expected the same of everyone. Morale in Woolsey's laboratory was extremely high.

Woolsey was a superb but infrequent lecturer, often teaching by demonstration. At that time, textbooks stated that complete removal of the neocortex in monkeys caused virtual paralysis. In the medical student physiology course, Woolsey once demonstrated a fully decorticate rhesus monkey, which he held on a stick chain while the monkey chased him around the lectern trying to bite him. This finding was, of course, much more than simply a demonstration. Travis and Woolsey showed that after bilateral removal of all neocortex in stages, monkeys could show considerable recovery of motor function and became capable of locomotion if given adequate postoperative physical therapy. Recovery of function following brain injury was of deep interest to Woolsey. I assisted Woolsey in preparation of two of the decorticate macaques (we did them in two stages) and in their postoperative care. Woolsey had developed a method of subpial surgical aspiration of cortex that made it possible to remove localized regions without damage to adjacent regions or of an entire hemisphere of cortex with minimal bleeding. He was a superb experimental neurosurgeon; my skill in this area is due to his teaching.

In Woolsey's lab, Ron Sindberg and I began mapping auditory and association areas of the neocortex in cat using chloralose anesthetic, which provided very responsive cortical tissue. At that time, several scientists in France, particularly Pierre Buser and Madam Albe-Fessard, had reported separate sensory responsive areas in association areas of the cortex. In this initial work, Ron and I looked at association areas (see Thompson and Sindberg, 1960) and at auditory responses in a region of ventral auditory cortex that we discovered. We used the difficult technique that Woolsey and Walzl had developed of electrically stimulating different regions of auditory nerve fibers in the exposed cochlea to determine tonotopic organization. In addition, I studied neuroanatomy with Konrad Akert and collaborated with Joseph Hind, W.I. Welker, Robert Benjamin, William Cox, Jean Hirsch, and others on various research projects.

The University of Oregon Medical School, 1959–1967

In 1959 I accepted an appointment as an Assistant Professor at the University of Oregon Medical School, initially in the Psychiatry Department under George Saslow as Chairman and subsequently in the Department of Medical Psychology when it formed as a separate department under Joseph D. Matarazzo as Chairman. My responsibilities were to do research and to teach a little to medical and graduate students. I was indebted to John Brookhart, Chairman of the Physiology Department, for providing much encouragement and advice and also my first laboratory—a small room in

the basement that quickly became both overcrowded and immensely stimulating. Ron Sindberg spent a brief time in my laboratory in Portland, and we completed our study of the ventral auditory cortex (Sindberg and Thompson, 1962).

The move back to Portland was exactly what I had wished for. Indeed, I was thrilled when Woolsey told me of the job and offered to write a letter, as did Wulf Brogden, Harry Harlow, and others. So I returned home. My mother had died when I was in Wisconsin, and I moved into my father's house. We lived very happily—he was a great cook and I know he enjoyed having someone in the house—he had been alone since my mother died. I was single, had a great place to live, had a great job, owned an Austin-Healy sports car, and really felt on top of the world. But I stress that my world was mostly science.

There were other reasons why the move back to Portland was important to me. Growing up, my closest friend was Michael Baird. We went to grade school, high school, and college together. When I went to Wisconsin he entered the University of Oregon Medical School, and when I returned he was just completing a residency in internal medicine. His father, David Baird, was Dean of the Medical School, and I knew the family well. Michael and I had become good friends with William Alden Spencer at Reed College. Indeed, Michael later married Alden's sister Jane. Alden also went to the University of Oregon Medical School and did elegant research with John Brookhart. After a rotating internship, Alden joined the NIH for the research equivalent of a residency in Wade Marshall's laboratory, where he and Eric Kandel did their pioneering work on hippocampal physiology. Alden later return to the University of Oregon Medical School in the Physiology Department in 1961. Alden and I developed a joint research program which I will describe later.

While working with medical students and my superb technician, Hilton Smith, I made the first discovery that was entirely my own. In the course of carefully mapping the sensory responsive regions in associative areas (cat), à la Woolsey, I realized that the responses were not sensory specific, but rather polymodal. The French scientists had always described them as sensory specific, but they were not—the areas of activation were identical for all three modalities of stimulation (auditory, visual, tactile) and the responses showed the same refractory periods both within and across modalities. I was very excited by this discovery and submitted an abstract to the XXII International Congress of Physiological Sciences in Holland in 1962, my first solo presentation at an international meeting.

When I stood up to give my talk, Madam Albe-Fessard came to the front of the room, stood directly in front of me with her arms crossed, and glowered at me throughout my presentation. At the end she accused me in no uncertain terms of stealing her ideas. I was devasted; it was my first real encounter with the dark side of science. Vernon Mountcastle was in the

audience and has told this story more than once. The bottom line, however, is that I appeared to be correct (see Thompson et al., 1963a,b).

In the summer of 1959 I met my wife-to-be, Judith Pedersen, at the Psychiatry Department picnic at Merwin Dam in Washington. At that time, Judith and I were both very strong swimmers. Together, we swam way out to a log border in the lake and got to know each other. Judith was born and grew up in Denmark, and spent part of her life during the Nazi occupation. At 18 she came to the United States on a scholarship to the University of Oregon in Eugene. She was very good in science, particularly chemistry, biology, and math, and would have gone to medical school except at that time medical schools were only admitting one or two women a year. Consequently, Judith majored in pre-nursing and obtained her B.S. and R.N. in the joint program between the University and the Medical School in Portland. At the time I met Judith, she was on the staff in the Psychiatry Department. Because office space was tight, my office was actually, on the ward, so I got to know Judith and the other nurses and aides and many of the patients. It was my first real experience with psychosis—our ward was experimental and our typical patients were very bright, young adult schizophrenics.

