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The History of Neuroscience in Autobiography

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Arnold B. Scheibel . Gerald Westheimer

Volume 5

Edited by Larry R. Squire



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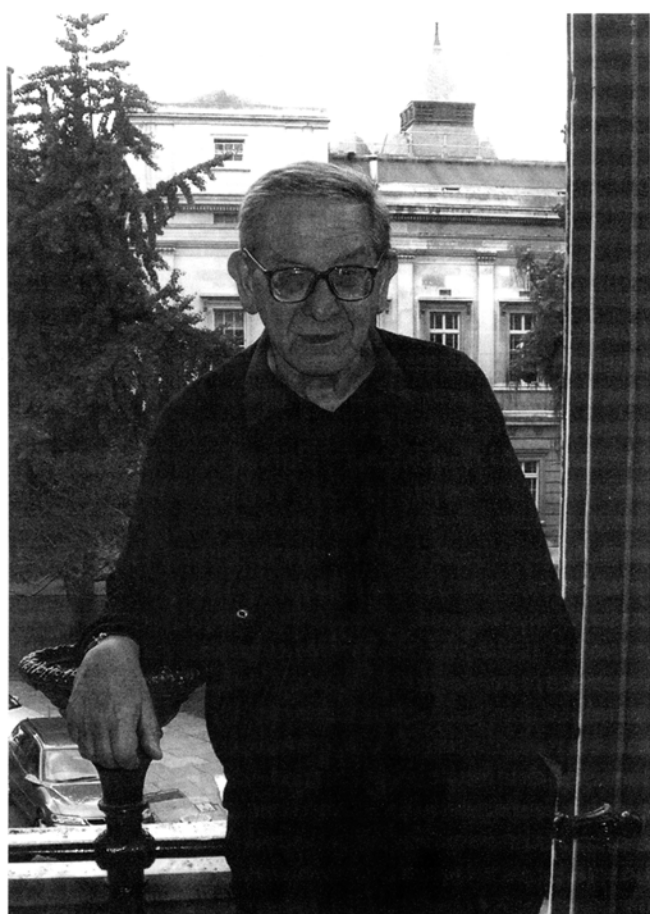
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Mitchell Glickstein

BORN:

Boston, Massachusetts
July 13, 1931

EDUCATION:

Bucknell University (1948–1949)
University of Chicago, B.A. (1951)
University of Chicago, Ph.D. (1958)

APPOINTMENTS:

Research Fellow, California Institute of Technology (1958)
Research Fellow, Stanford (1960)
University of Washington (1961)
Brown University (1967)
MRC, London, England (1980)
University College London (1987)

Mitch Glickstein began his studies with Garth Thomas and Roger Sperry.

Using mainly neuroanatomical methods, as well as physiology and behavior, he studied the organization of the cortical visual pathways in mammals and found that the lateral geniculate nucleus projects widely beyond what had been thought to be its sole cortical target. Subsequently, he identified projections from visual cortical areas to the pontine nuclei and from visually driven pontine cells to the cerebellum. His work has illuminated the role of the cerebellum in the sensory guidance of movement.

Mitchell Glickstein

Although I began writing this preface on the day after my 73rd birthday, I feel that I must be no more than 30 years old. Well, maybe 40. I have been around for a long time, been to a lot of places, and met many people. I hope that my chapter might be of as much interest to those that read it, as it was to me to write it.

In addition to the usual stuff of autobiography “I was born...,” I want to talk about the schools and universities that I attended and the places that I worked. I want to describe the people—teachers, bosses, colleagues, and students—whom I have been privileged to know. Some were inspirational teachers and remarkable bosses. I hope that I can convey some of my gratitude for the gifts that they gave me.

Universities are, I think, the finest institution that people have conceived and built. What a magnificent idea! A place for scholars to study and teach and for students to learn. I feel lucky to have been attached to one or another university or research institute in four countries for most of my life. I know something of how subjects are taught, academic appointments are made, and students are examined in those places. Although the idea of a university is a magnificent one, all real universities have flaws and limitations. I am sometimes surprised at how little some of my colleagues know about higher education in systems other than their own. My personal history might help others to know a bit more about institutions other than those they grew up with.

I love universities, even though I was often a mediocre student in high school and early years in college, scraping by and sometimes in danger of dropping off the educational ladder. In this brief autobiography, I propose to describe my early education, the teachers, colleagues, and students I have known, and the research I have done. I focus principally on my earlier years, although I still maintain as active an interest in neuroscience and its history as I did when I began.

Early Life

I was born on July 13, 1931 in Roxbury, a lower middle class district in the south of Boston. My neighborhood at the time was almost entirely Jewish. In Boston at the time the ethnic borders were clearly drawn, although they shifted from decade to decade. Roxbury had once been an upper middle

class suburb; first of Yankees and then Irish immigrant families on the way up. John F. Kennedy's grandfather, "Honey Fitz" Fitzgerald had once lived in the house next door to the one that I grew up in on Warren Street. That house had since been divided into six flats, my own house into three, with another little apartment tacked on at the back. Roxbury, Dorchester, and Mattapan are three contiguous regions of greater Boston. Jews occupied much of Roxbury. Black people lived to the north and west of my neighborhood. Malcolm X, in his autobiography, described that area of Roxbury as sugar hill, where successful black people lived. Further east, in South Boston, the Irish lived, and remotely, in the North End and in East Boston, the Italians. The Jewish neighborhood stretched from Roxbury, southward through Dorchester, to Mattapan. There was little mixing with the other ethnics, except, of course, for the fights at the borders. Blue Hill Avenue, the artery that ran through all three of the contiguous Jewish districts could have passed for a pre-war Polish ghetto; small kosher butcher shops, a synagogue, and a pushcart whose proprietor sold needles, thread, and shoelaces and called continuously "anything at all, I've got any kind you want."

My father was the cantor at the large synagogue Mishkan Tefilla (house of prayer). He was a wonderful tenor, recruited by the reasonably well-to-do congregation from his post at the principal Conservative Jewish Synagogue in Budapest where he had grown up. My mother was born in Newark, New Jersey. She had many brothers, whom we visited often. Downstairs in our house lived my father's sister, Aunt Esther, her husband, Uncle Philip, and their two boys Eddie, whom everybody called Sonny, and his brother David. My father's mother, a matriarch, lived downstairs with Aunt Esther, where she continued to dominate the family until she died when I was in the second grade. I had two older sisters: Helaine (whom everybody called Honey), 5 years older than me, and Judy, 4 years older. The only boy, I was loved by my mother and indulged by my sisters.

Early Schooling

From kindergarten to the sixth grade, I was a pupil at the Garrison School. William Lloyd Garrison was a 19th century abolitionist, an early campaigner against slavery. As a byproduct of the almost complete segregation of Boston neighborhoods, the school's pupils were 99% Jewish. There might, on occasion, be one non-Jewish kid in a class of 30 or so, mostly not. The teachers at that time reflected the Boston school district's rules. Spinsters all, they could not be married, although widows were acceptable. There was only one male teacher in the school, but I do not know whether the same rule against marriage applied to him. I did not like school and did rather poorly in all the subjects. Some absurdities of the methods of

teaching remain unexplained to me today. We were taught that we must write using the "Palmer method." The technique involves holding the pen firmly but writing by moving the arm from the shoulder NOT using your fingers. I suspect that maybe through some murky subconscious route, my interest in the motor control of the fingers may have had its root in that absurd technique. As a kid I would note, secretly, that the teachers did not use the Palmer method. They moved their fingers when they wrote. Do as I say, not as I do. I have only the faintest recollection of what was actually taught, but I do recall that the only reasonable question I can remember asking in 6 years of elementary school failed to elicit a sensible reply. The teacher had solemnly explained to us that rain came about because the winds, as they traveled over the ocean, picked up moisture, which later fell over the land as rain. "Why," I asked, "isn't rain salty?" In retrospect I think that the teacher did not have any idea of why. She dismissed the question as a silly one.

With changes in the people living in the Roxbury/Dorchester neighborhood from predominantly Jewish to predominantly black, the Garrison School reflected that change with a nearly all black set of pupils. Jonathan Kozol later taught at the Garrison School, and it became the subject of his angry book about the deficits in the teaching of black kids by the Boston School Department.

Every day after school for 6 years, I went to the nearby Hebrew school. We had about a half-hour from the time that the Garrison School let out until the Hebrew School began. That half-hour was almost always devoted to playing marbles ("aggies" in our argot) on the sidewalk across the street from the Hebrew School. Most of the play involved bowling aggies along the pavement. The practice was to set up a string of marbles and offer a certain number of marbles if you could hit the string from two paving stone distances away. Alternatively it could be "hit the penny and keep it." I devised a winning system. I set out a very long string of marbles; "hit the marbles and get two." Because the probability of hitting the string of aggies was less than .5, I acquired a vast collection of marbles.

Compared to the traditional ghetto cheder, in which boys learned to read the Hebrew alphabet and to recite the prayers, the Hebrew School was modern. Girls as well as boys learned not just to read Hebrew but also grammar and to translate the Bible into English. In Hebrew School, as in the Garrison School, I did not shine as a pupil. I never could settle down at either school to work. Later in the school—I think it was my last year there—we had an exam on translating Second Samuel. (Shmuel Bais in the Ashkenazi Hebrew we learned.) My father, having been told by my teacher of my generally poor performance, encouraged me with a bit of wordplay. "If you get a bad grade on Shmuel Bais, Yitzchak (My father) will be bais, Yiddish for angry. I got one of my only Bs and ran home to tell my father the good news."

Boston Latin School (Founded 1635)

Boston Latin School is the oldest school in the United States, outdating Harvard College by 1 year. I am not clear on how its selective admission policy worked. Clearly it could have not been related to my performance in elementary school. Maybe there was a test, but I do not recall. My sister Honey had gone to Girl's Latin School. I applied to and was accepted at Boys' Latin. The school lasted from the seventh grade to senior high school, 6 years in all. The incoming students were called the sixth class, and you worked your way through the classes to the first, or graduating class. Many, if not most of the graduates of Boston Latin School went on to Harvard. I failed in the second class, and never graduated.

I squeaked along through the successive years. Even though it was wartime, the teachers were all men, often elderly or strange. In the sixth class (the seventh grade) we had as a homeroom teacher Mr. Sullivan, who also taught us introductory Latin. "You can work out whether a phrase is in the passive voice, by thinking; 'by Mickey mouse' after it." A kindly, elderly man with silver hair, he was also a fount of great wisdom. "I think it's a good policy in life not to ask questions if you can find out the answer for yourself."

In the sixth class, and all subsequent classes, I remained a mediocre student. I could, when required, memorize conjugations of verbs or declensions of nouns, usually on the evening before a test. I never shone. Each year three prizes were awarded within each homeroom group: the classical prize (Latin and Greek), the modern prize (French, German, etc.), and the "fidelity prize," whose function I still do not know. My friend Sumner Kirshner won the fidelity prize one year. I never came close to any prize.

The fourth class (first year of most high schools) was no better. I managed to keep a low profile, to survive, but never to excel. Our Latin teacher that year, Mr. Roche, was known throughout the state. A short man, he delivered a never-ending stream of invective at the class, alternatively reproaching us for sweating (we came to Latin after gym) or wondering why we came at all; "Latin is for the amusement of the rich; you are neither rich nor amused. Why don't you all learn to do something with your hands." Most of us had an illicit translation of Caesar, the text for the year. Most of us were skilled at simulating a halting translation, not Doherty. He read his translation directly from the book he had bought and duly received a reprimand and a misdemeanor mark. A certain number of misdemeanor marks netted you a censure. Three censures and you were expelled.

Latin school was politically incorrect. What now might be the subject of angry letters to the school by a parent, and perhaps a reprimand to a teacher, was a routine occurrence. In the 10th grade Mr. Brickley,

our homeroom teacher and English master called the roll on the first day. “William Stone.” “Here sir.” “William I see that you come from the West End. Tell me William, have you ever seen a tree?” Military drill was a required part of the curriculum. Our drill teacher, called the roll alphabetically. When he got to David Yee, he stopped. “David, does your father have a restaurant?” “No sir.” “He must have a laundry. Pity, I thought I might go and get me some chop suey.”

Sailing

I love boats. My best friend for most of my years at Boston Latin School was Sumner Kirshner. In the summer we would sometimes take the subway and buses to Revere Beach, just north of Boston. On one afternoon when we were 13 years old, we watched a sailboat in the water off the beach, and both of us became infected. That winter we shoveled snow to earn money, keeping our earnings hidden in a glass jar in Sumner’s house. In the spring we had saved \$60, enough to buy a boat, a Swampscott Dory, which we found in a boatyard at the mouth of the Neponset River just south of Boston. We learned about boats and about sailing by making mistakes, many mistakes. We knew that dry seams between the planks had to be filled. We used Webtex, a roofing compound to fill them. We could figure out no way in which the boom fitted onto the mast and were too embarrassed to ask anyone. We finally overcame our shame and asked. We bought the appropriate fitting, a gooseneck, and managed to put it on the mast. Dory sterns are not easily adapted to fitting a rudder. Our boat had a peculiar arrangement in which a yoke on the rudder was connected to a yoke on the tiller by a pair of wires. The wires would snap easily under tension, which they did routinely. Our ignorance of hardware was matched by our ignorance of sailing. We took along Eddie Stoller on our first sail in the river mouth, just off the boatyard. Eddie shouted, “Head er up.” Not knowing what that meant, we did nothing, and the boat capsized. It almost always capsized, but someone would usually come out and tow us and the boat back to the boatyard’s shore. The next year we sold the dory (called Salty) and bought a larger boat with a tiny cabin, a Massachusetts Bayer, built, we were told, by a Mr. Shivricks on Cape Cod. We were not much more skilled at repairs or sailing, but we did manage to get it out of the mouth of the Neponset River, to tie up briefly, unwelcome, at the Dorchester Yacht Club. Boats were my salvation from a complex home life and mediocre school performance.

Dropout Year

My father died when I was 15. A chronic smoker, he died of cancer that probably originated in his lungs but was billed as cancer of the pancreas.

