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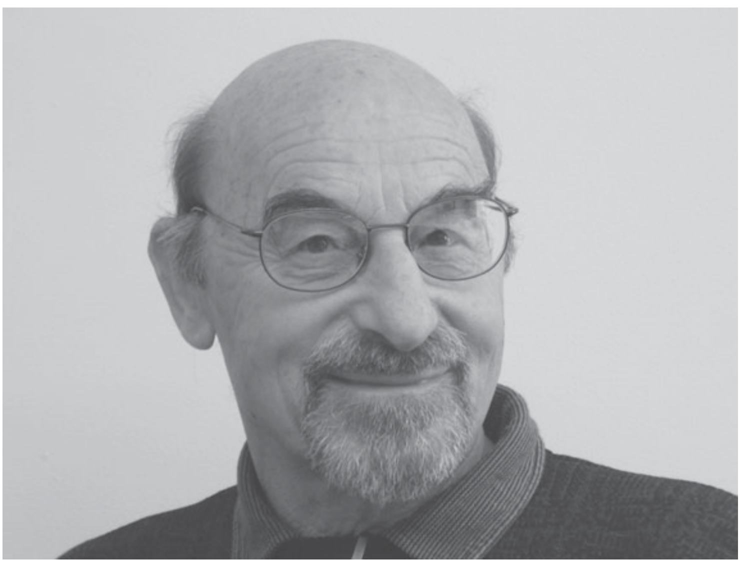

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Peter H. Schiller, in collaboration with numerous investigators, has carried out research using psychophysical methods, single-cell recordings, microstimulation, and pharmacological manipulations. The research has examined (1) the neural underpinnings of visual illusions and visual masking, (2) retrograde amnesia, (3) the neural control of eye movements, (4) the functions of the midget and parasol systems that originate in the retina, (5) the functions of the ON and OFF channels of the retina, and (6) the functions of extrastriate areas in visual processing. Studies at the present time are engaged in assessing the feasibility of creating a prosthetic device for the blind based on electrical stimulation of area V1 and in specifying the neural mechanisms that underlie depth processing.

Peter H. Schiller

Beginnings

In the early 1930s my father and my mother moved to Berlin, Germany, from Budapest, Hungary, because my father had obtained a fellowship to work with Wolfgang Köhler, an eminent Gestalt psychologist, who at that time was head of the Psychological Institute at the University of Berlin.

I was born in Berlin in 1931 and lived there during the first 2 years of my life. It was only natural, therefore, that the first language I had learned was German. Speaking predominantly in German continued after we had moved back to Hungary. This was due to two prime reasons. We spoke German at home because my father, who had written many of his papers and some of his books in German, wanted to remain highly proficient in that language. The second reason was that due to the very busy life my parents led, they successively hired several fräuleins to take care of me. They were all German. Consequently, my Hungarian language skills were quite limited when I entered grammar school. As a result, the first 2 years in grammar school were rather difficult for me. In Hungarian education, a great deal of emphasis is put on memorization. For example, we had to commit many poems to memory. Poetry plays a notable role in Hungarian life, to the extent that sometimes it is said that in Hungary everyone is a poet. And the culture has indeed created numerous wonderful, outstanding poets. So one of the tasks we had in grammar school was to memorize poems, which we then had to recite in class. Because of my limited language skills I had great difficulties with this, in particular with poems containing infrequent words. It was almost like trying to memorize nonsense syllables. As a result, for a while I was considered to be mentally retarded. Countering this deficiency of mine I immersed myself in memorization. In the ensuing years I memorized hundreds of Hungarian folk songs as well as numerous piano compositions by Bach, Bartók, and Kodály. I especially loved Bartók's works based on Hungarian folk songs, and I still have a copy of one of his music books entitled *For Children*. I am proud of the fact that I had actually met Béla Bartók in my early teens. His house was just down the street from where we lived.

In spite of my father's busy life, he devoted considerable time to my upbringing. He taught me to ski and skate from a very early age, he started me playing the piano, and then made sure I had the best piano teachers. He also supervised me as I was learning to write. I am left-handed and my father was determined to make me write right-handed. Initially he gave me copying assignments and instructed me to use my right hand. He would then leave the room briefly to attend to other tasks. Being rather obstreperous already then, I quickly switched hands to complete the assignment. Soon my father caught me doing this, so for each session he proceeded to tie my left hand down to the chair in which I was sitting. So in the end my father won out and I learned to write right-handed. This training had its benefits because it made me more or less ambidextrous.