Judith and I were married in May 1960 and moved into an apartment near the Medical School. At Christmas time we went to visit her family in Denmark and also traveled through France and Italy. We joined Alden Spencer and his wife Diane for a week in Pisa—Alden was doing a postdoctorate in Moruzzi's lab. During this week Alden and I developed our joint research plans—he had already accepted his appointment in the Physiology Department at the University of Oregon Medical School. We decided to focus on mechanisms of behavioral and synaptic plasticity in the spinal cord, where neurophysiological analysis was possible (see below).

Judith entered the graduate school of nursing in 1961 to obtain a Masters degree in psychiatric nursing, supported by a Public Health Fellowship. We discovered she was pregnant about Christmas time of 1961, and so that year we bought a house in Beaverton, a mixed blessing. It had an unheated swimming pool, usable about one month in Portland (although we did ice skate on it one winter), a septic tank that backed up, and a large overgrown backyard. Our first child, Kathryn, was born in August 1962, and I abandoned my family to attend the aforementioned International Congress in September. Judith and our newborn baby moved in with a nursing friend while I was gone. Then, in November, we lived through the "Columbus Day" storm. It blew down many of the trees at the end of our yard and took quite a few shingles from the roof. We were without power for about a week and sterilized the baby bottles on the barbeque.

Meanwhile, Judith had finished all her course work before Kathryn was born and was able to concentrate on her thesis. She received her Masters degree in the summer of 1963. She was appointed an Instructor at the University of Oregon School of Nursing. Our second daughter, Elizabeth,

was born in 1964. (Our third daughter, Virginia, was born in Newport Beach in 1968). Judith interrupted her own career to devote more time to the children. In later years, Judith joined me in the laboratory, and we have now worked together for many years. Judith became a superb neuroanatomist, completing a number of pathway tracing studies. She, along with a graduate student, Jo Anne Tracy, received the D.G. Marquis Behavioral Neuroscience Award in 1999 (American Psychological Association) for the most outstanding research paper of the year (Tracy et al., 1998).

When I joined the medical school in Portland, I obtained an NIH grant, which I held for many years. I have been most fortunate in having adequate grant support over the years from the NIH, NIMH, NSF, ONR, and other sources. Indeed, I have had continuous federal research grant support since 1959 and am currently supported through 2007. In 1962 I received a Career Development Award from NIMH which permitted me to devote even more time to research.

Our small Department of Medical Psychology at the medical school developed a Ph.D. program in "biopsychology." A critical factor was the hiring of Judson Brown, a distinguished behavioral scientist from the University of Iowa. Thanks to Jud, I gained a better appreciation of the importance of behavioral analysis at both empirical and theoretical levels. Jud came out of the Hull-Spence tradition and was a leading theorist in the field of motivation. He and I discussed and argued at length about the value of neuronal analysis of behavior and attempts to interrelate neural and behavioral phenomena. My paper on stimulus generalization (Thompson, 1965) illustrates this approach; indeed, it was much influenced by discussions with Jud. I felt this was my most important "theoretical" contribution to that time. Unfortunately, it was published as a chapter in a book. Judging from responses from colleagues, perhaps five people read it.

As a result of teaching courses in neurophysiology and behavior to our small but very capable group of graduate students in our Ph.D. program in Portland, I felt the need for a modern text in physiological psychology. My goal was to "explain" neurophysiology to psychology students and attempt, as far as possible, to analyze behavioral phenomena in neuronal terms. The result was my first (and best) text, *Foundations of Physiological Psychology*, written during the period 1964–1967 (Thompson, 1967). Our small graduate program, incidentally, produced a number of excellent scientists, e.g., Joel Davis, Mary Meikle, Timothy Teyler, and Richard Vardaris (Joel and Mary were my students).[1] David S. Phillips, my first postdoc, joined me

[1]I list in the footnotes the graduate students, postdocs, visiting professors, and others who worked in my laboratories at several institutions. If I have omitted anyone I apologize. Students in my laboratory at the University of Oregon Medical School (including MD-MS students) 1959–1967: Lew Bettinger, David Bliss, Joel Davis, Linda Fitzgerald, Richard Johnson, Robert Kramer, Mary Meikle, David Phillips, Robert Sack, Jon Shaw, Hilton Smith, and Ellen Zucker.

in 1962; Dave is now and for many years has been a full Professor at the medical school. The Department of Medical Psychology evolved into the current Department of Behavioral Neuroscience, a basic science department at the medical school. In October 2001, I had the great pleasure of being one of the speakers to dedicate this new version of our old department and graduate program in the medical school at the now Oregon Health Sciences University.

Alden Spencer and I began our collaboration in 1962. Alden had a basement lab adjoining mine. We had opted for the study of processes of behavioral plasticity in the acute spinal preparation. Thanks, in part, to the work of Eccles and his many associates, more was known at that time about the synaptic physiology of the spinal cord than other neural systems. Our goal was to develop spinal reflex models of behavioral processes of learning and memory so we could analyze synaptic mechanisms—in short, to develop simplified neuronal *models* of complex behavioral phenomena. I believe this was the first explicit attempt to develop the model system approach for analysis of the neuronal mechanisms of learning and memory. At least we thought so. In a broad context our approach was not, of course, entirely new; Pavlov had a somewhat analogous approach, using the conditioned reflex to study "psychic" processes.