I knew he was ill, but I had no idea of how ill. The only death in the family that I had experienced before was that of my grandmother some years earlier, to whom I was not attached. The year after my father died, I fell apart. I was truant most days. Scollay Square in Boston is now sanitized as Government Center. When I was 15 it contained two burlesque houses: the Old Howard and the Gayety. The Old Howard burlesque was a wonderful alternative to school. It began at the same time and ended at about the same time as the school did each day. For the price of admission you could see two movies, a sequence of strippers, a chorus of would-be strippers, several comics, and sometimes a trick dog act. All infinitely more appealing than school. On days that I did not go to the Old Howard, I wandered the length of Atlantic Avenue looking at boats. The fishing boats came in from the Grand Banks of Newfoundland loaded with cod in the hold and covered with ice. My schoolwork reflected my truancy. That year I managed to achieve the lowest grade in some subjects ever recorded in the school. My mother was copeless. My sisters arranged for me to go to Cheshire Academy that summer, where there was a remedial program for the lost year of high school. My sisters came to tell the teachers at Boston Latin that I was going to a private school. The Latin master said; "I think that he should go to reform school."

Cheshire Academy

Cheshire, Connecticut and Cheshire Academy are located about 14 miles north of New Haven. It was a good choice. The structure was what I needed. Each evening you went to your room and were meant to study until lights out. In the summer I made up the lost year, thanks to being required to stay in my room in the evening. Cheshire Academy was cosmopolitan. About 10% of the class were Latin American boys. A lively lot, we had a good soccer team and some great fellow students. They came from all of Latin America, from Mexico to Argentina. Gus Aguero was from Camaguey in Cuba. He had a sign over his bed that said "Gus, the great." He was. So were Santiago Flores, Esteban Rock, and Louie Uncein, whom we quickly designated Louie Insane.

Classes were small, and the work was easy. My father had left an insurance policy for educating his children, and there was enough money to support me at Cheshire for another term. After repairing the lost year in the summer term, I stayed on in the fall term, which gave me enough credits for a high school diploma. I graduated midyear first in my class, for the first time an academic success.

For the first months of 1948 I lived at home. I had a job at a soda fountain in the Parkway Pharmacy in Milton. Each morning I took the trolley car as far as Mattapan Square and walked across the bridge up to the drugstore. I learned to make the ice cream sodas and drinks that were

asked for, and I learned the beginning of a foreign language. A milkshake in Boston was a pallid thing of syrup and milk mixed and frothed in the mixer. If ice cream, was added, it was called a "frappe." The Parkway Pharmacy was on one of the main routes from Boston to Providence. Rhode Island people would stop in asking for a cabinet, Rhode Island-speak for frappe.

University

When I graduated from Cheshire Academy I applied to Yale but was not admitted. I also applied to Bucknell University, which shared Lewisburg, Pennsylvania with a fine federal prison. Once again I backslid. I did minimal work. Although I did very little work, my life was enriched by friends I met there and by my ownership of an absurd vehicle. A Chevy of dubious vintage circa 1929, it had a sheet metal body and no top. My sister, Honey, bought it for me in Connecticut where she was a teacher in the Cherry-Lawn School. The car retained its Connecticut plates (registered to one Kenneth O'Connor, whom I never met).

Bucknell's administration basked in their Baptist heritage. "We think Baptists are better than anyone else or we wouldn't BE Baptists!" Except for one bland mixed fraternity, all were segregated. We Jews had our own chapter of Sigma Alpha Mu, "Sammy." I duly 'pledged' for a few months. A silly business, I soon quit. I still feel guilty about not working at all at Bucknell. Manning Smith taught chemistry. A kindly professor, he gave me my deserved very low grade in chemistry but then turned up to visit me at home on his way through Boston.

Despite my mediocre performance at Bucknell, I was accepted as a transfer student at the University of Chicago.

University of Chicago

My high school friend Sumner Kirshner had been at the University of Chicago for a year. We loaded my old topless Chevy and drove the thousand miles or so to Chicago. For the first few weeks, we boarded in the home of a kindly old German-Jewish couple but soon moved out in search of livelier student life. We found it. I joined Whitman House, a coop. Unusual for its time, Whitman house had both men and women as members. Twenty-five people lived in the house. Ten more, in the food-group, were full members, but only ate there. Most of the people in the house were students, but it was not technically a student cooperative. We members of the house owned it. Whitman was one of four houses, jointly called "United Cooperative Projects." Whitman House was what I came to Chicago for. The membership was opposite in character to Bucknell's fraternities. Where each fraternity was structured so as to include the narrowest of backgrounds among its members, Whitman house had all sorts of people: every

variety of socialist, anarchist, and democrat. We even had one Republican member. At Bucknell, Jews joined the Jewish fraternity. The few black people at Bucknell could join only the one non-nationally affiliated fraternity. Whitman house had black people and white people, Jews, a few practicing Christians, southerners and northerners. Almost everyone was studying something or doing something. One of our members, Mickey Frank, was the cook, and we all ate dinner together. The food was pretty awful, but it did not matter. Mickey was among the most lovable of people, so no one cared much about her standards of cooking. Food was available in the refrigerator for breakfast or lunch; you signed up for what you used. One of our members was the work manager, and jobs rotated among the members. I have never known a more tolerant, interesting, or congenial group of people. Why study when there was so much to talk about, and so many good people to talk to? Evenings we might listen to Marlene Dietrich or Edith Piaf records, drink cheap wine, and drive to the Indiana dunes just before dawn to watch the sunrise. If anyone had some money we might get up a group to go to Granato's, a pizza restaurant west of Halstead where the pizza seemed wonderful and the company great. Although McCarthyism was in full swing around the country and state, Robert Maynard Hutchins, the chancellor of the university, publicly affirmed his policy that "No University of Chicago professor would be dismissed for any offense short of rape or murder committed at high noon with three witnesses."

Politics was everywhere at Chicago. One of the factions of the U.S. Trotskyist movement was led by Max Schachtman. Schachtman's followers had an active group on the campus. They organized a debate between Max Schachtman and Alexander Kerensky (yes THAT Kerensky; leader of the provisional government in Russia just before the Bolshevik revolution) on the topic; "Was the Bolshevik revolution democratic?" Schachtman; "Yes"; Kerensky "NO!"

The university never noticed if you turned up for class ("discussion groups") so mostly I did not. Each course had a single comprehensive exam at the end of the academic year. In the last few weeks of the academic year I read the assigned material continuously and managed to scrape by, yet again. Two of my friends, Bill Donaho and Dave Stevens, shared a room on Woodlawn Avenue in the house of a lady who kept student boarders as well as 30 or so cats. They gave me their room to study in. Bill moved into my room at the coop. Dave moved onto the beach on the Lake. For 3 weeks I read almost continuously, just about completing all of the years assignment. I passed without distinction but well enough to repeat the process in my second year at Chicago.

The University of Chicago remained a great place to be. I supplemented my modest income from my father's will with a job as a relief night clerk in The East End Park, a local residential hotel. The manager of the hotel

stood in some awe of the hotel's bookkeeping. A relative anumerate, he was convinced that it took years of training and experience to cope with hotel bookkeeping (called "transcript"). There were a few residential hotels on the south side of Chicago near the university, and a number of students had jobs as relief night clerks. We taught one another transcript in about an hour or so. Because the manager of the East End Park could not believe that we could know transcript unless we had experience, we gave as a reference Mike Nichols' mother who ran a Hotel in New York State called the Continental House. In addition to doing the day's bookkeeping, the night clerk manned the desk, ran the elevator, and operated the switchboard. All three took very little of the 10 or 12 hours. Some studied. Some held long discussions with other student night clerks on the nature of truth or the correct interpretation of a passage in Dostoyevsky.

Chicago's undergraduate college at the time offered 14 undergraduate courses. When you arrived you took a placement exam. If you passed one of the placement exams, you were exempted from 1 of the 14 courses. I passed seven exams, so I needed to take seven courses for the degree. I took four courses the first year and three the second. The third-year humanities course was offered in a variety of options. I took the Latin option along with three other students. Mr. Clarke, the teacher, was English. A superb teacher, his hobby was translating poetry from English into Latin. It often did very well indeed, translating T.S. Elliot's "When Mr. Apollinax Visited the United States . . ." into "*Ad civitates foederes dum Apollinax . . .*"

My second-year exam results were only marginally better than my first-year results, but I passed, and got the curious B.A. that Chicago awarded. "But what did you *major* in?" It was useless to try to explain.

When I finished the undergraduate course at Chicago, I applied to the psychology department to be a graduate student. I had a somewhat vague interest in becoming a clinical psychologist. I was politely refused. The secretary kindly suggested that my undergraduate grades were not high enough. So I traveled.

Weltreise

I went back to Boston in the fall of 1951 to stay with my mother. I found the very cheapest way to go to Europe: \$125 for a ticket on a Panamanian-registered, Greek-owned ship, the *Olympia*, from Canada to Europe. The ticket was from Quebec to Cherbourg. Most of the passengers were Canadian soldiers, bound for Germany, where they were to relieve some of the British occupying forces.

There were only a very few civilian passengers, so we were treated with great indulgence by the ship. Five meals a day and a small German ship's orchestra playing "*Du bist die schönste am Strandkaffee*" or a maudlin song about a boy whose mother had just died: "*Mamati, schenke mir*

ein Pferdchen; Ein Pferdchen wär mein Paradis...” One of the other young people on board was a Cypriot, Andy Georgiades, on his way from McGill to medical school in Paris. Andy had recently seen Ingrid Bergman as a psychiatrist in the movie *Spellbound* and was planning to be a psychoanalyst. Although my ticket said Cherbourg, the ship decided not to call there, and off-loaded us passengers in Southampton, providing us with a ticket on the night ferry to Le Havre. Six hours in Southampton, and I became an authority on England and all things English.

We left for France late that night. There was a deep thrill in closing the French coast in the morning. I was, at last, in a really foreign place. One of the other passengers taught me how to say “matches” in French, and I asked for “des allumettes” at a kiosk at the train station in Le Havre. Magic. She understood! Andy Georgiades and I roomed together at a pension in Paris while he found a permanent place to live, and I prepared to move on. I was scheduled to meet a friend, Dave Padwa, in Paris. We had arranged three sequential times and locations to meet: 3 PM at the Palais Dorsay on the Quai Dorsay, failing that 9 PM that evening under the Arch of Triumph, and if he was not there under the arch, we were to meet at 3 PM the next afternoon at the American Express office. Dave never showed up. I struck out on my own.

There was an easy camaraderie at the youth hostels and ready companions to travel with. We would hitchhike together or maybe beg a meal on a ship in a harbor. I worked my way first south to Nice and then to Genoa and Naples, then across Italy to Brindisi and a boat to Piraeus, where I arrived on New Year’s Day 1952. Aside from the Parthenon, I never saw much of Greece. After 3 days in Athens, I left aboard the *Abazia*, an Italian passenger liner for Israel.

I spent 2 months in Israel working at various kibbutzim. In one kibbutz, there was an American friend. In another, I fished for the same fish as Jesus’ disciples on the Sea of Galilee, with bright lights as lures and nets to catch them. I spent 2 weeks at Urim, a Kibbutz on the edge of the Negev desert in the south of the country. At the time our diet consisted mostly of bread, oranges, and yogurt. At Urim, I opened and shared the contraband tin of ham I had smuggled into the country in contravention of the Israeli laws at that time against importing pork. We ate the ham at a small party one evening.

Israel was a fantastic place at the time. All of us were cousins. I asked a soldier directions at the train station in Haifa. We rode on the same train, and I ended up staying the weekend at his sister’s kibbutz.

In February, I learned that there might be a chance for a job on an American ship in Haifa. The chief steward of a C2 freighter had become ill and was flown back to the States. Everyone in the steward’s department moved up one, leaving a space at the bottom. I signed on the Pacific Far East

Line ship, the *Indian Bear*, as saloon pantryman. The job involved making salads and coffee and washing the dishes in the officer's mess. Light duty except in the 132°F that we encountered in the Red Sea. The ship loaded chemical fertilizer, 10,000 tons of it in Savona Italy, and then proceeded eastwards briefly stopping in Cyprus, through the Suez Canal, Aden Arabia, Colombo Ceylon, and Singapore. When the ship was safely anchored in the outer harbor at Singapore, I asked (respectfully of course) the beefy-faced British pilot if it was safe to swim off the small platform next to the ship in the harbor or were there sharks. "It's not the sharks you have to worry about, sonny, it's the crocodiles wot eats them." He may have been joking, but I did not test it. We offloaded the fertilizer in Pusan, Korea, then still a war zone, and proceeded to Yokohama where we loaded dishes and took on as passengers two families of missionaries that had been evicted from China, who were enroute home. In Yokohama, I saw a tiny bit of Japan. On the way back to the States we encountered a typhoon—high winds and very high seas. One of the old able-bodied sailors, a northern Italian who had been shipping out most of his life, attributed the storm to the fact that we were carrying missionaries. "Dey all Jonahs; you always git dis wedder wit dem on board." We headed east from Yokohama to our homeport in San Francisco. It was thrilling to see a faint glint of gold in the far distance that got larger and larger as we approached the American coast. The ship passed under the Golden Gate Bridge into San Francisco harbor. I had never been west of the Mississippi river before. Here I was in California.

I left the ship with a magnificent \$1000 in cash. I bought an old car for a \$100 and headed east. The car died in Bakersfield. I carried on by "travel bureau," an office where you could arrange to pay for a ride with someone driving in your direction, to Amarillo and then by bus to Houston, where my sister Judy was living, and from Houston by bus to Chicago, where I checked back in briefly at my co-op house and then on to New York.