My oldest child, my son David, is also left-handed. But I have never had the inclination to force him to learn to write right-handed. Back in the days of my youth left-handed people were often considered inferior and clumsy. My father's motivation was perhaps to prevent people viewing me as a clumsy dolt.

My mother worked in the Hungarian equivalent of the Library of Congress. She would bring home numerous books for me to read, making it one of her projects for me to become an avid reader. My favorite author at that time was Jules Verne. I had read almost all of his books translated into Hungarian. *20,000 Leagues under the Sea* sticks out in my mind probably because this book was also turned into a movie I have seen.

In Hungary one of the most popular vacation sites is Lake Balaton, which is the largest lake in Central Europe. My parents and I had spent time there repeatedly during some of the summers because my father was engaged in research at an institute in one of the smaller towns along the lake named Tihany; some of this work was carried out on fish. My father was also a pilot and loved gliding. I joined him on numerous occasions, as I also did later in my life when we lived in Florida. Soaring silently in the sky in gliders was an exhilarating experience.

After the first two grades in grammar school, I was sent to a private boarding school. I learned subsequently that this happened because my parents had decided to get a divorce. This private school was located in one of the plushest sections of the Buda, on the top of a hill with a very large garden. It was a secure place, originally the property of a rather well-to-do family, surrounded by a beautiful high iron fence. The entrance gate was always locked. The road up to the palatial house was serpentine. Three-quarters of the way up there was a striking, large statue of Venus overlooking the valley below. This statue had gained a special significance for me. Although I was only 9 years old at the time, at this boarding school I fell madly in love with one of the girls named Ágnes. We managed to get together on several occasions in the evening at the base of the Venus statue. In my mind's eye I can still see Venus basking in the light of the full moon.

Sadly, some 30 years later when I returned to Budapest for a visit after the Iron Curtain had been lifted, I visited this school, which by then had reverted to a private home. The entrance gate was all rusty and askew. I walked up the hill to Venus only to see that one of her upper arms had broken off and parts of her legs had also crumbled, revealing the rusted metal posts underneath. Looking at this sad scene, I was reminded of my passionate love, which had long faded into the past. After leaving this school for upper school, I never saw Ágnes again. I still wonder occasionally what happened to her.

At this school I also made friends with two boys who were identical twins. I got to know them well enough to be able to tell them apart. We played many games together. One day, playing soccer on the large terrace adjoining the house, one of the twins kicked the ball over the railing. We ran to the edge hoping not to lose sight of the ball only to see it land on the ground and gain speed rolling down the long hill and disappear. This was a major crime and we had to do anything to find the ball. The twins, in desperation, suggested that we walk down the hill and while doing so keep chanting "The devil will help us find it." Well, we spent quite a bit of time doing this, but the devil was of no help. By this time several other students joined us to find the ball. Not much caring for this chanting ploy to find the ball, I now suggested an alternative. We got hold of another soccer ball and I had my friend kick it in the same manner as he did initially. The rest of us, spread out, watched the descent of the ball. We kept running down the hill as the ball kept rolling. Eventually it came to rest near the fence close to the entrance gate. And, lo and behold, there was the other ball just a few feet away. This event gained me accolades and played a role in my becoming sort of a leader of our little group of boys attending the school.

Our teacher, named Rózsa-néni, was a very tough, sometimes mean-spirited individual. She was a firm and forceful teacher from whom we learned a lot. I did make her very angry once. During one of our spelling lessons she asked the class why the word *hallani*—which means to hear—is spelled with two l's. In Hungarian, learning how to spell is actually quite easy because the words are spelled much as they are pronounced. She pointed to me to answer her question and I stood up as required. At a loss, I finally blurted out "because we have two ears." This prompted laughter in the class. Our teacher felt I was making fun of her and ordered me to the front. Once there she told me to hold out my hand—I extended my left hand—which she then smacked sharply with a ruler. The right answer, of course, is "because it sounds that way."