We selected habituation of the hindlimb flexion reflex of the acute spinal cat as our model system. Flexion reflex habituation was a very robust and repeatable phenomenon. We first showed that habituation of this model system had all the properties of behavioral habituation in intact organisms (Thompson and Spencer, 1966). In the course of this work, we discovered that dishabituation was actually a superimposed process of sensitization, both in our preparation and in intact vertebrate behavior.

At the same time, we analyzed sites and mechanisms of plasticity underlying short-term habituation and sensitization (e.g., Spencer, Thompson, and Neilson, 1966). For habituation, we ruled out muscle fatigue, sensory adaptation, and changes in motor neurons and in primary afferent fibers. Our results were consistent with a process of synaptic depression in interneurons, although we could not prove it. Later, Kandel and associates demonstrated this to be the case in a monosynaptic system in *Aplysia*, and we did so in a monosynaptic pathway in the isolated frog spinal cord (e.g., Farel and Thompson, 1976). At the University of California, Irvine, Philip Groves, a graduate student, and I elaborated all these findings and results from our spinal interneuron recordings into the "dual-process" theory of habituation (Groves and Thompson, 1970). The Thompson and Spencer 1966 paper on the parametric properties of habituation (later a citation classic) and the dual-process theory had a significant impact on the field and indeed are still cited to this day.

In 1966 I took a six-month sabbatical in the neurophysiology laboratory of Anders Lundberg at the Salgrenska in Göteborg, Sweden. At that time,

Lundberg was perhaps the leading scientist in spinal neurophysiology. During the time I was there, I was fortunate to work on a project with Anders, Charles Phillips from England, and others on the patterns of monosynaptic Ia connections to hindlimb motor nuclei in the baboon (see Hongo et al., 1984; yes the data were collected in 1966, but not published until 1984). I learned a great deal more about intracellular recording in this project. Because baboons are, of course, very valuable and the experiments were acute, the work was intensive, with each preparation (and all the experimenters) going for 36 hr or more. Judith and our daughters spent much of this time with relatives in Denmark.

University of California, Irvine, 1967–1973

In 1967 I accepted a professorship in the Department of Psychobiology at the University of California, Irvine, at that time chaired by James L. McGaugh. When I moved to Irvine, I was awarded a Research Scientist Career Award from NIMH, which I held until I left Irvine in 1973. The period at Irvine was very productive, both in terms of research and scholarship and in terms of the growth and increasing importance of the Department of Psychobiology. I had an outstanding group of graduate students and postdoctoral fellows during this period.[2] Indeed, the graduate program we developed was one of the first and most successful programs in the broad field of behavioral neuroscience. While at Irvine I continued research on the neurobiology of habituation and on the organization and functions of cerebral cortex and developed a research program on neuronal mechanisms of associative learning, using the somewhat controversial spinal conditioning preparation (e.g., Pattersen, Cegavske, and Thompson, 1973). We actually began this work in Oregon (Fitzgerald and Thompson, 1967). We did indeed demonstrate an associatively induced increase in the amplitude of the flexor reflex (acute spinal cat); however, unlike associative learning in intact organisms, there was no change in response latency with learning. As with habituation, we were able to rule out changes in motor neurons and sensory afferent terminals, but could go no further.

During the time at Irvine, I collaborated and interacted with a number of colleagues: Carl Cotman, Gary Lynch, James McGaugh, Marcel Verzeano, Norman Weinberger, Richard Whalen, and others. I particularly valued, and still do, my discussions with McGaugh, Lynch, and Weinberger and my collaborations with Verzeano. Intellectually, it was an exciting time as we

[2]Graduate students and postdoctoral fellows at the University of California, Irvine, 1967–1973: Lew Bettinger and Joel Davis moved with us; Herman Birch, Craig Cegavske, Ray Demarco, Paul Farel, Michael Gabriel, Fay Glanzman, Dennis Glanzman, Philip Groves, Dexter Irvine, Kathleen Mayers, Michael Patterson, Richard Robertson, Richard Roemer, Edwin Rubel, Timothy Teyler, Knut Wester, and William Wheeler.

developed the graduate program and our own research programs. During the time at Irvine, I collaborated with Harry Harlow and James McGaugh in writing an introductory psychology text that emphasized the biological point of view (Harlow, McGaugh, and Thompson, 1971). I also began editing a series of volumes on methods in physiological psychology and, in collaboration with James Voss, edited a book on learning and performance dedicated to W.J. Brogden and written by Brogden's students (Thompson and Voss, 1972). We were able to present a typescript copy of the book to Wulf Brogden at a Psychonomic Society meeting in St. Louis before he died. Although in poor health, Wulf, in typical fashion, wrote a critique of each chapter for each author. But we could tell he was very pleased. I know how he must have felt. Just this past year many of my former students and colleagues wrote and published a book dedicated to me (Steinmetz, Gluck, and Solomon, 2001). My students also wrote articles for a full issue of the journal *Neurobiology of Learning and Memory* (2001, 76, pp. 225–461).

At Irvine and later at Harvard, I collaborated with Gardner Lindzey and Calvin Hall in writing yet another introductory text in psychology (Lindzey, Hall, and Thompson, 1975). I had gotten to know Gardner via committees; he was then at the University of Texas, and he played a key role in convincing me to accept the position at Harvard, where he had agreed to serve as Chair of the Department. Gardner was extremely knowledgeable and influential in psychology and very stimulating. Calvin Hall was also a most impressive intellect. I greatly enjoyed my interactions with these more senior individuals.