New York

I arrived in New York in June of 1952 and proceeded to settle in. My old Chicago friend, Bill Donaho, and I found a precious rent-controlled flat in the old Spanish Harlem at First Avenue and 107th street, \$24 a month with the bathtub in the kitchen. I still had a few hundred dollars left from my payoff on the *Indian Bear*, and I spent most of it paying for summer courses in math and psychology at NYU. The psychology courses were deeply boring. The math I found wonderful. Ignorant, I started with a course in analytic geometry and then a continuation night school course in calculus. Calculus was marvelous. I did all of the problems in the book. My sister Honey was married and living in nearby Bayonne, New Jersey, pregnant with my niece, Martha. Honey taught Latin in the Bergen School,

a small private girl's school in Jersey City, but she was leaving to look after Martha. I was offered her job, teaching Latin and history at \$1900 a year. My Latin schoolteachers would have been appalled. I found the job pleasant and easy. I gave an inspired lecture to my eight students in second-year Latin on the passive periphrastic. Miss Wood, the headmistress, had her office next door, and she said she would stop and listen to my history classes because she enjoyed them. So did I. That summer I had a job as a sailing counselor at a camp on Lake George. My duties consisted of sailing all day with campers and teaching about the nature of winds and boats. Evenings, the other sailing counselor and I would take his sailing canoe out, over-rigged with a massive mainsail and a cut-down tent for a jib, and fly over Lake George until we capsized.

My grades at NYU were good, and so I reapplied to the University of Chicago graduate school in psychology. This time they accepted me.

Graduate School

Bill Donaho and I divided our joint possessions. He got my half of the furniture. I got full possession of our 1942 Chevrolet station wagon. I arrived in Chicago with a half tank of gas and \$2. The universal advertising spot was then the tree in front of Woodworth's Bookstore on 57th Street. There was a job listed as a home-helper with the MacFadyens, who lived in a big house about a mile north of the university. The main responsibility was to ferry their adolescent son to school in the morning. They were a delightful couple; Mrs. MacFadyen taught piano at a local college. They let me come down to listen in the evenings when she played chamber music. My other job was as a night emergency worker with the Red Cross. My main responsibilities were to arrange emergency leave for servicemen or to alert the disaster team when there was a fire. The Red Cross job paid enough so that I could afford to rent a place of my own and I left the MacFadyens in good graces. The Red Cross job lasted for 5 years. I was sacked in my last year of graduate school for sleeping through a five-alarm fire—a warehouse, no one was injured or needed shelter. I was offered the chance to shift to the day work, which I politely declined.

First Year in Graduate School; The Core Curriculum; Roger Sperry; Austin Riesen and Ekhard Hess

Chicago's psychology department had a fixed course in the first year, centered on a Proseminar in General Psychology. The proseminar dealt with all experimental psychology. At the end of the academic year we took prelims. You could pass the prelim exams at a doctoral level or a master's

level, or you could fail. In the latter two cases, it might be with or without permission to retake the examination.

For the second time in my life I worked very hard at my studies. I attended and took notes in every class. I read and summarized all of the assigned readings in my notes. Three people lectured us in the first part of the proseminar: Austin Riesen, Eckhard Hess, and Roger Sperry. All three taught us about vision. We were ignorant, but we could tell that all three could not be right. Riesen spoke about his dark-raised chimps, Snark and Alfalfa who, he said, slowly learned to see after being raised for several months in complete darkness. Vision, he argued, must be learned. Hess told us about his experiments on prism displacement in chicks. Newborn chicks were fitted with a rubber mask containing laterally shifting prisms. Over the first 3 days of their little lives, the chicks pecked more and more accurately at exactly the wrong spot to pick up a single bit of grain. Vision, Hess argued is innate. Sperry told us about his experiments on rerouting nerves. The nervous system, Sperry argued, is fixed, with little chance for its functions to be modified. He had a memorable clinical example of a woman who had a nerve that normally controls salivation shifted to a tear duct. She wept when she saw an apple.

We students were ignorant, but we recognized that at least one of our teachers must be wrong. A similar challenge was presented by the “transposition experiment.” Rats were trained to choose one of two triangles; one was 2 cm high and the other 4 cm. When tested with a pair of triangles 4 and 8 cm in height, they chose the taller, 8-cm triangle. They had learned a relationship: “the larger triangle” not an absolute size. The only theory that seemed to offer an explanation for the transposition experiment and for Riesen’s data was in a book recently published by Donald Hebb, *The Organization of Behavior*. In the argument between nativism and empiricism in vision, empiricism was saved by Hebb. I was a Hebbian for about a year. The following year I began working at Michael Reese Hospital where Jack Orbach, a physiological psychologist, worked. Jack had been Karl Lashley’s last post doc at the Yerkes lab, when it was still in Jacksonville, Florida. Orbach also admired Hebb, but he gave me a 100-page monograph by Gordon Walls to read: *The Problem of Visual Direction* (Walls, 1951). I became, and remain, a nativist.

I took the readings and the concepts we were taught in the first year of the psychology course seriously. Along with my classmates, I read Hull and Spence, and I found them underwhelming. Learning theories that taught me little or nothing about learning. I was particularly put off by reading Miller and Dollard—an attempt to blend Freudian ideas with learning theories, to the benefit, I thought, of neither. We were assigned, and I read, 300 pages of Kurt Koffka’s book on the principles of Gestalt psychology. I took 30 pages of notes, but I also found many of Koffka’s principles hard to accept. Koffka’s notion of “good gestalt” seemed especially arbitrary

when it was used to account for the appearance of the constellations. The Gestalt psychologist had put forward vague ideas about a role for electrical fields in the functions of the cerebral cortex. Sperry had directly challenged the postulated electrical fields as the basis for form perception. Sperry inserted gold, which would have shorted them; mica, which would have insulated them; or cross hatching, which would have interrupted short cortico-cortical connections. None of these assaults on the visual cortex abolished form vision.

We took prelims in the late spring of the first year of graduate school—29 of us. There was a fine tradition of older students serving drinks, coffee, etc. while you took the exams. I had worked hard, and my notes and memory were both intact, so I did not worry. The day before the prelims I tried to bring one of my fellow students over to Billings Hospital with me to hear a lecture on the adrenal cortex. He refused to leave the library; an unfortunate choice, because one of the questions was on the material of the lecture. I was one of the fortunate nine students that passed at the doctoral level. The department made it clear that there would be no more hassle. Take whatever courses you choose. Write the dissertation you wish to, and you will get a Ph.D. degree.

Second-Year Graduate Student

Having passed the prelims, I could carry on at Chicago; I planned to be a clinical psychologist. The clinical psychologists in the department organized their own second-year program. Hedda Bolgar taught us personality theory, with a serious amount of Sigmund Freud. Soskin taught us Jung. We had courses in Rorschach testing from Sam Beck and a course on the TAT test with Bill Henry. Sam Beck gave me a job as a research assistant; an easy enough task, writing short précis of the literature on schizophrenia. My high school German was sufficient for the task. I also helped by translating one chapter of Ewald Bohm's text on the Rorschach test. I translated the chapter on "The Special Responses" in which I learned that "white shock," or a slowed response to a white space on the card, always meant fear of the female genitalia—maybe. I also started seeing two clients in Carl Rogers' counseling center, a responsibility I liked. Forget the theory. In one of my two clients, I was convinced that the opportunity to talk to a neutral, but interested and sympathetic person, was helpful.

By now I was convinced that I did not want to be a clinical psychologist. I liked the work, but I wanted to be in a field that made orderly progress—one in which the small grain of sand I might add to the pile was based on what had gone before and would be of interest, and perhaps even of importance, for those that followed. My clinical psychology teachers were intelligent and insightful, but there seemed little chance that knowledge would become cumulative.

Third- and Fourth-Year Graduate School

Michael Reese Hospital was about half way between the loop and the University of Chicago. It had attached to it a relatively new Institute of Psychiatric and Psychosomatic medicine, headed by Dr. Roy Grinker. Grinker came from an old German Jewish family in Chicago. His father, Roy Grinker Sr., had been a neurologist. As a young physician, Roy Jr. was a neurological wunderkind. He wrote an excellent textbook of neurology, rare for someone so young. The medical school at the University of Chicago had a checkered history in hiring a head of psychiatry. The hot area of the time was psychoanalysis. They would hire a psychoanalyst to head the department, but he would soon leave, feeling undervalued by the real doctors. The higher-ups had a great plan. Send Roy Jr., a real doctor, to Vienna for analysis by Freud, and bring him back as Chairman of the Psychiatry Department. They sent him. He went and had a fast psychoanalysis with the master himself. Grinker came back to Chicago, but he too soon left the university to found his own empire attached to Michael Reese Hospital. As a psychiatrist and director of the Institute at Michael Reese in the 1950s, there was still much of the rigor of a neurologist in Dr. Grinker. He wished to study psychiatric problems in a rigorous way and set out to study anxiety. Patients would spend a period of time in a testing room, where a sequence of biochemical and psychological procedures and interviews would be carried out. Heart rate and blood pressure were monitored continuously. Heart rate was measured by electrocardiogram (EKG) written onto a Grass penwriter. My job in those precomputer days was counting heartbeats. The plan of the experiments seemed straightforward—several procedures, each preceded and followed by a rest period, then a stressful interview with Dr. Grinker, designed to elicit anxiety, followed by a repeat of the procedures prior to the interview. Did heart rate go up after the interview?

I had been studying and was obsessed at the time with factor analysis. Because L.L. Thurstone had recently left Chicago, Lyle Jones taught the factor analysis course. In the first lectures, Lyle Jones introduced us to two unsolved problems: how many factors to extract from a correlation matrix, and how should the factors be rotated. In the precomputer time, we did our factor analyses using a desk calculator. Because it was relatively simple for hand calculation, the major technique we used was Thurstone's centroid method for factoring. We also were introduced to Thurstone's semi-intuitive criterion for rotation: to "simple structure." I began immediately trying to develop a more rigorous mathematical solution for both problems. I developed some possible solutions, including significance testing of the factors. I also developed a unique solution for the worst rotation, which I thought would be 45 degrees away from the best rotational solution; I could rotate a solution to the *least* simple structure. I never

published either, but I applied factor analysis to the data I had collected at Michael Reese. Factor analysis was not known by my senior colleagues, so I developed a teaching device to illustrate its use. Suppose you had a simple test of measuring a patient's heart rate. You could, for example, ask the patient to exercise briefly by stepping up and down on a chair and measure heart rate before and after the exercise. If you averaged the data from 100 subjects you would doubtless find the trivial result that heart rate on average goes up significantly with exercise. But suppose that a subset of the 100 subjects, say 10, had a paradoxical decrease in heart rate. The data would be lost in the group measurement. A matrix of the correlations between all pairs of subjects would preserve the average data but also allow you to identify the aberrant response. I applied this logic to the data I had collected and showed that the Michael Reese patients could be divided easily into two groups with grossly different patterns of response. The work on heart rate and blood pressure formed the basis for my doctoral thesis and was published along with the other members of the Michael Reese group as coauthors in the *Archives of Neurology and Psychiatry*—my first publication (Glickstein et al., 1957).

In my last year in graduate school I was drifting away from factor analysis, but I remained painfully aware of the pitfalls and limitations of the method. My last effort in clinical psychology was a negative one. J. Wittenborn (1950) had published a factor analysis of Rorschach scoring categories. The Rorschach Test is open-ended. You can say as much or as little as you choose in response to each card, which seriously influences the factor solution. Wittenborn had published the original correlation matrix in his paper, so it was possible to use partial correlation to evaluate the influence of this open-ended aspect of the test. I showed that the number of responses accounted for almost all of the variance in the test. Removing this factor revealed another statistical artifact of the factor analysis. Response categories are mutually exclusive. If you give, for example, a "whole" response, you cannot give a "detail" response. In the limiting case of a true-false test, there must be a correlation of minus one of true with false answers. The reduced matrix of partial correlations reflected the imposed negative correlation between categories. There seemed little more in the data than randomness. Brash, I published my analysis as a "Note on Wittenborn's Factor Analysis of Rorschach Scoring Categories" (Glickstein, 1959).

In my fourth year in graduate school I spent two nights a week in the lab of Nathaniel Kleitman. Eugene Aserinsky and Kleitman (1953) had discovered and described the phenomenon of rapid eye movement sleep (REM) and its association with dreaming. Bill Dement was both a medical and graduate student in physiology at the time, continuing the sleep research. I was happy to work there. I would typically sleep in the lab one night as a subject or run the experiment on another night with Bill Dement or

some other student as sleeper. Good fun, we studied the possible effect on the electroencephalogram (EEG) of hypnotic suggestion on the perceived brightness of light. In other studies, we tried to influence dreams by external stimuli. Mostly we could not, but in a few cases we could clearly do so. In one subject we played a series of low, bass notes from a sound generator at an irregular interval. The student dreamed that he was in his cousin's house, learning guitar. His cousin would play a low bass and interleave it with high melodies between bass cords. In another experiment we sprayed the room during REM sleep with a cheap perfume we had bought that afternoon in Steinway's drugstore. The subject dreamt that he was a male prostitute, waiting for his next client.

Chicago seemed a place where everybody made an important discovery. Eugene Aserinsky had discovered REM sleep; Ronnie Myers, a medical and Ph.D. student working with Roger Sperry, had shown that it is possible to establish two nonconflicting memory traces in the two hemispheres. Myers cut the corpus callosum and optic chiasm of cats in the midline. He taught the cats to choose one of two visual patterns for a food reward with one eye masked. When tested using the opposite eye, the animals were naïve. They could easily learn to choose the formerly negative cue. Cats with the corpus callosum cut, and with visual information restricted to one or the other hemisphere, had no difficulty maintaining two opposite memory traces. Depending on which eye was open, the cat would choose the cue that had been learned on that side of the brain. With Aserinsky and Myers as examples, it seemed that every graduate student at the University of Chicago had made a fundamental discovery. I was jealous.

Final Year of Graduate School

By now I was convinced that the answer to any of the questions I had lay in the study of the brain. I knew very little about the brain, so I asked three people for a job so that I could learn more about it. K.L. Chow, Jim Toman at Michael Reese Hospital, and Garth Thomas, who had been one of my teachers at the University of Chicago and was now working in the basement labs at the Illinois Neuropsychiatric Institute (INI). My job as a research assistant for Garth Thomas was mainly to train rats in a shuttle-box avoidance task, testing the effect of hippocampal lesions on acquisition and retention. We ran many subjects. My other jobs were to assist in stereotaxic surgery and to perfuse the animals after testing was completed. I also removed the perfused brains for sectioning. The INI lab had several active research groups working on various aspects of neuroscience. Ralph Gerard and Gilbert Ling had worked there in the past and had developed the use of microelectrodes for single unit recording.