This teacher had one interesting habit. She often had some sliced bread on a plate when she was teaching, and she would tear off a central piece and proceed to knead it with her fingers. Eventually she would discard the well-kneaded piece of bread only to repeat the process. My twin friends got into the habit of collecting the discards and put them on a shelf inside a wooden cabinet in our common bedroom, where the 15 boys attending the school had slept. The dozens of these odd creations looked a bit like little modern sculptures with captivating, highly varied shapes. Today they could probably be sold in an antique store.

Our teacher, who was born in one of the small towns of central Hungary, Öcsöd, had two sisters who still lived in that little town. One of them, named Eti-néni, often visited at the school. For reasons I cannot remember, we became quite friendly. This led to another significant set of experiences in my early life. I spent several summers with this family in the town of Öcsöd, which exposed me to an entirely different form of life steeped in agriculture. I made a good friend there, Pinka János, whose father was a carpenter. János and I ended up spending a lot of time in his father's shop. Initially, father Pinka was most reluctant to let me touch anything there because I was left-handed and he considered lefties clumsy and inferior. But eventually he realized that I had considerable manual skills—I was in fact more skillful than János—so he ended up giving me numerous little tasks, as a result of which I learned a great deal about woodwork and carpentry that had many long-term benefits in my life.

War Years

When in the early 1940s I entered secondary school in Budapest, called *gymnasium* in many European countries, I became a close friend with a fellow student. We used to meet before classes started in the morning and frequently took walks in a park near the school. One day we talked about friendships and he proclaimed emotionally, "We will always be best friends!" I agreed with him heartily. A few days later, when we met again, he was wearing a yellow star on his jacket. I looked at it and my first thought was, being rather naive and ill-informed, that he had won some sort of award. He then explained to me that he was Jewish and a new rule had just come into effect: every Jew in Hungary, as in several other European countries, was required to always wear the yellow Star of David. A few days later my friend did not show up to meet me in the morning. I have not laid eyes on him ever again.

Shortly after this incident, the bombing of Budapest started in earnest. Hundreds of planes flew over the city, mostly at night, dropping thousands of bombs causing extensive damage and killing many. During part of this period I lived with my grandparents on my father's side because they had a large apartment overlooking the Danube River that was closer to my school than the homes of my parents. I adored my grandmother who was a vivacious, beautiful woman with whom I had discussed many things about life, especially about the nature of war. She was a fine pianist and a great art collector. One of her favorite art productions was the Sicilian Triskelion symbol, which appears in many different forms, always consisting of three interlocked legs or spirals, often with a central human face. The symbol is part of the Sicilian flag, is the basis of the roundel of the Irish Air Corps and a great many other displays throughout the world. My grandmother's prime collection consisted of various pieces of China-ware decorated with the Triskelion. She even had a pendant made with this symbol that she always wore.

The warning signals for the frequent bombing raids were sirens going off throughout the city. When this happened, we were instructed to go down to the basement for safety. My grandmother was claustrophobic and refused to comply. So instead, perhaps spitefully, she often took a walk on the deserted streets during the raids. One day, after the sirens had sounded the second time, indicating that we could leave the basement, my grandmother was not in our apartment. In fact, she never came back and was never found. There was extensive bombing damage in the neighborhood the night this happened, and we presumed that she had become a victim. Subsequently, I spent time trying to find her body without success. I had thought I could locate her because of the Triskelion pendant she had always worn.

After this terrible incident I moved back to my father's and stepmother's place in one of the suburbs of Budapest, the so-called Hüvösvölgy. This was a beautiful house with a large garden that had numerous fruit trees. It had belonged to my stepmother's well-to-do parents. Her father was the CEO of the Hungarian Railroads. Shortly after I moved there, the Russian invasion of Hungary started. After further bombing raids and the relentless sound of the slowly approaching cannons, the Russian Army reached Budapest. A prolonged battle arose between them and the Germans, who gradually withdrew, except for a small contingency that had set up fortifications in the Castle of Buda, which ended up resembling wars in the Middle Ages where castles were surrounded and then invaded. The Castle was under siege for several days. The Germans then broke out in an effort to escape. Every one of them was killed. By this time the city had been devastated. There were thousands of burned-out vehicles and tanks along many of the main roads and dead bodies everywhere. To slow the advance of the Russians, the Germans had blown up all the bridges on the Danube that connected Buda and Pest, and they also destroyed endless miles of railroad tracks using a specially designed giant railroad car that had a device on it that broke the tracks every few yards with a twisting motion.