It was also during this period at Irvine that I became involved in editorial activities, beginning as Editor-in-chief of the journal *Physiological Psychology* published by the Psychonomic Society. In this context I got to know Cliff Morgan well; he was an extraordinary person. I became one of the Associate Editors of the *Annual Review of Neuroscience* in 1981; I enjoyed my interactions with Max Cowan and the other Associate Editors. In 1981 I agreed to become Editor of the *Journal of Comparative and Physiological Psychology (JCPP)* (1981–1982) published by the American Psychological Association, but with a condition. At that time there was serious strife between comparative and physiological psychologists; their methods, approaches, and interests had become quite divergent and the *JCPP* was suffering. The *JCPP* had a long history as *the* psychological journal in the field. My condition was to separate it into two journals, *The Journal of Comparative Psychology* and *Behavioral Neuroscience*. I was thus the "founding" Editor of *Behavioral Neuroscience* (1983–1990). Several senior people in the field were rather outraged by this change in title, but the separation worked. *Behavioral Neuroscience* is now the leading journal in the field.

During this period at Irvine, I was not satisfied with spinal conditioning as a model for analysis of mechanisms of associative learning and memory in intact mammals and cast about for other approaches. At that time, Michael

Patterson, a postdoc in the lab, argued persuasively for eyeblink conditioning (actually nictitating membrane conditioning) in rabbit, with the preparation developed by his Ph.D. mentor, Isidore (Dore) Gormezano. I was, of course, familiar with his work and a great admirer of it; Dore and I had been fellow graduate students at Wisconsin. Mike set up the instrumentation, and we trained a few rabbits. I was enormously impressed with the very robust and reliable learned behavior and the possibilities for neurobiological analysis.

Harvard University, 1973–1975

In 1973 I moved to the Department of Psychology and Social Relations at Harvard University, where I held the professorship previously held by Karl Lashley—a very special honor, since Lashley had been a particular hero from undergraduate days. Harvard provided me with superb laboratory facilities and support, and I found, as expected, that the intellectual atmosphere, students, and colleagues at Harvard were truly outstanding.

While at Harvard we discovered the massive engagement of hippocampal neurons in eyeblink conditioning (Berger, Alger, and Thompson, 1976). We characterized this result at length: the increase in neuronal activity had all the properties of a memory trace except that, as we knew from the earlier literature, the standard delay eyeblink conditioned response (CR) was neither prevented nor abolished by removal of the hippocampus. This seeming paradox bedeviled us for years (see Berger, Berry, and Thompson, 1986; Thompson et al., 1976). Theodore Berger was and is an extraordinarily talented scientist.

Actually, we set out to map the entire rabbit brain in 1-mm steps in well-trained animals using unit cluster recordings. Since the amplitude-time course of the behavioral eyeblink CR forms the envelope of the unit cluster response in the motor nuclei, and this motor CR response has to be driven from higher systems, we looked for similar patterns in unit cluster recordings throughout the brain. We did not, of course, look randomly, but brain structure/system by system. The hippocampus was the first structure we mapped. But in the end, we mapped all the major brain systems. Other than the hippocampus and, of course, brain stem motor nuclei, the cerebellum showed the most prominent neuronal model of the CR, both in areas of cerebellar cortex and in the nuclei (see, e.g., McCormick, Lavond, and Thompson, 1983). This mapping led us to the cerebellar memory system (see below).

Timothy Teyler played a key role in our research program at Harvard. Tim had been a postdoc in my lab at Irvine. He then took a further postdoc in Per Andersen's laboratory in Oslo, Norway, where he learned the hippocampal explant (slice) preparation and long-term potentiation (LTP). I was able to hire Tim as an Assistant Professor at Harvard. He set up a hippocampal slice lab in the floating room built initially for von Bekesy in my laboratories.

During that time, Gary Lynch visited our lab and learned the slice technology from Tim. I believe that Tim's lab at Harvard and Philip Schwartzkroin's lab at the University of Washington (he had also done a postdoc in Oslo) were the first two hippocampal slice labs devoted to physiology and synaptic plasticity in the United States. At Harvard I had outstanding facilities and a large number of spectacular undergraduates, outstanding graduate students, and postdocs, and we mounted a number of different research projects.[3] When I left Harvard I held a dinner party at the faculty club for my people; I believe there were about 50 in attendance.

Although my wife and I liked Harvard very much, and indeed, Judith began working with me in the lab there, neither we nor our daughters liked living in the Boston area at all so we returned to the University of California, Irvine and to Newport Beach in 1975. In 1977 I was elected to the National Academy of Sciences, the honor that pleased me the most in my career.

University of California, Irvine, 1975–1980

At Irvine we continued work on hippocampal substrates of eyeblink conditioning (Theodore Berger came with me to Irvine to complete his thesis and stayed on as a postdoc). Yet again, I had superb graduate students and postdocs in the lab.[4] Steve Berry discovered a key relationship between hippocampal EEG frequency and learning (eyeblink conditioning) (Berry and Thompson, 1978). Ron Kettner made what I have always thought to be a major discovery, namely, that at absolute acoustic detection threshold (rabbit eyeblink CR) neurons in auditory nuclei detected the signal equally on behavioral detection and non-detection trials (thus ruling out auditory nuclei as a site of memory trace formation), whereas hippocampal neurons (and cerebellar neurons) only responded on detection trials (Kettner and Thompson, 1982, 1985). Paul Solomon (a visiting professor) and Don Weisz (a postdoc) made a key discovery we had been waiting for: hippocampal lesions markedly impaired learning of the trace (but not delay) eyeblink CR (Solomon et al., 1986; although not published until 1986, the initial lesion

[3]I had undergraduates, graduate students, and postdocs at Harvard University, 1973–1975: Craig Cegavske, Fay and Dennis Glanzman, Richard Roemer, and William Wheeler moved with us; Timothy Teyler rejoined us as an Assistant Professor; Bradley Alger, Theodore Berger, Theresa Harrison, William Levy, Patricia Mensah, Jacqueline Metzler, Sheryl Spinweber, and Richard Young.