Garth Thomas was a splendid boss. He was newly converted from psychophysics to neuroscience, and he shared his knowledge and his

enthusiasm with me. When the smelt run on Lake Michigan was in full force, I would go with Garth to the lakeshore in the evening with the appropriate net, a small alcohol stove, and a bottle of whiskey to greet the incoming fish that arrived in the millions.

Two of my acquaintances from the university were medical interns working upstairs at INI. We jointly decided to study the effect of temperature on the EEG. We reckoned that the natural choice for a subject for our experiment was a cold-blooded animal, so we bought a small alligator for the purpose. We discovered that alligators have a low threshold for barbiturates. When our first subject died from an overdose, we abandoned the project.

I had the use of an EEG. I collaborated with another group who wanted to study electrical activity in mealworms. One of that group had devised a cunning plastic holder for the mealworm. A pair of metal plates was connected to lead wires and was adjustable on either side. Fantastic. We placed a mealworm in the restraining apparatus and recorded low-voltage activity, which slowed when we cooled the mealworm. Then someone suggested a control. Take out the mealworm. The electrical activity persisted, so we abandoned that project.

Others in the lab included Dr. Meduna who had previously discovered Metrazol shock therapy for psychiatric patients. Meduna's reasoning had been a bit fallacious. He said that although he had seen many epileptic patients and many schizophrenics he never had seen a patient suffering from both. Epilepsy and schizophrenia, he suggested, are the opposite of one another. The solution would then be to give a schizophrenic an epileptic fit. In Meduna's first attempts, he produced the fit using the convulsant drug, Metrazol. The technique of producing seizures was later modified by Cerletti and Bini in Rome who used electrical stimulation to produce the seizure. Meduna's original thinking was a bit flawed. If the random probability of a person being epileptic is, say 1 in 100, and the random probability of someone being schizophrenic were also 1 in 100, and if the two conditions are independent of one another, the joint probability would be 1 in 10,000. No matter. Meduna was now studying the effects of inhaled CO₂ on psychiatric patients.

A good colleague in the lab was K. Koketsu who had worked previously with John Eccles in Australia and was actively studying spinal reflexes with another Japanese colleague, S. Nishi. Working with them was a very pretty technician called Yoko. Koketsu taught me and the others in the lab how to hold and use chopsticks. Another one of the senior colleagues in the lab was Alexander Geiger. Geiger was from an earlier era when physiology and biochemistry were still united. He had developed a preparation for studying brain metabolism by isolating the cerebral circulation. Geiger made replacement blood from ox blood, substituting the normal circulation with his made-up solution. He could then measure the

concentration of substances going into the cerebral circulation and compare it to that in the venous outflow. Active neurons use more oxygen and absorb more glucose. Before the development of the 2-deoxyglucose technique for studying glucose uptake, Geiger had the idea to use tritiated glucose in order to study active sites in the brain. I collaborated by making test rats anxious, fearing the onset of a foot shock. The first cases that we looked at seemed promising. The hippocampus and entire limbic system were lit up in the very first rats we tested but so were the controls. Geiger was one step away from the optimal method of using a form of glucose that would remain in the cell. Perhaps a better-controlled behavioral study might have shown up the difference between rats in our study.

Geiger's method had another use for me. There was at the time some speculation that the EEG might have nothing to do with neuronal activity but was simply a mechanical artifact, a sort of jiggling of the brain pulsed by a flood of blood and shaking within its cerebrospinal fluid (CSF) bath. The perfused brain was an easy way to evaluate the idea that the EEG is a mechanical artefact, because the pump that perfused the brain was a smooth one. The EEG appeared to be entirely normal.

By now I was committed to a career in neuroscience. I had not completed my qualifications as a clinical psychologist, but I was encouraged by Howard Hunt, the Chairman of the Psychology Department at Chicago, to accept a clinical psychology internship at Billings Hospital: "We would very much like to have one of our people in that internship." I agreed to a one-third-time internship and rather liked it, although I was not deflected from my plans to be study the brain. One person that I was asked to evaluate was a middle-aged lady of rather limited intellect. The woman had been living with her brother's family. Could she survive on her own if a caretaker were to share a flat with her? Was she just of limited intellect, or was she also psychotic? The tests convinced me that she was just mentally slow, not psychiatrically ill. In a sentence completion test I began "I want to know . . ."; she said "What's news?" As part of the intelligence test, I asked her "Why should people pay taxes?" She said, "I don't know; my brother takes care of all that."

I was faced with the good question of where to go to continue to study the brain. One possibility that Howard Hunt suggested was to apply to work at National Institute of Health (NIH) with Mort Mishkin and Hal Rosvold. Roger Sperry had moved to Cal Tech, where he was now the Hixson Professor of Psychobiology. I remembered Sperry's lectures and wrote to him. He agreed to have me.

Cal Tech

Cal Tech was a marvelous choice. When I arrived I knew very little about the brain but was eager to learn. I also knew little or nothing about

what was going on in Sperry's lab. Sperry himself was in a sanitarium when I arrived, recovering from a bout of tuberculosis. Norma Sperry, his wife, relayed messages from Roger to us in the lab. I had some vague acquaintance with Ronnie Myers' thesis research at Chicago, but I can clearly remember my own confusion when Norma kept talking about "split brains." I had no understanding of what she was talking about.

Sperry's lab had attracted some excellent people, and Cal Tech was a lively place for biology. When I arrived, Colwyn Trevarthen and Chuck Hamilton were both graduate students with Sperry. Harbans Arora was a post doc. That summer Mike Gazzaniga, whose parents lived in the Los Angeles area, worked in the lab between his junior and senior years at Dartmouth. He became a lifelong friend. Gilbert French had left recently and Al Schrier was just leaving for Brown. Later, Ted Voneida came after working with Marcus Singer and Walle Nauta. The technicians were equally excellent. Lois MacBird trained monkeys, as did the animal caretaker, Mike Saxlund. Mike confided in me that he would sing while training the animals and that they liked it. I am sure they did. Others came while I was there. Domenica (Nica) Attardi arrived in Pasadena with her husband and 8-year-old son, Luigi ("My name is Louie!"). Her husband had come to work in the virus lab of Renato Dulbecco. Nica wanted a part-time position during the hours that her son was in school. At the same time as Nica appeared, Sperry's histology technician, Octavia Chin, apologized to him that despite her best efforts she could not get the regenerating fibers to stain the same color as the normal fibers. Sperry put the two people together and the result was a beautiful study of regeneration of the fish optic nerve (Attardi and Sperry, 1962). Nica made regional ablations in the fish retina and cut the optic nerve. She showed that the regenerating fibers came to three successive choice points. All of the optic fibers decussate, but as they approached the tectum, half proceeded medial to it, half lateral. As they traveled along the edge of the tectum they would choose the appropriate point to turn along its surface. There was a third choice point when they stopped at a point on the surface of the tectum to synapse.

The lab had two foci. One was the study of nerve regeneration, a continuation of Sperry's brilliant earlier work. The other was on the functions of the corpus callosum. I knew very little about either. I spent the first weeks in the lab looking for an appropriate source to help me to learn about the callosum. I found it in Bremer's *Physiologie et Pathologie du Corps Calleux* (1956). That was the good news. The bad news was that it was in French. I bought a dictionary and plodded through it, writing out all 50 pages in English—a good move. At the end, I knew a lot more about the callosum, and I could read French.

Ronnie Myer's discovery of the role of the corpus callosum in inter-hemispheric transfer had been made while he was a graduate student with Sperry at Chicago. He had continued those studies with Sperry at Cal Tech

for a short while before being called up in the doctors' draft, where he was assigned to Walter Reed Hospital. There was more to do. Sperry suggested that I test the generality of the failure of interhemispheric transfer in callosum-sectioned animals by studying tactile learning. I trained monkeys to reach out of a training box and feel two objects that they could not see, placed over wells in front of the box. My monkeys readily learned to displace one of two three-dimensional objects for a food reward; for example, a high vs. a low cube or a cone vs. a pyramid. In order to rule out a trivial deficit caused by a brain lesion, I arranged the testing situation so that it was an advantage to have no corpus callosum. I would train the monkey to use one hand to select one of two paired objects. When I tested the second hand, I reversed the positive cue. If the cone had been positive with the first hand, the pyramid was now correct. Normal monkeys start at 0% correct with the second hand, because they know the problem. Callosum-sectioned monkeys start at 50% correct. When the animals were retrained using the second hand, I tested the original hand with the original values. The cone would again be correct. Now there was an even clearer advantage in not having the callosum. The normal monkey again performed at 0% correct. The callosum-sectioned monkey remembered the training on the original hand and remained at the criterion level of performance (Glickstein and Sperry, 1960).

Although the knowledge of which of two stimuli was correct did not transfer, the habit of testing did. The callosum-sectioned monkey did not know which of the two objects was correct, but he did know that there were two objects. He would reach out to feel the two from the outset, when first using his untrained arm and hand. I believe that I later found an explanation for this puzzling form of interhemispheric transfer, when I began to study the anatomical connections of the cerebellum.

I did another experiment with Sperry and Harbans Arora in my second year at Cal Tech (Glickstein et al., 1963). Since Jacobsen's work it was known that monkeys with bilateral lesions of the dorsolateral prefrontal cortex are profoundly impaired in performing tasks involving delayed response or delayed alternation. Both tasks require immediate memory. Monkeys with unilateral lesions are relatively unimpaired. In order to analyze the anatomical circuits involved, I followed a procedure that Mort Mishkin had devised to study functional connections between the striate and the inferotemporal cortex. I made a unilateral lesion of the frontal cortex combined with a section of the ipsilateral or contralateral optic tract. Vision was now restricted to one hemisphere, with the intact prefrontal cortex either on the same or opposite side of the brain. When I cut the corpus callosum in animals in which the two areas were on opposite sides of the brain, they were impaired in performing the delayed response task.

Sperry's lab was enriched by people coming to learn techniques or collaborate in experiments. I remember Michael Gaze coming in the summer

after I arrived. He later told me that he had been alerted to Sperry's work by David Whitteridge, then professor of Physiology at Edinburgh, who later became my close friend.

Although he had a natural tremor, Sperry was a skilled surgeon. His model for experimental surgery was not human surgery but zoological dissection. He sterilized the dissecting table. He made irregular-shaped wooden blocks that he would wrap in a sterile towel and weighted inside with lead to stabilize his wrists. He routinely operated using a dissecting microscope. Sperry was an excellent lab director. He was completely supportive of any research plans of mine or of others in the lab. He was, however, often angry about any claims for priority made by his students after they left the lab.

Cal Tech's biology department had no assistant or associate professors at the time, only full professors. The biology lab had been founded by the great geneticist Thomas Hunt Morgan, originally from Columbia. Among the full professors there were nine geneticists, several of whom, like Sperry, went on to win the Nobel Prize. Sperry was one of three neuroscientist professors when I arrived. The other two were Anthony Van Harreveld and Kaas Wiersma. Van Harreveld was a kind and generous man. At the time he was interested in the mechanism of spreading depression and the distribution of fluid and ions in the brain. Controversial at the time, Van Harreveld questioned the conclusions of many electron microscopists on the amount of intercellular space in brain. Van Harreveld was most helpful to younger colleagues. I knew very little anatomy when I arrived. He lent me a copy of Winkler and Potter's beautiful 1912 *Atlas of the Cat Brain*, a fixed cat brain, and a knife. At his suggestion, I made cuts roughly in the plane of the atlas and studied the structures I could see. Van Harreveld had three post-doctoral students working with him when I arrived. Johannes Schade had been at the Brain Research Institute in the Netherlands and was studying spreading depression. Joe Bogen was training as a neurosurgeon, that year working in the lab with Van Harreveld studying the pharmacology of an awful drug called bulbocapnine. Nico Spinelli was also with Van Harreveld, interested in the physiology of spinal reflexes. An imaginative electronic designer, Nico made his own stimulator, which had dozens of switches and dials. None of the dials or switches had labels, but the apparatus worked, and it did what he wanted it to do.

Wiersma was the third neuroscience professor. Wiersma studied invertebrates, particularly crayfish. A pioneer in invertebrate physiology, Wiersma developed some of the concepts that were later taken up and elaborated by others in the field. Eric Kandel credits Wiersma as being the pioneer.

The introductory biology course at Cal Tech was designed to be a show-piece. Cal Tech undergraduates were among the most highly selected high school kids of any institution in the United States. Most came planning to

study physics or engineering. The introductory biology course was meant to convince these very bright young people that biology is as exciting and rewarding as any science. Most of the lectures were given by the full professors. Sperry never really liked lecturing and designated me to deal with his part of the course. There was an informal popularity contest among the lecturers for student ratings. The first year I came second after James Bonner, an outstanding and articulate plant geneticist. The second year I had the highest student ratings for my lectures on the brain. The students were not passive. I used a lot of slides in my lectures. One of their clever tricks was to invert the optics of the projector, so that the image was minified, a tiny postage stamp, rather than a full screen.

Cal Tech's geneticists were world leaders. George Beadle was abroad the first year that I came. While at Oxford, Beadle learned that he had been awarded the Nobel Prize for his studies of yeast genetics. The graduate students promptly sent him a congratulatory telegram in DNA code.

When I arrived at Cal Tech I was told that I must give a talk; a Cal Tech tradition for new people. I felt that I knew nothing of any interest, so I declined. But further encouraged, I agreed to speak on REM sleep, then still recently discovered. I began my talk by drawing a 2×2 table on the blackboard to illustrate the probability of people reporting a dream while their eyes were moving, as opposed to when their eyes were still. I had barely finished putting the table on the board when Max Delbrück got up to say; "Oh no that's wrong!" I said, "No, it's right." He thought a bit, and said "Oh yes, that's right."—lively seminars always.

Cal Tech attracted scientific visitors. In an early thaw with Eastern Europe, Jan Bures came and spoke. A charming and most intelligent visitor, I liked him enormously, enough to discuss the nature of politics in his country. At the time Jan was a member of the party in Czechoslovakia. Somewhat drunk in the faculty club that evening, I said, sympathetically, that Czechoslovakia had been betrayed in 1938. He agreed and told me that at the height of the German occupation a large number of Czech citizens were in forced labor or concentration camps. I sympathized but asked him, "How many are there now?" He said, "None; but it is unsafe to criticize my government or your government."