During the battle in Budapest, as the Russians advanced slowly, our house in the Hüvösvölgy became a headquarters for the commanders of one of the Russian divisions. We were confined to one room in the house. The conduct of the Russians was merciless. Rape was one of the most common occurrences. On one occasion, upon entering the large kitchen of our house, I got a momentary glimpse of such a rape. Three soldiers held down the stripped body of one of our help, a young woman whose job had been to look after my little sister, while a fourth soldier kneeled between her legs with his pants down. A fifth solider quickly slammed the door in my face but not soon enough to obliterate this image that is still vividly in my head.

The Russians caused major damage to our house, breaking dishes, toilets, and bathtubs. One drunken night—their alcohol consumption was obscene—two of the officers sat down in front of our beautiful grand piano, on which my father had started my piano lessons, and used a hammer to hit the keys, breaking them irreparably.

Mercifully, the Russian army left after a few weeks, advancing toward Germany, leaving behind devastation. Due to the fierce combat and profuse killings, in addition to the burned-out vehicles and tanks, there were weapons and explosives strewn everywhere. To prevent their reuse, the Russian soldiers would remove the firing pins and throw them away. Being at loose ends at this time since the schools were not running, a good friend of mine and I got involved in all sorts of nefarious activities. One of our favorite games became to find the thrown-away firing pins and match them to the rifles and machine guns strewn all over the place. We had some success and actually had put together a little weapons arsenal, including stacks of various bullets. We hid these in the basement of a nearby deserted, bombed-out house. We never fired any of these weapons but, going into the nearby woods, we would take rifle ammunition and after removing the bullet would lay down the casing, pour out a bit of the gun powder, and then light it. We then quickly crouched behind nearby trees until the explosion took place which, of course, had not much of an effect on anything. My favorite weapon in our arsenal was a shiny little pistol—pistols were very rare in the rubble—but we never managed to find bullets for it.

Perhaps one of the goriest undertakings during this period was to bury the thousands who had died during this phase of the war. The smell of death was rampant as the dead bodies began to decompose once spring approached and the snows melted. Groups were organized to find the bodies and take them to collection sites. Because of the acute shortages in Budapest, the wood to make coffins was also in short supply. To minimize this problem, one unseemly, but unavoidable practice became to construct foreshortened coffins into which the decomposing bodies had been placed with the lower legs bent over 180 degrees at the knees. Gradually the city was cleared of the dead and their odor dissipated.

Another consequence of the extensive damage to the roads and the destruction of the railway system was acute food shortage. One item that remained in reasonable supply was dried beans. To prevent us from developing an aversion to them, clever means had been devised in many households to prepare them in all sorts of different ways. Beans were often prepared for breakfast, lunch, and dinner. But to this day I find it next to impossible to eat beans.

About 6 months after the Russian invasion, the city was cleared of the dead, and the roads were repaired as were the railroad tracks. Reconstruction had begun and the schools reopened. Life gradually returned to normal but did so without ever erasing the impressions and memories of these war years. A new government was formed dominated by communists.

Around this time I spent another summer in Öcsöd. With so much of Europe devastated, these were difficult times. I joined a little workforce whose task was to raise silk worms for the purpose of harvesting silk for a company that made clothing. We were told that our reward, after several weeks of hard work, would be a new pair of shoes for each of us. This undertaking had its source in the fact that one of the most common trees, many of which still line the roads on the Hungarian Plains, is the mulberry whose leaves silk worms love to eat. So we spent our days climbing these trees collecting leaves in big sacks. The worms were ravenous. Their demand was so great that by the latter part of the summer most of the trees in the area had become bare. We had to walk to progressively more distant locations to collect leaves, which wore out our shoes; so we were really looking forward to our promised earnings. Mercifully, the worms eventually got to the stage of weaving their silk cocoons. Once completed, the cocoons were packed into large boxes and were carted away to the factory that created silk clothing. Disappointingly, after our work had been finished, we were informed that the undertaking was less successful than had been anticipated. As a result we did not receive shoes. Instead, they gave each of us a pair of leather shoe soles. In those days all shoes were made of leather and their soles often had to be replaced.