[4]I had graduate students and postdocs at the University of California, Irvine, 1975–1980: Theodore Berger, Fay and Dennis Glanzman, and Patricia Mensah moved with us; Steve Berry, Gregory Clark, Steve Coates, Fred Hoehler, Ronald Kettner, Brenda Lonsbury-Martin, Laura Mamounas, Glen Martin, Russell Richardson, Patricia Rinaldi, Robert Shannon, Paul Solomon, Donald Weisz, and Bo Yi Yang.

work was done at Irvine). The role of the hippocampus in trace conditioning in animals and humans has developed into a field, thanks in part to a subsequent study by Jeansok Kim and Robert Clark in my lab at the University of Southern California (USC) (Kim, Clark, and Thompson, 1995) and to work by John Disterhoft, Larry Squire, Robert Clark, and others. It may provide a simple approach to the study of awareness.

In 1978–1979 we spent a year at the Center for Advanced Study in the Behavioral Sciences at Stanford. Gardner Lindzey was now Director of the Center and encouraged me to come. We developed a special interest group in learning and memory. During this year at the center, Leslie Hicks and I, with the long-distance help of V.B. Shvyrkov, wrote up the proceedings of a joint Soviet–U.S. symposium on brain substrates of learning and memory I had hosted at the University of California Irvine in 1978 (see Thompson, Hicks, and Shvyrkov, 1980). This symposium was preceded by a rather difficult visit to Moscow Judith and I made as a part of a delegation from the U.S. National Academy of Sciences to the Soviet Academy of Sciences to arrange a series of such joint symposia. Arranging the meeting at Irvine was extremely difficult. We (U.S. side) had insisted that Evgeny Sokolov, their most distinguished scientist in this field, be included, but in the end the Soviet authorities refused. (Evgeny tells me that now he is free to travel as he pleases, but no longer has adequate funds from the Russian government to do so.) Over the years, I made several trips to the Soviet Union and more recently to Russia. Although events during visits in the Soviet days could be complex, even mysterious, I have always enjoyed my Russian colleagues and my visits there.

Stanford University, 1980–1987

Judith and I and our daughters very much liked living at Stanford and, of course, Stanford University. I accepted a position at Stanford University in 1980 as Bing Professor of Human Biology with a primary appointment in the Psychology Department. I had developed some interest in administration and chaired the Human Biology program (a popular undergraduate major) for five years. Although the program was successful during my reign—the number of majors virtually doubled and many of the students were great—I felt it took far too much time away from my research. Of course, the Psychology Department at Stanford was and is outstanding, and I greatly enjoyed my colleagues there and in the university-wide neuroscience Ph.D. program. (I served as acting Chair for a semester.)

It was at Stanford that we discovered the essential involvement of the cerebellum in standard delay eyeblink conditioning (McCormick et al., 1981). I will never forget the day Dave McCormick showed me the polygraph record from the first successful cerebellar lesion. The conditioned eyeblink response was completely gone, even on CS (tone) alone test trials and the

reflex eyeblink response to the corneal airpuff US was unchanged. We had hints from recording studies by McCormick (see above) and by Kettner and lesion work by David Lavond that the cerebellum was involved in eyeblink conditioning, but the cerebellar lesion data were decisive. Key players in our cerebellar work at Stanford also included Paul Chapman, Gregory Clark, Nelson Donegan, Michael Foy, Mark Gluck, Barbara Knowlton, Christine Logan, Michael Mauk, Laura Mamounas, Ronald Skelton, Joseph Steinmetz, and Diana Woodruff-Pak.

I make special mention of several of my associates in the cerebellar work at Stanford. Mark Gluck introduced me to computational modeling and developed several useful connectionist level computational models of the cerebellar learning circuitry, models that made specific, verifiable (and verified!) predictions about the circuit (Gluck, Reifsnider, and Thompson, 1990; Gluck et al., 2001). David Lavond showed that kainic acid lesions in the correct place in the interpositus nucleus not much larger than 1 mm^3 abolished the eyeblink CR, thus ruling out fibers of passage and demonstrating extreme localization (Lavond, Hembree, and Thompson, 1985). Michael Mauk showed that high decerebrate animals could retain the CR and provided key evidence re the US pathway (Mauk, Steinmetz, and Thompson, 1986). David McCormick was the key player in the initial recording and lesion studies identifying the essential cerebellar circuit (McCormick and Thompson, 1984). Joe Steinmetz, more than anyone else, was the key player to identify the CS pathway and, with David McCormick and Michael Mauk, the US pathway and showed that electrical stimulation of mossy fibers as a CS and climbing fibers as a US resulted in normal behavioral learning (Steinmetz, Lavond, and Thompson, 1989). Diana Woodruff-Pak argued persuasively and demonstrated empirically that eyeblink conditioning in rabbits and humans provided an extremely useful model for studying the neurobiological effects of aging on learning and memory (Woodruff-Pak and Thompson, 1988). Laura Mamounas demonstrated the key role of GABA in cerebellar memory processes (Mamounas et al., 1987). Most of these scientists continue to work on the neuronal substrates of basic associative learning and memory in their current research programs.