The next day when Jan Bures came by the lab again, he admired some of the wire that Colwyn Trevarthen and I had bought to record EEGs. Very thin and flexible, 12 of the wires would fit into a quarter-inch laboratory tube. "Take one," I told Bures. "I must pay." "No just take one and put it in your luggage." Jan said, "I must choose the red wire, no?" Some years later, after the Russian invasion of his country Bures reminded me of the incident with the wire some years earlier and said, "If you were to test me again with the wires, I'm not sure which color I would take."

Sperry did not suffer fools gladly—two occasions come to mind. One was a talk by a young woman who had an elaborate, almost

incomprehensible, learning-theory approach to avoidance training. Sperry snorted and said "Oh I could do it much better than that. All you have to do is throw a rock at a cat. He will avoid you forever." Another time a visitor came with a theory of how the cortex works. Tiny magnetic domains circle around continuously and constitute the basic mechanism of cortical function. I kept looking at Sperry, whose previous work ruled out any such mechanism. He passed me a note, saying, "Why are you looking at me?" Someone asked, "What would be the consequence of inserting conductors or insulators into cortex?", experiments Sperry had done and published. "Oh that would be equivalent to decortication!" As we left the seminar room Sperry said quietly "I wonder if he's crazy."

Although we had speakers from time to time, Cal Tech did not have as active a neuroscience seminar series as UCLA, so we would arrange to invite many of the UCLA lecturers to speak at Cal Tech. I had the dubious joy of being in charge of the seminar one year, snagging people from the UCLA list. The Long Beach lab where I picked up the speakers was about 50 miles from Pasadena, much of the driving on city streets. Returning them to their motel in the evening I clocked 200 miles of city driving, but I had a good chance to ask questions of the speaker and learn more neuroscience.

On the occasions when we went to UCLA to hear a seminar, Joe Bogen, Nico Spinnelli, Colwyn Trevarthen, and I might stop at Taix, a cheap country-style French restaurant on our way. Jim Olds' pleasure centers were new, and the surgeons were not far behind, stimulating the human brainstem on their way to making a basal ganglia lesion for Parkinson patients. They would stimulate at a subcortical site and ask the patient how it felt. One surgeon reported that his patient said, "I feel great pleasure; it is 'appiness; I feel 'appy on one side of my body."

The Los Angeles coast is not a particularly rich one for sailing, but Catalina Island was a favored goal for weekend trips. I remember a fine voyage on a Chinese junk with Jennifer Buchwald, Carlos Guzman, and Henry Lesse.

Stanford

I had spent 2 years, from 1958 to 1960, with Sperry at Cal Tech. I was eager to learn new techniques and to work in a new lab. I wrote to Karl Pribram at Stanford and arranged to work there in the following year, 1960 to 1961. Karl was based in the psychiatry department of the Stanford Medical School. Jean Koepke, an Iowa Ph.D., Jim Dewson, and Tony Deutsch were attached to Pribram's lab, as was Muriel Baghaw, a pediatrician. I remain grateful to Karl for teaching me surgery and to Miriam for teaching me how to look after a monkey after surgery. Pribram was an excellent surgery teacher. At first, I would do the initial incision and final closure in an

operation. The next step was to do the first two procedures, and the final two closures, and so on, until I was doing the entire operation on my own. Sometimes we would operate on two monkeys simultaneously, with Karl at one end of the surgical table and with me at the other. If I wanted to ask a question, or needed help, he was available and gowned. Karl also knew and taught the thalamus. At the time the standard work on the monkey thalamus was Earl Walker's book *The Primate Thalamus* (1938). Karl would hold seminars in the lab or in his house, teaching major thalamic groups and their subdivisions. I also learned from Karl how to do careful reconstructions of a cortical lesion and the associated retrograde degeneration in the thalamus.

While at Stanford one of my old teachers, K.L. Chow came to join the neurology department. It was good to see him again. He took me and my wife to a local Chinese restaurant, saying that it served the best Peking duck he had eaten since he left Peking. Sadly, it had gone down from an A minus to a B plus on the night we ate there.

Seattle

It was time to look for a real job. I turned up three possibilities. One was to join one of the giant soft-money pyramids at Harvard Medical School, a second was to become an Assistant Professor of Psychology at Wesleyan University in Connecticut, and the third possibility was a joint appointment in physiology and psychology at Seattle. A happy choice, I opted for Seattle. The job was supported by a training grant held jointly by the two departments for a joint Ph.D. in physiology and psychology. The major force behind the plan was Theodore "Ted" Ruch, who had been Chairman of the Physiology Department at Seattle since the medical school was founded about 10 years earlier. Ruch had brought with him from Yale several of the promising young people to join him in the new department. Under Ruch's leadership it was generally rated as one of the best in the United States. Professor Ruch's brother, Floyd Ruch, was a psychologist, which may have influenced T.C. Ruch's view that the two sources of outstanding young physiologists were from psychology and physics, hence his enthusiasm for the joint program. Seattle is an attractive city, and the job was an attractive job. There were many applicants narrowed down to a short list of three. I have no illusions about the reason for my appointment. It seemed from late informal discussion after I was appointed that the two departments had opposite ratings of the three short-listed candidates. I was offered the job because I was not unacceptable to either department.

My responsibilities were to teach in both departments and to look after the students who were enrolled for the joint Ph.D. degree—a pleasure. The five students who were in place when I arrived were Ron Adkins, Harry Carlisle, Chris Davis, Joe Miller, and Gene Taylor. The physiology

department also had a grant for training post docs, many from psychology, to learn neurophysiology. In the first years I was at Seattle, the post docs were Bill Stebbins, Bob Reynolds, Dwight Sutton, and later Dick King. These were among the best years of my academic life. Each of us knew something different. Each of us came to Seattle with a strong wish to learn neurophysiology. We all got on well. Daily informal seminars in the bullpen knocking Skinner out of Bill Stebbins and a residual Freudianism out of me. The following year Karen (Greene) arrived from Brown University as a graduate student, and the next year her fiancé, later her husband, Mark Berkley joined the department as a post doc. Mark became one of my closest friends.

Seattle was a magnificent opportunity but paradoxically limiting. While at Cal Tech and Stanford I had haunted electronic surplus stores and built a most rudimentary physiological lab: an electronic stimulator, a restored old amplifier, and an oscilloscope from a Radio Shack kit. My aim was to do physiology as a hobby, perhaps studying the giant nerve cord of earthworms. My enthusiasm for physiology was dampened by the offer of state of the art equipment, with professional level stimulators, amplifiers, oscilloscopes, and a Grass camera. I stayed with my behavioral and, later, anatomical experiments.

I had only minimal knowledge of anatomy when I arrived. Seattle and its people taught me much more. Ide la Bossiere was a superb technician in the histology lab. She had been taught to do degeneration staining by Orville Smith, who was a fellow Assistant Professor. Orville taught me how to read Ide's Nauta-stained sections. My first attempt with the method was controversial. I had been aware from the old German literature that there might be a crossed thalamo-cortical pathway. Although thalamic projections were thought to be strictly to the ipsilateral cortex, there was some behavioral evidence that there might be a weak projection from the thalamus to the contralateral side of the brain by way of the corpus callosum. The existence of such a pathway would bear on the anatomical basis of interhemispheric transfer. My first attempt at using degeneration staining was to look for a crossed geniculo-cortical pathway. With Joe Miller who had become my graduate student, I made lesions in the geniculate of cats, waited an appropriate length of time, and with the help of Orville Smith, studied the distribution of degenerated fibers in the cerebral cortex. The results were surprising. Most striking, was the very widespread distribution of geniculo-cortical fibers on the ipsilateral side of the brain. We also found degenerating terminals at the border of V1 and V2 on the contralateral cortex. We published a note in *Science* on "The Lateral Geniculate Nucleus and Cerebral Cortex; Evidence for a Crossed Pathway" (Glickstein et al., 1964). The finding was questioned by another group; they attributed our findings to direct damage to the corpus callosum.

Although we had varied the trajectory of the injections to avoid the caudal corpus callosum, the widespread ipsilateral geniculo-cortical projections seemed of far more importance. Rather than pursue the argument, Dick King, Joe Miller, Mark Berkley, and I followed up the more striking features of our result. In addition to the expected projection to area 17, we saw a massive geniculate input to area 18 of Otsuka and Hassler, V2 of Hubel and Wiesel, and to the lateral suprasylvian cortex "The Clare-Bishop area" (Glickstein et al., 1967). The physiological implications of our anatomical findings seemed important. The dominant view of the way in which visual receptive fields are constructed was that neurons with simple receptive fields in V1 project to neurons with complex receptive fields in V2. But if geniculate cells have only center-surround receptive fields, and if there are no simple cells in V2, there had to be another way in which complex receptive fields are formed.

Some time later, Mark Berkley, Ellen Wolf, and I studied the problem in more detail. We published a study that the three of us were proud of, but which, we felt, nobody ever read. Mark and I had become close friends as well as colleagues. We enjoyed working together. As a part of our joint study of the geniculocortical projections in cats, Mark mapped gross evoked potentials to flash in several cats. Otsuka and Hassler (1962) had described the variations in the morphology of the cat visual cortical areas: their types I, II, III, and IV. The major distinction among them was the depth of the lateral fissure. In some cats, the fissure is represented as only a slight depression on the surface of the lateral gyrus. Bob Doty (1958) had earlier described a "high amplitude strip," a large evoked potential he recorded to flash on the surface of the lateral gyrus. Mark showed that the high-amplitude strip corresponds exactly to area 18 of Otsuka and Hassler. The highest amplitude evoked potentials are in area 18 not in area 17.

In other cats, we made a small stereotaxic lesion in the geniculate under sterile operative conditions. Several days after we made the lesion, we reanesthetized the cat, and Mark mapped the distribution of gross flash-evoked potentials on the cortex and then prepared the brain for studying degenerating fibers. I charted the distribution of degenerating fibers in the cortex. We worked independently on the physiology and the anatomy. We compared the two maps; my map of the degenerating fibers in area 18 and Mark's map of the "holes" in the expected gross potential to flash. The match was perfect. Where there were degenerated geniculo-cortical fibers in area 18, the high-amplitude response was abolished. In other experiments we showed that the high-amplitude response was unaffected if the corresponding region of area 17 was removed. Mark Berkley, Ellen Wolf, and I published the results in *Experimental Neurology* (Berkley et al., 1967), where it languished, unread and unloved except by its authors.

I had not abandoned my interest in interhemispheric transfer. With J. Secrist, I started to study whether more complex rules could

be transferred between the hemispheres as well as simple visual discriminations (Glickstein and Secrist, 1972). We studied interhemispheric transfer of a learning set. I first cut the optic chiasma in the midline. We trained the monkey with one eye open in a reversal learning set. The monkey learned to choose one of a pair of two-dimensional patterns. When he reached criterion, we reversed the value of the stimuli. The former positive cue, was now negative, and the animal was now at 0% correct. Eventually he relearned to choose the formerly negative cue. Once again, when he reached criterion we switched the value of the two patterns. Over time the monkey takes less and less time to reacquire the correct choice. Fully trained, he is almost always correct by the second try. He has learned a rule "win stay; lose shift." When the monkey was tested on the formerly closed eye, the learning set was immediately available. Either the set was present in the second hemisphere, or it could be accessed by way of the callosum. I cut the callosum after only a few trials, and the animal still knew the set when tested with the formerly closed eye. The evidence suggested that the learning set had been stored in both hemispheres.

Bill Stebbins had studied reaction time in rats while he was on the faculty of Hamilton College, before he came to Seattle. He had developed a simple and effective behavioral technique to teach rats to respond as quickly as possible to a stimulus as soon as it was presented. Monkeys could also be trained using Bill's methods. Joe Miller, Bill Stebbins, and I (Miller et al., 1966) added an additional rule to ensure rapid responses. We set an initially long time within which responses would be reinforced. If the monkey responded in a time that was shorter than the setting, it was rewarded. If it took longer than the preset time, it was not rewarded. After every trial the minimal time was shortened if it succeeded and lengthened if it failed to go as fast as required. We adjusted the ratio of increases and decreases, so that the monkey never quit working and never got into a lazy habit of accepting 50% reward. The monkeys performed the task rapidly to either light or sound stimuli. The same behavioral contingencies worked well for us humans in the same apparatus. Helped by Chuck Stevens, Joe Miller designed an optimal configuration for bipolar stimulation of a restricted region of the striate cortex. We placed a bipolar stimulating electrode permanently over foveal striate cortex in a monkey that had previously been trained to respond rapidly to the onset of a light. It took only three trials before the monkey would respond rapidly either to a light or to a short train of bipolar stimulation of visual cortex. We then tested systematically the latency of reaction time to lights of different intensities and to electrical stimulation at different current levels. At the shortest asymptotic speed of performance, stimulation of visual cortex gave us average reaction times that were about 40 milliseconds shorter than responses to light. The savings were about equal to the evoked latency of the light (Miller and Glickstein, 1964, 1967).

The lateral geniculate nucleus is prominently laminated in humans and the Old World primates. There are other animals in which the geniculate is also laminated but in which the input to the layers was unknown. The literature assured us that the large parvocellular mass of the squirrel monkey geniculate had only two layers. In an attempt to clarify the inputs, Bill Calvin, then a graduate student in the physiology department, and I made a unilateral enucleation of a squirrel monkey, waited for a year, and studied the resultant long-term transneuronal degeneration in the geniculate. Rather than a four-layered geniculate that had been postulated by previous authors, we found that the lamination is similar to the inputs in humans and the Old World primates. The contralateral eye projects to layers 1, 4, and 6; the ipsilateral eye projects to layers, 2, 3, and 5. Unlike humans and the Old World primates, there are no prominent interlaminar fiber layers within the parvocellular LGN. When we had this result, we heard that Bob Doty had done a similar experiment with the same conclusion, I wrote to him, suggesting that we publish the results jointly, which he agreed to do (Doty et al., 1966).