Getting back to Budapest at the end of that summer, I went to live with my mother in her family's villa in another beautiful part of Buda. This villa, which was also on large grounds, had three floors. My mother and I lived on the ground floor and my cousin Andrea, with whom I became close friends, on the top floor.

My grandfather, who had the villa built originally, well before the war, was a powerful, innovative, and fearless individual. He was the CEO of the Anglo-Hungarian bank and consequently was financially well off. He also bought a car at that time, a Mercedes. The single-lane driveway to the garage was a long one and he did not like having to drive the car that distance in reverse to get back onto the street. So he had the garage modified to contain two rotaries. Once the car was driven onto one of them, pressing a button rotated the car around 180 degrees with an electric motor. He had two of them built, I suppose, because he was planning to buy a second car—something that was seldom done in those days. Creating these rotaries may have been a clever idea, but the system kept breaking down until it could no longer be repaired. So my grandfather just parked his car at the beginning of the driveway when he got home from work in the evening.

Another unusual idea that my grandfather had came about because he snored loudly at night, which made the life of my grandmother miserable. He wanted to continue having the two of them sleep together, so he had a huge new bed built in their bedroom with a central partition that could be pulled down from the ceiling. The partition was reasonably well sound proofed. My cousin Andrea and I tried this out one day when my grandparents were away. We lay down on the bed and then I started to make loud snoring sounds. She then pulled down the partition and yelled, "Can you hear me?" Indeed, she was barely audible.

My grandfather never did buy a second car and soon he became fatally ill and passed away shortly before World War II got under way.

Once I moved into the villa with my mother after the war, my cousin Andrea and I became inseparable. We had many friends in the neighborhood and frequently we played a game in our yard that was popular at the time called Number War. The game has two teams, a defending one and an attacking one. The site of the defending team is generally marked by a flag, which was the object to be seized by the attacking team. We wore cardboard plaques attached to our heads with four numbers on each. The two teams were identified by virtue of having different color plaques. Whenever the numbers worn by an individual were correctly yelled out by a member of the opposing team, the warrior was declared to be dead and had to leave the area. To prevent the reading of the numbers, the participants hid their heads behind trees, bushes, and buildings, peering out sideways to peruse the scene. This was, and probably still is, an absorbing game, which at the time was especially popular among Boy Scouts.

Andrea's father, my uncle, often took exception to my conduct, sometimes deservedly so, and meted out punishment by forbidding me to play with my cousin. One of these arose when I figured out a way for speeding up my descent from the top floor of our villa where Andrea lived to the ground floor where I stayed with my mother. The elegant circular staircase had an inner railing with a nice smooth polished wood balustrade secured with glazed iron posts to a continuous marble ledge next to the inside portion of the steps. I learned to hook my arm around the top of the railing and place the soles of my shoes onto the marble ledge. This allowed me to slide down to the first floor rapidly. The speed of descent could be controlled by varying the force with which I squeezed my arm. Due to my frequent slides down the staircase, the inner portion of the marble ledge gradually became quite shiny in contrast with its outer portion. One day my uncle came home as I was whizzing down the staircase. He had already noticed the shininess of the marble but did not know its source. He told me I must stop this unseemly practice, but of course I did not obey him. He caught me again flying down the steps a few days later and furiously forbade me to see my cousin Andrea for a week.

On another occasion the lights went out on the top floor and my uncle accused me of being the culprit. I had nothing to do with this, and in short order I fixed the problem by replacing a burned-out fuse. This did not help things and I received another week's punishment.

To combat this frequently occurring separation from Andrea, I tried to come up with some way of communicating with her. At this time there were still numerous bombed-out buildings in the neighborhood which had not yet been repaired. Some of the ruined material was stacked at the edge of streets for eventual removal. Common here were discarded wires, some of them telephone wires. For reasons I cannot remember, I started to collect such wires. I then had the idea that perhaps I could communicate with Andrea using the Morse code, which at that time was a prime communication system. Many of us had memorized the code. Andrea's room on the top floor of the villa was on the same back side of the building as mine on the ground floor. So after a lot of fiddling, I had put together two telegraph keys that produced an audible click with each press. I then connected our rooms, leading the wires I had twisted together through the windows and up the outside wall next to a down spout. Soon we were communicating with each other using this system, although it was not uncommon that we had difficulties understanding each other. When this happened, we would rush into the stairway and yell toward each other from the ground floor to the top floor. The most common yell was, "What did you say?"