Our cerebellar discoveries were not met with unanimous acclaim. Indeed, several cerebellar physiologists, among others, not only did not believe our findings, but attacked us in every conceivable way, both legitimate and otherwise—another lesson in the dark side of science. However, we or at least data from our lab and subsequently from other labs as well (e.g., Yeo et al., 1985) prevailed. A fact that often gets lost because of the emphasis on eyeblink conditioning is that our cerebellar findings apply to classical conditioning of *all* discrete responses learned with aversive events, e.g., limb flexion, head turn, etc. The studies by Theodore Voneida at the Northeastern Ohio Medical School on cerebellar substrates of forelimb flexion conditioning

in the cat are an elegant example (e.g., Voneida, 1999, 2000; Voneida et al., 1990).

Yet again, I was able to assemble an outstanding group of undergraduates, graduate students, postdocs, and visiting professors at Stanford.[5] During the eight years we were at Stanford, we identified the entire essential circuitry for delay eyeblink conditioning, ran a number of control studies ruling out various alternative hypothesis, and completed some computational models of the cerebellar circuitry. Much of the work during this period is summarized in Gluck, Reifsnider, and Thompson, 1990; Steinmetz and Thompson, 1991; Thompson, 1986, 1990; and Woodruff-Pak and Thompson, 1988.

There was considerable interest some years ago in electrical stimulation of cerebral cortex as a CS. Robert Doty reported several such studies using limb flexion conditioning. At the time, it was thought that the memory trace was formed in the cerebral cortex, but definitive evidence was lacking. For her thesis at Stanford, Barbara Knowlton used electrical stimulation of the auditory cortex of the rabbit as a CS in eyeblink conditioning. She was able to show that, as with peripheral stimuli, the critical structure was the cerebellum, and, with Judith, she identified the CS pathway: from auditory cortex to a region of the pontine nuclei and to the cerebellum as mossy fibers (Knowlton and Thompson, 1992; Knowlton, Thompson, and Thompson, 1993). It was very satisfying to bring this earlier unresolved literature to closure.

The issue of the role of the cerebellar cortex in eyeblink conditioning was tackled in detail by Christine Logan for her thesis at Stanford University using rabbit eyeblink. She obtained the first really decisive data showing that very large cortical lesions including the anterior lobe result in a dramatic decrease in CR latency in addition to impairing learning (Logan, 1991). We had earlier seen a suggestion of this, but not so clearly (McCormick and Thompson, 1984). These general results—impairment in acquisition and amplitude of CR and a decreased latency with very large cerebellar cortical lesions—have been replicated in many other studies. On the other hand, the only lesion that consistently and completely abolishes the behavioral CR is a lesion of the interpositus nucleus.

While at Stanford I developed a collaborative research program with my colleague in the Psychiatry Department, Seymore (Gig) Levine. Gig was (and is) a world authority in the field of stress. Michael Foy had joined my lab as a postdoc after receiving his Ph.D. with Tim Teyler at Northeastern Ohio

[5]I had an outstanding group of undergraduates, graduate students, postdocs, and visiting professors at Stanford University, 1980–1987: Gregory Clark, Ronald Kettner, Laura Mamounas, Russell Richardson, and Bo Yi Yang moved with us; Paul Chapman, Nelson Donegan, Michael Foy, Mark Gluck, Deborah Haley, Lee Holt, Barbara Knowlton, David Lavond, Christine Logan, John Madden, Michael Mauk, David McCormick, Merle Prim, Ronald Skelton, Mark Stanton, Joseph Steinmetz, and Diana Woodruff-Pak.

Medical School, where he mastered the hippocampal slice and LTP. Mike had the idea that behavioral stress might be important in LTP, perhaps accounting for the variable results across laboratories in the degree of LTP reported at that time. Together with another postdoc, Mark Stanton, we completed a study where we first acutely stressed rats (immobilization and tail shock) and then prepared hippocampal slices and induced LTP (Foy et al., 1987). The results were striking; prior behavioral stress completely prevented the subsequent induction of LTP in the slice (CA1).

When I moved to USC (see below), Mike Foy accepted a position in the Psychology Department at Loyola-Marymount University in Los Angeles, where he is now a full Professor. He continues to work with us on hippocampal plasticity. By the time I moved to USC, we were joined by a superb postdoc, Tracey Shors, who also worked on the project.

University of Southern California, 1987–present

In 1987 I was given an offer I "could not refuse" from USC. They were in the process of developing a neuroscience program and had raised the money to build a research building. In addition to the usual setup funds, my offer included a substantial permanent research fund, a position for Judith, and other forms of support. I was appointed Keck Professor of Psychology and Biological Science, with a light teaching load. We had rented out our house in Newport Beach when we moved to Stanford, so we moved back yet again to Newport Beach. This time, however, there was a formidable commute.

Development of the Neuroscience Program at USC was due to the vision of a remarkable man, William Wagner, then Dean of Natural Sciences and a physicist by training. He labeled the program NIBS—Neural, Informational and Behavioral Sciences—with a strong focus on cognitive and computational aspects of neuroscience. I agreed to become Director of the program in 1989 and set about hiring. I had a budget of over one million dollars that was designed to self-destruct. Each time we hired someone for the NIBS program, that person had to have a primary appointment in a department and the first year of his/her salary came as a permanent reduction in the NIBS budget, thereafter to be picked up by the University. So NIBS and the home departments had to agree on the appointments. It was also the case that setup funds for each new appointee would come from my budget and then be replaced in my budget the following year.

In the first several years, I hired or facilitated hiring of an outstanding group of scientists: Michel Baudry, Theodore Berger, Irving Biederman, Roberta Brinton, Mary Ellen MacDonald, Mark Seidenberg, Larry Swanson, and Alan Watts. Together with Michael Arbib and Christoff von der Malsburg, already in the program, we were well on our way to becoming an outstanding neuroscience program with foci on synaptic plasticity and learning and memory and with a strong emphasis on cognitive and computation approaches.