I did a similar study on the tree shrew, *Tupaia*, an animal that also has a prominently laminated geniculate (Glickstein, 1967). Like monkeys and humans, the individual laminae receive segregated input from the ipsilateral and contralateral eye. A puzzle presented itself, still unexplored. The tree shrew eye is placed far laterally in its head. Consistent with the Newton-Müller-Gudden principle, which states that it is the contralateral visual field that is represented in the geniculo-cortical pathway, the optic nerve arising from each retina is almost entirely crossed. There is very little overlap in the visual input from the two eyes, with only a tiny representation in the ipsilateral optic tract. But the territory occupied by the inputs from the left and the right eye are of roughly equivalent volume in the geniculate. There are, I believe, only two possible explanations for this apparent paradox. One possibility, which I do not believe, would be that there is massive convergence onto geniculate laminae from the contralateral eye and divergence from the ipsilateral eye. A more plausible explanation is that the geniculo-cortical pathway is virtually restricted in this animal to the representation of the binocular field.

I have always been blessed with technically skilled students. Erich Luschei had been an undergraduate in psychology at the University of Washington. Erich was accepted as a joint program graduate student, and he chose to work with me. At the time, Evarts had recently developed techniques for recording single unit activity in behaving monkeys. Erich developed a technique for single unit recording on his own. We set out to study the will. Erich found a two-channel tape recorder that would play backwards. He recorded a monkey's lever press on one channel and cell firing in the motor cortex in the other channel. With Bob Johnson, then a medical student, we studied performance in a reaction-time task. We could

tell whether the response of a given unit was more closely linked to the stimulus or to the response by summing unit responses forward in time from the stimulus or backward in time from the response. The results seemed promising. We published a short account of the work in *Nature* (Luschei et al., 1968).

At the time it seemed that it would be a straightforward task to track neural activity from primary sensory cortex to motor cortex by recording from structures along the way. We never got quite that far. What appeared to be the simplest of behavioral tasks is not so simple. In order to study the muscle activity in reaction time performance, we sanded our own arms to get low-resistance electromyograms (EMGs) from agonist and antagonist muscles. With Carol Saslow, we studied muscle potentials while we performed the same reaction time task. The task of withdrawing our arms from a telegraph key turned out to be a more complex act than we had envisaged. The first response we detected was a diminution in the activity of the major antagonist muscle. This was followed by a burst of activity in the agonist, which brought our arms and finger off the key. Finally, we recorded a braking activity in the antagonist muscle that slowed and then stopped the movement. There was an 80-millisecond spread from the first sign of the response to the final end of the movement. Thus, it was hard to relate individual cell activity to specific aspects of the movement (Luschei et al., 1967).

The Zoo Connection

Seattle had a modest-sized zoo. The zoo had an occasional problem. Animals are shown only if they are normal-appearing and in good physical health. In order to extend our study of the cortical representation of vision, Mark Berkley and I were able to study the visual cortex of large cats that were scheduled for killing by the zoo. We studied the morphology of the cortex in a leopard, jaguar, and a young lion. In all three, the brain was entirely cat-like. Where there is usually only a hint of a fissure in most domestic cats, there is a deep fissure on the lateral gyrus of the great cats.

The Other Faculty

T.C. Ruch was head of the physiology department, universally addressed as “professor” by all of us juniors in the department. When I first arrived in the Seattle department, I was scared. Here I was in one of the major physiology departments in the United States, and I knew very little physiology. Only a matter of time before they find me out. Within the first week of my arrival, T.C. Ruch suggested we go to have a coffee together. Here it is, I am done for! Now is when he finds me out. Rather than interrogate me on my knowledge of physiology, T.C. asked my opinion on woven wire vs. hardware cloth. “For what?” I bravely asked. “For monkey

cages." Ruch was ordering more cages, and his habit was to sound out his own ideas with a younger colleague. After a monolog on the advantages and disadvantages of the two types of cage, he changed the subject, and addressed me directly. "You don't know any physiology; don't worry, you will learn it here. We will start you as an assistant in the nurse's course. You will be lecturing in the medical school course in three years."

I have never known a more effective chairman. Entirely selfless, he worked for the good of his department. When an NIH study section was due to make a site visit, the visit was announced well in advance with the coda, "Don't let the presence of the site visitors interfere with any plans you may have made to do an experiment on that day." A typical Ruch three-line whip.

Ruch's chairmanship influenced the other members of the department to be supportive of one another. If you needed help in understanding a problem, designing apparatus or building equipment, the other members of the department were always ready to assist. In my second year at Seattle, Chuck Stevens arrived as an Assistant Professor. Much of my education in neurophysiology began with his help and his excellent *Primer of Neurophysiology*. Among the memorable colleagues was Art Brown. A converted physicist, Art is as intelligent as any colleague I ever knew and as skilled. He also set a high moral standard for the department. I remember when we were considering whether we should accept someone as a student who came with a reputation of being difficult, perhaps a political dissident. The sense of the department meeting was to adopt a vague "We don't have room" solution. Art was not having it. He insisted that if we reject someone for his politics, we must be explicit and tell him so. We accepted him, but he did not come.

When I first got to Seattle, the university was completing the construction of a Primate Center whose director was Professor Ruch. The dean of the medical school gave him an ultimatum, "You cannot manage two big jobs at once; physiology or the primate center, choose." Ruch chose the primate center, and he was succeeded in the Chair of Physiology by Harry Patton.

Pat was a marvelous lecturer. His lectures to the medical students were models of clarity. They were much more than that. Pat taught, among other things, the neurophysiology of reflexes. Not just what we know about spinal mechanisms but *how* we know. He taught physiology in a historical context. What was the sequence of experiments and clinical observations that led to current understanding? Pat was a major influence in my own thinking about how to teach.

Isolated in the northwest corner of the United States, we relied on one another for interaction. One of the best programs was the "Neurological Study Unit." Every 2 weeks a topic was selected that had both clinical and basic science relevance. A member of the clinical and of the

basic science departments would each present about a half-hour talk, followed by discussion. Through the Neurological Study Unit, I got to know some of the clinical problems and several of the outstanding people in the clinical departments.

One of my favorites was Elsworth (Buster) Alvord, the Professor of Neuropathology. We disagreed once on the interpretation of macular sparing after lesions of the visual cortex. The disagreements did not make us enemies but good colleagues. Alvord was a most helpful source of advice on how to deal with artifacts in histological sections, for example, how to get rid of an annoying reddish contaminant in our Nissl stains.

The Psychology Department

My appointment was as an Assistant Professor in two departments. As a member of the psychology department, I taught courses and seminars in my first years at the university. The psychology department was neither as successful nor as supportive as physiology, so I spent most of my time in the medical school. Shortly after I arrived in Seattle, the university appointed a new Chairman of the Psychology Department. His proposals for revising the structure of the department's teaching and hiring policy soon were vigorously opposed by two thirds of the members of the department. About a third of the members thought the new chairman's ideas were excellent and supported him. So did I. The administration listened to the complaints of the majority, and the chairman left.

I was put up for promotion to Associate Professor by the Physiology Department. By university rules, my promotion had to be supported by both departments. One of the members of the psychology department had been a physiological psychologist before becoming a dean many years ago. No longer the dean, he was back in the psychology department. In order to become familiar with current issues, he had taken my seminar on association cortex. When my name came up for promotion, I had unanimous support from the tenured members of the physiology department but not from psychology. I was opposed by the former dean on the grounds that my position was not needed, "What would he teach?" Happily, his influence was insufficient to block my promotion.

Ben Everett Buys My Other Half

I was put off by my experience in psychology. I was pleased when Ben Everett, the Chairman of the Anatomy Department, offered to take up the other half of my appointment. I cheerfully left the psychology department and devoted my full time to teaching and research in the medical school.

Seattle is set in one of the most beautiful regions of North America—paradise, but it rains a lot. Sometimes, even in midwinter,

the rain would stop. Very rarely, the sky would be completely clear. The mountains on all sides would become visible—the Cascades to the east, Mt. Baker to the north, “The Brothers” to the west in the Olympic Peninsula, and, best of all, Mt. Rainier would also appear in the southeast. On those rare winter days, we stopped work in the lab and went out on my little 19-foot sailboat to experience the joy of the place we lived in. The waters around Seattle are protected. Happy times with friends were when we took my sailboat up Puget Sound. A fine voyage with Bill Stebbins and Dwight Sutton, catching fish, anchoring in pleasant little harbors, and arguing about the brain.

The Move to Brown

My wife was unhappy in her job in Seattle and saw brighter prospects in the East. We had been married in 1955, when she was a resident in psychiatry and I was a graduate student. She had been following me through three successive places, so when the Brown University psychology department offered me a job, I accepted it. We moved from Seattle to Providence in 1967. Two of the people that I worked closely with in Seattle came with me. Ide La Bossiere was an outstanding histology technician. Erich Luschei was my graduate student. Both helped me set up a lab at Brown. One of the pleasant surprises was finding Ford Ebner in an adjacent building. Ford had studied interhemispheric transfer at Walter Reed with Ron Myers. Ford was a fine colleague and has remained a close friend. Brown had a collection of excellent undergraduate students, several of whom worked with me in my lab or assisted in a tutorial course. Dennis Butcher studied reaction time and Barbara Brown studied finger use in monkeys with cerebellar lesions.

Lorrin Riggs and the Vision Group

My closest colleagues in the Brown Psychology Department were in the vision group: Lorrin Riggs, Dean Yaeger, and our students. Two of Lorrin Riggs’ students, Mark Hollins and Kay Fite, spent a postdoctoral year with me. Sylvia Thorpe, Dean Yaeger’s student, worked with me on a translation of Cajal’s monograph on the retina (Cajal, 1972). Lorrin Riggs is the best professor I have ever known. A quiet scholar, he had made fundamental discoveries on vision and on its relation to eye movements. Lorrin was also a superb teacher, not as a lecturer but as a guide for younger people. Under his care, average students became good scientists. Excellent graduate students became outstanding scientists. Lorrin’s students and post docs loved him rather than liked him. He was kind in his dealings with others, but somehow managed to remain incisive and clear in his scientific judgments. When a new student arrived, a typical scene would ensue. Most had been

excellent undergraduates, and most talked fast. In their first interview with Professor Riggs, they would often ask him a question. Lorrin never shot from the hip. If you asked him a question, he thought about your question. While he was thinking he did not say anything. The student would then fill the silence by asking him another question. Lorrin would now think about that question. Aware of the danger, older students began to give new students advice on how to proceed. If you ask Lorrin a question, wait! He would answer it, but only after he has thought about it.

Retinoscopy and Eye Size

With Ide La Bossiere, I continued to add to a collection of sections of eyes and brains that I had started in Seattle. The collection of eyes proved useful for solving a puzzle in interpreting the literature on refraction in animals. Every week or so Lorrin, Dean Yager, and I and our students would have an informal vision lunch, where we would discuss vision, sports cars, or anything else. One of Lorrin's students, Ross Beauchamp, was using the retinoscope for refraction. Ross raised the question in the vision lunch, "What would the consequences be if the moving shadow seen in the retinoscope were to be reflected from a layer other than the receptors?" No one knew. Because retinas are thin, it did not seem to matter much. It does. To a good approximation, all mammalian retinas are about the same thickness. Myotis, the little brown bat, whales, and elephant's eyes are vastly different in volume, but the retinas are about the same thickness. The retina of the baleen whale, *Ballaenoptera physalis* is more than 15,000 times the volume of the bat eye, but the retina of each is about a quarter of a millimeter in thickness. Because the retina has a roughly constant thickness in all mammals, the error in retinoscopy can be calculated for a simplified eye. The dioptric power of a simplified eye is equal to one over the square of the focal length times the refractive index: $D = uf^{-1}$. Differentiating this equation: $dD/df = -uf^{-2}$. Thus, the error in diopters should be proportional to the inverse square of the focal length of the eye. Michel Millodot, who was a graduate student with Lorrin at the time, and I began to assemble published data from the literature and to refract the eyes of various creatures. We plotted measured refractive state against corneo-retinal length. The plot in log-log coordinates is linear with a slope of -2 , suggesting that the argument about a possible source of error in the measured refractive state was correct. We could now calculate where the reflection comes from. We concluded that the shadow seen in retinoscopy is due to a specular reflection from the retina-vitreous surface. Contrary to the literature, rats are not 7 diopters hypermetropic, and rabbits are not 2 diopters hypermetropic. Both are probably emmetropes. We published the results in *Science* (Glickstein and Millodot, 1970).

Paul Yakovlev's Lesson

When I was still at the University of Washington, I heard a lecture by Paul Yakovlev, then Professor of Neuropathology at Harvard. Now that I lived nearby, only an hour's drive from Boston, I boldly telephoned Professor Yakovlev with an unusual request. I had read Yakovlev's papers on brain control of movement. They seemed original and imaginative, but I was not sure I understood them fully, so I phoned to ask him if I might visit and have a tutorial with him on his ideas about the nature of brain control of movement. He agreed. After a splendid, 2-hour lesson, I asked if I could give him a present in return for his teaching. He asked what I had in mind. I had in mind to give him a set of slides for his collection of comparative brain material. He sniffed at my offer of a monkey brain but accepted my suggestion that I give him a set of seal brain sections. He praised the beauty of the cell stains but sniffed at the fiber stains. He said "I will put in collection and label Glickstein contribution."

Corticopontine Projection

We had identified several parallel independent cortical targets of the lateral geniculate in cats. The projection from the geniculate to V2, area 18, is as dense as the projection to V1. Lesions of V1 do not abolish the photic evoked response to flash on V2. V1 and V2 are in parallel not in series. Why? We speculated that one of the two areas might be involved in the processing of visual form, the other movement. Because cells in V2 are particularly sensitive to moving targets, this area might play a role in movement detection, possibly regulating the cat's own movements—either locomotion or independent use of the limbs. If this were so, a logical target for fibers that arise from cells in V2 would be the cerebellum. Projections from the cerebral cortex to the cerebellum relay in the pontine nuclei, so we set out to study the differential projection of V1 and V2 to the pons. We made lesions in area V1 or V2 and plotted the resultant degeneration in the pontine nuclei. We found a heavy projection from V2 to the pons. In our initial studies we failed to see a projection from V1. (Glickstein et al., 1972). As Per Brodal later pointed out, there is also a corticopontine projection from V1 but much weaker than that from V2.

Some years later with Janet Cohen, Bryan Dixon, Alan Gibson, Mark Hollins, Ide La Bossiere, and Ric Robinson (Glickstein et al., 1980), I studied the pontine projection from striate and prestriate visual areas in monkeys using degeneration and orthograde tracing techniques and, later, with Jack May and Barbara Mercier using retrograde tracing (Glickstein et al., 1985). There are great differences in the extent of corticopontine projections among the monkey cortical visual areas. Cells in the

dorsolateral area 17, the primary visual cortex, and cells in the inferotemporal areas did not appear to send fibers to the pons. The massive visual projection arises from dorsal extrastriate areas, beginning in area MT (V5 of Zeki) and including MST and the LIP and the adjacent visual areas in the parietal lobe. Jack May and I summarized the differences in the projections from extrastriate areas (Glickstein and May, 1982). We suggested that the medial, parietal-centered areas probably serve in the visual control of movement, and the temporal areas serve in the analysis of color and form. In the same year, Leslie Ungerleider and Mort Mishkin (1982) proposed a similar dichotomy among extrastriate visual areas, suggesting that the ventral areas are involved in identifying objects and the dorsal areas in registering their location. Some years later, Mel Goodale and David Milner proposed a distinction rather more similar to the one that Jack May and I had suggested (1992).

Oxford 1970–1971

Around 1970, my marriage began to break up. In order to help get over the attendant depression, I decided to work abroad for a year. I had written to David Whitteridge when he was Professor of Physiology in Edinburgh some years earlier. In 1970, he was now Professor of Physiology at Oxford. Why Whitteridge? I became aware of Whitteridge's scientific work from a footnote in the 1960 Freiburg symposium on Physiology and Psychophysics of Vision (Jung and Kornhuber, 1962). Doty had questioned the evidence for accurate spatial mapping of the visual fields on the primary visual cortex of cats. Whitteridge disagreed. In a footnote in the proceedings, Doty wrote that Professor Whitteridge had invited him to stop in Edinburgh on his way back to the United States, "... where we put the question to two cats. I must say that Professor Whitteridge had the better of the argument." Oxford seemed as if it would be a good place to work. It was. Whitteridge wrote, agreeing that I might visit him on my way home from a meeting that I had attended in Slovakia. I arrived in England and stayed with John Sundsten, an old friend from Seattle who was on sabbatical leave working in Bristol. I phoned Professor Whitteridge to arrange my visit. He said "I am absolutely up to my eyebrows in examinations, and I must go to St. Andrew's on Tuesday; I can give you only one hour." I suggested that he was obviously much too busy, so we might make it another time. He replied; "No, No, No, you must come." John Sundsten and I drove across southern England in a fierce rain storm to Oxford where I was ushered in to the presence of the professor. Whitteridge began, "What do you want?" I replied that I had come to see his lab. He said "I haven't got a lab" whereupon I got up to go. Realizing that he had gone a bit too far he said, "What have you been doing?" We began to discuss the eye, and he showed me some beautiful pictures of the retina that had been published nearly

100 years earlier by Lindsay Johnson. Whitteridge had recently arranged to have several republished. Two hours into the visit he said, "Actually, I have got a lab. Let's go and have a look at it." And then "Will you need money?" I reassured him that I had an NIH fellowship. After that peculiar beginning, we went from being good colleagues to closest friends. I miss him still. When I am near Oxford, my first thought is often to visit David—alas no longer possible.

I determined that I would start to work right away when I arrived in Oxford. So I packed and shipped two trunkfuls of lab equipment weeks before I left the States. My aim was to start working within a day or two of my arrival. I came with two possible plans for research. One was to record the receptive field of single cells in V2 before and after I had removed area V1. The other possibility was to see if I could record visually driven cells in the pontine nuclei.

The first try was a disaster. Whitteridge suggested that I work with a medical student on the first problem. We studied the receptive fields of cells in V2 cells after I had made a lesion in V1. The relationship between the student and me did not work. Eager for a discovery, as we recorded from cells in area V2, he said that he thought that the surround mechanism of the cells was now absent or weak. I did not agree. When he wrote that alleged observation in our lab book, I pointed out that a year from now he would believe what he had written, so I would write "I didn't see this" and sign it. Clearly not a recipe for a fruitful collaboration. The alleged dependence of V2 on an input from V1 came back to haunt me a year later when I spoke informally to some of Steve Chorover's graduate students at MIT after I returned to the States. I began my talk by saying, "It's not clear what the influence of V1 is on the receptive fields of cells in V2." "Oh yes it is! V1 provides the surround mechanism for the receptive fields of cells in V2." "Fascinating," I said, "Whose lab is that from?" "Whitteridge's lab," they chorused. I pointed out that they might be telling me about my own research. The conclusion had been put forward in a talk the student gave at Cambridge and further simplified when it was discussed by another colleague from Cambridge visiting MIT. I still do not know the answer to the question of whether the input from V1 influences the response of cells in V2 of the cat.

That collaboration did not work. Professor Whitteridge knocked on another door, that of John Stein, recently appointed medical tutor at Magdalen College, and said, "You two might have something to discuss." We did. We still do. It was a happy collaboration. One or two days a week we would prepare a recording experiment all day, and record unit activity in the pons all night. In the morning, we would go around to John's house for breakfast. At first we turned up nothing; no visually driven cells. We modified our procedure. John had previously studied the larynx and

knew how to remove it in an acute anesthetized animal in a terminal experiment. We worked with a supine preparation in which the larynx had been removed. We drilled through the bones overlying the brainstem and put a bit of graph paper next to the basilar artery for informal coordinates. During the first months of our collaboration, nothing worked. I encouraged John to give it up. He always pushed for one more go. One night, around midnight, we drove a cell visually. That was good enough news. Better yet, Professor Whitteridge was still in his office, so we could fetch him. David waved one of his wands with a black rectangle at the end, and he too drove our cell. Fantastic night. At the time we recorded results from experiments on long strips of positive photographic 35-mm film in a Grass camera. In order to dry the film we hung it from a wire on the top floor of the physiology building. The next morning, everyone could see that we had a visually driven cell.

I was introduced to the Physiological Society that year. Rather a solemn vote followed each oral presentation: "Is it the wish of the society that this abstract be published?" The audience votes as a committee of the whole. When John Stein and I reported our findings of visual cells in the pontine nuclei in a region that receives its input from the visual cortex, the audience approved its publication. However, one of the older members stipulated that, instead of the single word "Results," "Provided he will say, the combined anatomical and physiological results..."

In addition to David Whitteridge and John Stein, there were a number of other colleagues who went out of their way to be friendly to me during my year at Oxford. One of those people was Austin, now Abbie Hughes. Austin and his wife invited me to their house for dinner and took me sightseeing to Marlborough and Stonehenge on a weekend. Two of the most active people working in the physiology department were Guy Goodwin and Ian McCloskey. Guy was a graduate student with Peter Matthews; Ian was a fellow of Pembroke College. At the time, it was holy writ that muscle spindles act only in a servo-circuit. We are unaware of their output. Guy and Ian did a number of exquisitely simple experiments to challenge that conclusion. We are indeed aware of the output of spindles. They vibrated a flexor muscle on the upper arm. Subjects (including me) reported that they felt that their arm was extending at the elbow, as if the muscle had been stretched. They did several control experiments to validate their conclusion and proceeded to replicate and show the shortcomings of earlier studies that had allegedly provided proof that we are unaware of the output of spindles. Peter Matthews was Guy's lab sponsor. Peter is an outstanding scientist and scholar. Skeptical of the conclusions at first, he was finally persuaded by the evidence. One of the best lectures that I ever attended was one given by Peter at a meeting at Oxford. Without using slides, he demonstrated the key experiments on a semihostile witness. Giles Brindley had been one of

the principle exponents of the silent spindle, but he would not lie. If he felt a limb move, he reported that he felt it move. It was a magnificent session. Evidence counts.

Oxford teaches its undergraduates very well. All of the undergraduates had a tutor responsible for their education. All had tutorial sessions each week in which the focus was not on what the tutor said or wrote but what the student had written. I took the Oxford style of tutorial teaching with me back to Brown and taught with tutorials as best I could manage when I returned.

Back at Brown

I came back to Brown with enthusiasm and an eagerness to get back to work. Within a week or two of my return, Alan Gibson turned up, recommended to me by Mike Gazzaniga, who had been his Ph.D. supervisor. About the same time, Jim Baker arrived as a graduate student, recommended by Mark Berkley. One such student or post doc would have been a gift. Two were wonderful. Alan and Jim were both highly intelligent and technically gifted. I have never met a more effective lab person than Alan or as bright a new graduate student as Jim Baker. My research at the time was adequately funded, and it allowed for a one-twelfth time appointment so that John Stein could spend summers in the lab. Our plan was to record and characterize the receptive fields of pontine visual cells. John and I had found them at Oxford. We knew they were there, but we knew very little about their response properties. Our aim was to learn the nature of the visual information that is sent to the cerebellum. With Alan Gibson and Jim Baker, we set about recording from a large number of visual pontine cells. One fortunate fact was that Jim McIlwain was a next-door neighbor in the physiology department. Jim McIlwain had produced an accurate map of the representation of the visual field on the surface of the superior colliculus of cats. Our preparations were set up for recording of visual receptive fields. We would first establish the locus of the blind spot and other retinal details on a back projection screen. The visual cells in the pons are about 25 mm below the surface of the cerebral cortex. Even a slight error can lead to missing them in the pontine nuclei. It was Alan's insight that we stop the electrode at the surface of the colliculus and record the position in the visual field of the responding neurons. Thus, we had a way station about halfway down to the pons where we could confirm the trajectory of an electrode. If we were in the wrong place, we withdrew the electrode and used McIlwain's map to correct the stereotaxic placement. We always found visual pontine cells by the second penetration. Over time we were able to record and characterize the receptive fields of several hundred pontine visual cells. At first, we tried to drive pontine visual cells with stationary or moving bars and edges. They would fire but grudgingly.

The insight came when one of us walked in front of the preparation and the cell from which we were recording fired at a very high rate. We found that the editorial page of the *Providence Journal* also was an effective stimulus. Most pontine visual cells respond best to large, textured fields, at a preferred speed, moving in a preferred direction (Baker et al., 1976).

In addition to a cortical visual input, visual information is also relayed to the cerebellum by way of the superior colliculus. George Mower, another gifted graduate student, joined the lab in the following year. With George, we studied the target of collicular originating axons in the pontine nuclei and the response properties of pontine visual cells that are activated from the colliculus (Mower et al., 1980).

Pontine visual receptive fields differ from those of cells in the cerebral cortex. One problem that we addressed was the nature of the receptive field of cortical cells that provide an input to the pontine nuclei. The group at Penn had pioneered this approach, studying the properties of neurons in area 17 of cats that project to the superior colliculus. The technique was demanding and slow: electrically stimulating axon terminals in the colliculus and recording from antidromically activated cells in the cortex. One of the difficulties with the procedure is that you may not activate an antidromically driven cell on every penetration. Alan Gibson's technical skills gave us the results we looked for in a reasonably short time. Alan devised a four-electrode fork that we advanced through the cortex. The apparatus cycled, recording from each of the four electrodes in turn as we stimulated the pons. Our yield of antidromically activated cells increased almost fourfold. We recorded the receptive field properties of a number of cells in area 18 and the lateral suprasylvian areas whose axons project to the pons. Deep in lamina V, these cells have receptive fields that are entirely different from those that had been reported for cells in more superficial laminae (Gibson et al., 1978).

Joan Baizer, another typically bright graduate student, came to Brown from an undergraduate degree at Bryn Mawr. Joan joined me in studying the effects of cerebellar lesions on prism adaptation. If a laterally displacing prism is placed in front of the eyes, monkeys and people mispoint at first. After a few misses, they become accurate. When the prism is removed, they mispoint in the opposite direction. Charles Harris had argued convincingly that adaptation to a laterally displacing prism is not visual but probably involves recalibration of the position of a limb. The anatomical and physiological properties of the visual input to the cerebellum suggested that it would be a logical locus for such recalibration. Joan's monkeys viewed an array of lights through one eye and reached out rapidly to close a switch under the light. A laterally displacing prism was then placed in front of the eye. In the animal with a large unilateral lesion of the cerebellar hemisphere, prism adaptation was abolished on the side of the lesion (Baizer et al., 1999). The experiments had been done when Joan was a

graduate student at Brown. At the time the results were puzzling, because there seemed to be no obvious reason why some cerebellar lesions affected prism adaptation while others did not. Later, when I studied the visual input to the cerebellum, the explanation seemed clear. It seemed most likely that the cerebellar region in which the lesion was effective in abolishing the adaptation is coextensive with the major target of visual information that is relayed via the pons from the cerebral cortex.

We tested these same animals in other tasks. Barbara Brown was an undergraduate at Brown. She observed the same monkeys in a device similar to one that had been devised by Kuypers and his students for studying finger use. In the animal with the largest cerebellar lesion, the animal was unable to appose index finger and thumb. The entire hand was used as a scoop in picking up a raisin from the wells.

Joan Baizer and Barbara Brown joined me in teaching my undergraduate course. Labeled "Mind and Brain" it was historically based, with all of the assignments were to the original literature. We divided the class into three, and each of us tutored one third of the class about a third of the time. Thus, I could teach each student individually or in pairs for about one third of the time during the term.

On one of my visits to Oxford, I met Lydia Sinclair. She joined me in Providence in 1974. Lydia had been training as a solicitor. In the early part of 1975 she went back to complete her articulated clerk requirements to qualify as a solicitor. I joined Lydia for the spring term in 1975. Geoff Raisman and Pauline Field had moved to a Medical Research Council Lab at Mill Hill in the north of London, and Geoff kindly gave me a desk where I began to write a textbook, sharing my office with the laboratory pet, a rainbow boa constrictor.