Although it took some time and effort, I was finally able to establish a university-wide Ph.D. program in neuroscience in 1996. This has proved to be the glue that holds the neuroscience program together, at least until now. From the beginning there was a fundamental structural problem in the NIBS/neuroscience program. The initial budget for the program, including the Hedco Neuroscience research building (due in large part to a gift from the Hedco Foundation), came entirely from the School of Letters, Arts and Sciences (LAS), but the program was university-wide. The revenue sharing system at USC pits school against school, so problems were inevitable.

The NIBS program was strongly supported in the early days by then Dean of LAS, William Spitzer. However, he retired and support for the NIBS program declined rapidly under a succession of LAS deans who cut the budget, changed the rules on setup funds, and were generally not supportive. I was not able to make any more hires in the program, and we basically stalled. It was most unfortunate.

In 1999 our neuroscience program received an external review by an outstanding group (Leon Cooper, Fred Gage, and Larry Squire). Their report was very supportive of our program and its goals and very critical of the University for its lack of support. There was no response from LAS. Eventually, however, the Provost (with university-wide authority) intervened and provided much needed support in terms of graduate student stipends and operational costs. I stepped down as Director in 2001 to be replaced by Larry Swanson.

Although I enjoyed many aspects of administering the neuroscience program, it did interfere substantially with my research program. But, yet again, I was able to assemble an outstanding group in my laboratory.[6] In 1991 I was appointed a "corresponding" member of the Center for the Neurobiology of Learning and Memory at the University of California, Irvine. I have greatly enjoyed my continuing interactions with my many friends and colleagues at Irvine.

I will note here just a few high points of our research at USC. First, I must acknowledge my debt to two colleagues at USC: Michel Baudry and Caleb (Tuck) Finch. Michel is a superb neurochemist/physiologist and a long-time

[6]I had an outstanding group in my laboratory at the University of Southern California, 1987–present: Paul Chapman, Barbara Knowlton, David Lavond, and Christine Logan moved with us (we continued long-distance collaborations with several colleagues: e.g., Mark Gluck, Joseph Steinmetz, and Diana Woodruff-Pak); Gabor Bartha, Shaowen Bao, Gil Case, Chong Chen, Lu Chen, Kimberly Christian, Robert Clark, Michael Foy, Rene Garcia, David Gellerman, Hiroshi Gomi, Jeffrey Grethe, Stephanie Hauge, Richard Hinchliffe, Dragana Ivkovich, Tsugio Kaneko, Jeansok Kim, Jon Lockard, Yi Chun (Ingrid) Liu, Steve Maren, Matti Mintz, Shahriar Mojtahedian, Nancy Nichols, Alan Nordholm, Gorica Petrovich, Andrew Poulos, Xiaoxi Qiao, Oscar Ramirez, Karla Robleto, Andrea Scicli, Paul Shinkman, Tracey Shors, Steve Standley, William Sun, Rodney Swain, Georges Tocco, Jo Anne Tracy, Benjamin Tran, Noriaki Uenishi, Rosemarie Vouimba, Craig Weiss, Martha Weninger (ne Berg), and Kenji Yoshimi.

friend and collaborator who has done his best to educate me in molecular matters. Tuck is a leading scientist in the neurobiology of aging and a greatly valued friend and collaborator. At USC we continued to characterize the essential circuitry for delay classical conditioning of eyeblink and other discrete responses. I had decided at Stanford that a way to approach the issue of localizing the memory trace in the circuit was by reversible inactivation. A visiting professor in my lab at Stanford tried to develop a reversible cooling system, but without success. David Lavond became interested in this approach; he had moved with us to USC, where he was a Research Assistant Professor in my laboratory. (He is now a full Professor in the Psychology Department.) He successfully developed a cryoprobe using freon, based on a system initially developed at the University of California at Los Angeles (UCLA).

Meanwhile, a superb graduate student in my laboratory, David Krupa, developed a complementary approach by infusion of muscimol, a competitive $GABA_A$ agonist, an approach initially suggested to me at Stanford by Eric Knudsen. Muscimol hyperpolarizes and thus inactivates all neurons with $GABA_A$ receptors for a period of several hours, followed by complete recovery. Alan Nordholm, another excellent graduate student, utilized lidocaine for reversible inactivation (Nordholm et al., 1993). Judith worked with Krupa and with Nordholm on these projects. Using all these methods, we were able to localize the memory trace to the cerebellum.

More specifically, inactivation of the motor nuclei or the red nucleus during training did not prevent learning at all, even though performance of the response (CR for red nucleus CR and UR for motor nuclei) was completely prevented. Similarly, inactivation of the superior cerebellar peduncle, all the output from the interpositus (now using tetrodotoxin), does not prevent learning at all, even though performance of the CR is prevented during training. In marked contrast, muscimol inactivation limited to the interpositus nucleus completely prevented learning. Subsequent postinactivation learning occurred with no savings at all compared to an appropriate control group, even though all projections to the cerebellar cortex were completely functional (except, of course, for projections from the interpositus) (Krupa and Thompson, 1995, 1997; Krupa, Thompson, and Thompson, 1993; Krupa, Weng, and Thompson, 1996).