The work continued in my lab while I was away. When I returned, I had two more excellent graduate students, Farrel (Ric) Robinson and Jack May. Ric began the task of sorting out the differential projection from cortex and colliculus to the cerebellum of cats in order to identify the cerebellar targets of visually active pontine cells. He would label a visual region of cerebral cortex with a radioactive tracer and later inject a retrograde tracer into one or another region of the cerebellar cortex. He could thus identify those retrogradely labeled pontine cells that receive a visual input. One of the major cerebellar targets of visual information is the paraflocculus (Robinson et al., 1984).

The visual information to the cerebellum in monkeys arises from the dorsal stream; the extrastriate visual areas that include the angular gyrus of the parietal lobe. Jack May, Susan Buchbinder, another Brown undergraduate, and I studied the effects of lesions of these cortical areas and compared the effects to those caused by equivalent-sized lesions in inferotemporal cortex. There is a complete dissociation in the effects of lesions. As others had discovered, temporal lobe lesions produce severe

deficits in visual discrimination learning. They are without effect on skilled use of the wrist and fingers under visual guidance. The parietal lobe lesions produced the reverse effect; a severe deficit in visuomotor control without impairing visual discrimination learning (Glickstein et al., 1997).

The Offer from MRC; Leave of Absence

Training as a solicitor in England is different from that of an American lawyer. Graduates of a university in any subject can become qualified solicitors by passing a series of difficult law exams and apprenticing—in Lydia's case for 2 years—as an articulated clerk. In the spring of 1980, I was offered a position with a Medical Research Council Group on the Neural Mechanisms of Behaviour, based at University College London, headed by Ian Steele-Russell. Lydia and I moved to England to try it out. My salary with the MRC was about half of the one that I had earned at Brown, and housing cost more in London than it did in Providence. But the advantages were great. Our research budget in the lab was negotiated on a 5-year basis—no grant applications. Loosely attached to University College, I had the advantages of an academic position, with fewer responsibilities. I liked the first year, so I asked Brown University to extend my leave of absence for another year. I still liked it. Lydia was close to becoming a fully qualified solicitor, so we decided to stay. I asked Russ Church, then Chairman of the Psychology Department at Brown, "How do you resign?" He replied, "A single sentence will do; two if you wish to soften the blow."

In England, I was once again fortunate in the people that worked with me. Barbara Mercier had moved to a town near London from Oxford, where she had been employed as a lab technician. Skilled and intelligent, I hired her as a histology technician, and she went on to do independent work with me. Graduate degree programs are different in England from those in America. In America, there are usually taught courses, with exams to pass as well as a thesis to write. In England, Ph.D.s are usually research degrees. Students are given lab facilities and are expected to turn up a thesis in 3 years. In order to be allowed to register for an advanced degree, students usually need to have a first or upper second class honors degree in a related subject. Barbara had technical qualifications but did not have an undergraduate degree. She was allowed to work for a Ph.D. after she passed written and oral exams to confirm that she had an equivalent knowledge of neuroscience as someone with a degree in the subject. Barbara did a beautiful study of the differential projection from the rat barrel fields to the pontine nuclei and the basal ganglia (Mercier et al., 1990). Corticopontine cells that arise from the barrel fields are all located in lamina Vb. Cells projecting to the basal ganglia are located in lamina Va. We suspected but did not prove that there is a thin sublamina at the border of Va and Vb whose cells bifurcate to project to both targets.

A few years after I arrived, the Medical Research Council decided to discontinue our unit. There were several options open to the Council for dealing with its employees when a unit closes. One possibility would be to transfer them to another unit. But that was a nonstarter, because ours was the only one specializing in brain and behavior. The other option was for me to negotiate an academic position, and the MRC would continue to pay my salary until I retired. Chris Yeo, my colleague in the Neural Mechanisms of Behaviour Unit, and I both asked if we could stay on at University College. The chairman of Anatomy, Geoff Burnstock, and the provost of the college, Sir James Lighthill, agreed. There was a typical complexity in my actually being appointed. The University of London is a semifictitious organization that nominally includes nearly all the institutions of higher learning in the London area. University College is the oldest of these and it is, in fact, fiercely independent, but at the time, all senior appointments had to be approved by a university-wide committee of academics. The appointment procedure went through several silly steps. When the form was first sent to Senate House, where the committees meet, the word came back that I could not be appointed Professor of Neuroscience because I was not a recognized teacher in the University of London. The next proposal was that I be appointed a recognized teacher. This was bounced because I was at the time a visiting professor, and there was a statute against appointing visiting professors as recognized teachers. The College changed my status within UCL to that of Senior Fellow. Now, at last, I was a recognized teacher. But when the proposal to appoint me to a professorship was sent, it too was rejected because there were no funds to support such a chair, "What if he were to be hit by a bus?" There was, however, a consolation; "You might choose to convey upon him the *title* of Professor of Neuroscience." This was done. The whole procedure took only a couple of years.

When the MRC closed the unit, Barbara Mercier chose to accept the redundancy payment offered by the Council and find a job closer to her home in Kent, avoiding a long daily commute. Chris Yeo and I had MRC grant support, and I had a position vacant for a technician. Ines Hans applied. Ines had a degree in veterinary medicine from Zagreb. She was married to a British citizen and had come to live in London. Initially, Ines had a job in a veterinary practice. She applied for a position with me to try new things. Ines worked with me for some 12 years, initially as a technician. An intelligent and highly skilled lab person, Ines was accepted as a graduate student at UCL. Together with Dutch colleagues and John Stein, we studied ponto-cerebellar pathways in monkeys (Glickstein et al., 1994). For her doctoral thesis, Ines studied behavioral and anatomical organization of the rat barrel fields. One of the problems we studied was the organization of cortico-pontine fibers within the cerebral peduncles. We found a precise arrangement of the fibers within the peduncle at the level of the midbrain. Fibers from the temporal and occipital lobes travel in

the dorsolateral portion of the peduncles. Frontal lobe fibers travel in the ventromedial portion of the peduncles. Somatosensory fibers travel in the middle (Glickstein et al., 1992). With Charles Legg, who spent a sabbatical year in my lab, and Elisabetta Vaudano, who spent a year with me while completing her doctoral degree in Torino, we studied the distribution of cortico-pontine cells in the rat (Legg et al., 1989; Vaudano et al., 1991). In monkeys, only about half of the cerebral cortex sends a major input to the pontine nuclei. There is only minimal input from occipital, inferotemporal, and part of prefrontal cortex. In rats, all of the cerebral cortex projects to the pons. Like monkeys, however, the heaviest cortico-pontine projections arise from the motor areas of the cortex.

One of my duties at University College had been to organize an undergraduate degree program in neuroscience. In British universities, undergraduate courses are typically more specialized than they are in America. The usual degree course is only for 3 rather than 4 years, and there is seldom any requirement for distribution. But neuroscience is of its essence multidisciplinary, and I was asked by my chairman in the anatomy department to try to organize an undergraduate course covering the broad field of neuroscience. The course was jointly offered by five departments including zoology, physiology, pharmacology, and psychology as well as anatomy. In Britain, admission to an undergraduate course is like graduate admissions in the States. Each course admits its own students rather than a blanket admission to the university. Our first intake for the B.Sc. Neuroscience course was seven students: five from Britain and two from Greece. Another tradition in British universities is that students often stay on to do graduate work in the same university in which they did their undergraduate course. Ned Jenkinson was one of the seven of our first undergraduates. He asked to stay on and work for a Ph.D. in my lab. I was happy to agree.

Chris Yeo and Rabbit NMR

In addition to Ian Steele-Russell, the other senior researcher in the lab was Chris Yeo. Chris had a Ph.D. degree from Queen Mary University, where he had studied interocular transfer of conditioning in fish. He had come to the MRC unit before me, interested in mammalian learning. About the time I arrived in the unit, Dick Thompson reported the effects of cerebellectomy on conditioned nictitating membrane in the rabbit. A previously conditioned response was abolished after cerebellar lesions. Chris Yeo, Merv Hardiman, and I began to study the neuronal circuitry involved. We made small lesions in one or another cerebellar nuclei. We found a zone in the lateral anterior interpositus and adjacent medial dentate nucleus, in which lesions prevented acquisition of the conditioned nictitating membrane response (Yeo et al., 1985a). Chris went on to identify the associated hemispheric lobule VI as the focal area (Yeo et al., 1985b), and the effects

of olivary lesions (Yeo et al., 1986). The pattern of retrograde degeneration in the inferior olivary following HVI lesions was consistent with a circuit through the same region of the cerebellar nuclei (Yeo et al., 1985c). Since that time Chris has gone on to analyze further the critical circuitry and the effects of temporary blocking of structures in that circuit.

Barrel Field to Cerebellum in the Rat

With Barbara Mercier, I had studied the projections of the barrel field layer V neurons to the pontine nuclei in rats. Ned Jenkinson, who was one of the first University College neuroscience students, joined me as a graduate student. Ned trained rats to run down an alley in the dark, observing them through a night vision scope. Rats will jump a gap of 16 cm in the dark, a distance at which they can just reach the platform on the other side of the gap with their whiskers. If they cannot feel the distant platform, they refuse to jump. If they are trained in the light, so that they see the distant platform, they will attempt a much longer jump. Ned and I made small unilateral lesions in the cerebral peduncles of rats that had been trained in the dark as well as in the light. The lesion interrupted the input to the pons, hence to the cerebellum from one or another area of the cerebral cortex. If we cut the middle portion of the peduncles, blocking the connection from barrel field, and shaved the whiskers on the side with intact connection to the pons, rats behaved as if they had lost both sets of whiskers. They would refuse to jump, even though they could reach the distant platform with the surviving whiskers. If we spared the whiskers with intact connection to the pons, the rats continued to jump. In all cases, rats would jump much greater distances in the light (Jenkinson and Glickstein, 2000).

Jan Voogd and History

When I first came to live in London, one of the people I most wanted to meet and talk with was Jan Voogd, who was then living and working in Leiden. Jan had made one of the major discoveries about the structure of the cerebellum and its connections. He found that the cerebellar cortex is divided into long, parasagittal stripes that constitute a fundamental unit of the cerebellum. The stripes are parasagittally oriented in the vermis and bend outward in the hemispheres, always at 90 degrees to the course of the cerebellar folia. Jan Voogd has since become a good friend as well as colleague. We share an interest in the comparative anatomy of the cerebellum. We have collaborated in anatomical as well as historical studies. We wrote on the contributions of the Dutch anatomist, Lodewijk Bolk, to our understanding of the comparative anatomy of the cerebellum (Glickstein and Voogd, 1995).

Inouye; Manfred Fahle

The Japanese ophthalmologist, Tatsuji Inouye, was a physician attached to the Japanese army during the 1904–1905 Russo-Japanese war. His clinical responsibility was to assess the degree of visual damage to soldiers caused by gunshot injury. Inouye took the opportunity to study in detail the visual field deficits caused by gunshot wounds of the occipital lobe. The work was published in German in 1909. I had earlier written about Inouye's work with David Whitteridge (Glickstein and Whitteridge, 1987). I published a translation of the entire monograph with Manfred Fahle some years later (Inouye, 1909, translated by Glickstein and Fahle, *Brain*, 2000).

Visiting Parma

In 1983 Giacomo Rizzolatti invited me to come to Parma as *Professore a contratto*. I gladly accepted. The visit began an enthusiasm for Italy, which I still maintain. Some of the most fun I had when I was working in Parma was to study with Giacomo the life of Francesco Gennari, the first person to identify the nonhomogeneous structure of the human cerebral cortex. From the library in Parma, Rizzolatti and I had a copy of Gennari's monograph. From a local history book, I found that Gennari had come from Mattaleto, a tiny village about 25 kilometers from Parma. I phoned the priest at Mattaleto, who gave me access to the church archives, stretching back to the 16th century. The priest was very helpful, but he found it hard to believe that anyone of any importance could have come from his tiny village. In the church archives I found a record of Gennari's birth as well as the marriage record of his parents. Giacomo Rizzolatti and I published a short article about Gennari in *TINS* (Glickstein and Rizzolatti, 1984), and I incorporated some of our findings into an article in *Scientific American* on the discovery of the visual cortex (Glickstein, 1988).

I have been a visitor to several other labs in northern Italy. In Verona, with Giovanni Berlucchi, and Torino, with Piergiorgio Strata. I love the language, the people, and the food. It was, however, a severe setback to my self-confidence when my teacher in an Italian class at University College, Laura, refused to let me get by with an infinitive whenever a verb was needed independent of its tense.

Weizmann Institute

Yadin Dudai invited me to visit the Weizmann institute in Rehovot, Israel. There I met Shabtai Barash, who soon became a colleague and friend. Shabtai had a long-standing collaboration with Peter Thier in Tübingen, which began when they both were post docs in Richard Andersen's lab at MIT. Shabtai had been studying saccadic adaptation. If a person or monkey

looks at a fixation target and shifts to look at a new target as soon as it appears, they are highly accurate. If the target is shifted as soon as the eyes begin to move, the saccade is inaccurate. Within a single session, the amplitude of the saccade changes. If, for example, a target comes on at 15 degrees to the right along the horizontal meridian but then is shifted to 20 degrees when the eyes begin to move, monkeys and people compensate by increasing the amplitude of the saccade over time. In collaboration with Peter Thier, Shabtai and I made lesions in the oculomotor vermis of two monkeys that had been trained in the saccadic adaptation task. Despite extensive postoperative training, there was no recovery of the ability of the monkey to adapt to the altered position of the target (Barash et al., 1999).

A Few Conclusions

My research on cortico-cerebellar circuits makes me skeptical about the current emphasis in systems neuroscience on cortico-cortical circuits. Cells in each layer of cortex have powerful differences in their properties. The cortex is often best understood in terms of its subcortical connections.

My early academic history makes me sympathetic to people that experience a bad patch in their studies. I was lucky in the fact that I had sisters and that there were institutions that helped me recover. Some are less fortunate.

Despite the great variability in how they do it, all of the universities, public and private, American and foreign, at their best share in certain underlying principles. The solution to problems and disagreements is based on evidence. They are, and should remain, institutions where teachers are free to pursue their studies, and students are free to explore. I love the international character of scholarship, and science in particular. Knowledge is without boundaries, and friendships can be formed among the most distant of colleagues.

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