Paul Shinkman, a Professor in the Psychology Department at the University of North Carolina and an old friend, joined me for a number of summers and a sabbatical year to work on a most interesting project following up on a study my Wisconsin Professor, Wulf Brogden, published with W. Horsley Gantt in 1945. In brief, they reported that movements elicited by electrical stimulation of cerebellar white matter (e.g., limb flexion, eyeblink, etc.) could be conditioned to a neutral tone or light CS (dogs). With Rodney Swain, a graduate student, we replicated and extended these observations in rabbit (Swain et al., 1992). The responses elicited by cerebellar stimulation

relayed through the interpositus nucleus rather than by antidromic activation via the inferior olive or pontine nuclei and the effective stimulus appeared due to activation of climbing fibers. Indeed, we were able to condition the movements elicited by stimulating white matter (US) directly under an oval surface electrode stimulating parallel fibers as a CS, thus creating what we hope is an extremely localized memory trace (see Shinkman, Swain, and Thompson, 1996; Swain et al., 1992; Thompson et al., 2000).

An extraordinary group in my lab, Jeansok Kim (postdoc), Lu Chen, and Shaowen Bao (graduate students), established procedures for eyeblink conditioning in the freely moving mouse. We based this on earlier work by two former postdocs in the lab, Ron Skelton and Mark Stanton, who had initially developed procedures for eyeblink conditioning in the rat, infant rat, and mouse. Because of the large number of mutant and transgenic mouse strains available, a number of issues concerning possible mechanisms of learning and memory can be analyzed. In particular, the issue of cerebellar cortex versus interpositus nucleus (as the site of memory storage) could be addressed by use of the Purkinje cell degeneration (pcd) mouse. This mutant, with no functional cerebellar cortex at all, learns eyeblink conditioning, albeit more slowly, to a lesser degree and with shorter CR latencies (Chen et al., 1996), just as with large cerebellar cortical lesions or inactivation. But lesion of the interpositus nucleus in the pcd mouse completely prevents learning.

Lu and Shaowen, together with Xiaoxi Qiao and others, completed an important series of studies on the Stargazer mouse (e.g., Chen et al., 1999). This mouse, incidentally, was discovered by Xiaoxi Qiao and Ray Nobilis at the Jackson lab. It lacks BDNF in cerebellar cortical granule cells; these cells have no functional AMPA receptors and eyeblink conditioning is much impaired. We collaborated with Susumu Tonegawa, Shigeyoshi Itohara, Hiroshi Gomi, and others in studies of transgenic mice (see Kim et al., 1996).

In our cerebellar projects in the rabbit, Jeansok Kim and David Krupa were able to show that the behavioral phenomenon of "blocking" in eyeblink conditioning was mediated by the GABAergic projection from the interpositus to the inferior olive (Kim, Krupa, and Thompson, 1998). Jeansok was also much interested in hippocampal functions in eyeblink conditioning. As a graduate student with Michael Fanselow at UCLA, they showed that lesions of the hippocampus in fear conditioning (rats) abolished freezing to context, but only if made soon after training. In my lab, Jeansok, together with Robert Clark, obtained similar results for trace eyeblink conditioning in rabbits: large bilateral lesions of hippocampus immediately after training abolished trace (but not delay) conditioning. The same lesions made a month after training had no effect (Kim, Clark, and Thompson, 1995). Shaowen Bao, Lu Chen, and Jeansok Kim completed an extraordinary study using both mouse interpositus slice and intact trained rabbit and provided very

strong evidence that in standard eyeblink conditioning the basic memory trace is established in the interpositus nucleus (Bao et al., 2002). Currently, I have an outstanding group of graduate students focusing on cerebellar substrates of conditioning: Kimberly Christian, Ka Hung Lee, Shahriar Mojtahedian, Andrew Poulos, and Karla Robleto.

In our ongoing project on stress and hippocampal LTP, Tracey Shors completed a lovely study showing that stress impairment of LTP is truly "psychological." Animals were given shock escape training—they learned rapidly—and yoked animals were given identical shocks, but could do nothing about it. The escape animals showed little subsequent impairment of LTP (hippocampal slice), but the yoked animals, who could not control the situation, showed marked impairment of LTP (Shors et al., 1989). More recently, Jeansok Kim and Mike Foy showed that behavioral stress enhanced subsequent LTD (hippocampal slice) and that both stress impairment of LTP and enhancement of LTD required NMDA receptor activation (Kim et al., 1996). In current work with Mike Foy and in collaboration with our colleague Michel Baudry, we discovered that acute application of physiological levels of estrogen to the bath enhanced LTP, prevented stress impairment of LTP, and prevented stress enhancement of LTD (Bi et al., 2001; Foy et al., 1999, 2000; Vouimba et al., 2000).

Conditioned fear has always been of interest to me. We collaborated with our superb colleague in the School of Pharmacy at USC, Jean Shih, in showing that MAOA KO mice exhibited markedly enhanced conditioned fear, but no change in eyeblink conditioning (Kim et al., 1997). With our colleagues, Larry Swanson, Gorica Petrovich, and Andrea Scicli, we characterized enkephalin mRNA levels in the amygdala (Petrovich et al., 2000). In current work, Ingrid Liu is exploring the role of BDNF in conditioned fear.

In this essay I have focused on the "voyages of discovery" I have been so fortunate to make with my many students and associates. There is no intellectual thrill greater than discovering something entirely new that has never been known before. However, in the long run, I feel the most important thing to me is family—my wife, children, and now grandchildren (we have seven). In looking back, I so wish I had spent more time with my daughters as they were growing up. For many years I was too much involved in professional activities—committees of the National Science Foundation, the National Institute of Mental Health, the American Psychological Association, the National Academy of Sciences, the National Research Council, the Society for Neuroscience, and others. Such activities may be useful, but in my case they took far too much time away from my family.

I have been very gratified by the many honors and awards I have received. But in the end, I and most other scientists will be forgotten. The discoveries we have made will be listed in the textbooks as facts not associated with names, and this is as it should be. Unlike other approaches to knowledge, scientific knowledge is cumulative

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