During one of the punishment days when we were yelling like this my uncle entered the villa. Seeing us talking when we had been forbidden to do so resulted in another week's punishment. So we devised a safety procedure to minimize this happening: Whenever any of our parents came home unexpectedly while we were beeping away, we quickly sent an SOS signal (··· | — — — | ···). Fortunately, my uncle never found out about our Morse code system. Otherwise I might have been punished for life.

A few years ago Andrea, who now lives in Beirut, sent me a postcard. On the top of the face page are the words in bold, "Morse Code," and below are the letters of the alphabet with the dots and dashes of the code for each. I have posted this card on the wall of my office to the left of my computer. Looking at it now reminds me of these long-ago times and makes me realize how much the world has changed since then. No one nowadays knows much about the Morse code. New technologies in communication and the computer revolution have obliterated it.

Another fun thing Andrea and I did while we lived together in the villa, for which we were not punished, was stargazing. I had become enamored with the night sky and went on to memorize the constellations. Our yard in the villa was well suited for this purpose as it was located near the top of the hill, providing thereby an excellent view of the sky. We would spend hours outside at night with a map and a flashlight in hand; gradually we learned a great many of the constellations. Some years later I learned that David Hubel also had a passion for the stars. On one of our trips, as described in a subsequent section, we embellished this knowledge in Australia.

The political climate and the many changes instituted by the Hungarian government pressured by the Russian domination spelled an uncertain future. My father soon realized that his prospects in Hungary as a research scientist and university professor were in serious jeopardy. So he decided to leave the country. He was offered a position in America and so in 1947 he, my stepmother, and my half-sister emigrated legally. Their beautiful home in Budapest, following extensive repairs, was rented out to the U.S. Ambassador to Hungary.

Once my father, stepmother, and my sister Christina, who was 7 years old at this time, got settled in the United States, procedures began to enable me to join them. I was put through the emigration process and was very fortunate because, having been born in Germany, I was on the German quota system, which had more slots and thereby allowed more immigrants to enter the United States than Hungarians. So in 1948 I left Hungary. I took the train to Prague and then flew to London, where after a few days I boarded the *Queen Elizabeth* that landed in New York after five stormy days.

The *Queen Elizabeth* was a remarkable ship, the largest of its kind in the world at the time, 83,673 tons. It was extremely fast. During the war years it was used to transport troops. Due to its speed, it typically sailed solo because no other ship could keep up with it. Many years later when I flew to Hong Kong, as we were approaching the airport there, the pilot pointed out the hull of the *Queen Elizabeth*, which was lying on its side, half submerged in the harbor. The ship had been decommissioned and the intent was to turn it into a museum. Due to a major fire that had erupted during this conversion, the ship was destroyed. Her sister ship, also owned by the Cunard Line, fared better. This ship, the *Queen Mary*, has also been converted into a museum but with success. She is still beautiful and now resides in the harbor at Long Beach, California.

Initial Years in the United States

Once I arrived in New York, I was looked after by a friend of the family. They were wonderful and took me to museums, to the Statue of Liberty, and to the top of the Rockefeller Center. I was then put on a train that took me to Jacksonville, Florida, where my father and stepmother picked me up. We drove to Orange Park, some 12 miles from Jacksonville. This is the place where my father worked in the Yerkes Laboratories, which some of the locals called the Monkey Farm. The head of the laboratory was Karl Lashley.

While living in Orange Park, my father often took me to the Yerkes Laboratories, where I assisted him in his experiments, some of which at the time were concerned with examining detour behavior. This work was done in several species of animals. We tested cats at home in the evening in a maze I had built with my father. On many weekends we took trips to the Marineland Aquarium. Here my father carried out experiments examining detour behavior on octopi. It was most instructive for me to become familiar with this intriguing species.

The investigators at the Yerkes Laboratories formed an impressive group. I have met several of them: Karl Lashley, Henry Nissen, Josephine

Semmes, Edward Evarts, Karl A. Pribram, and Robert A. Blum. Blum and his wife, a childless couple, were rearing a really cute baby chimp in their home. I learned later, as is so often the case, that as this chimp grew older it became unmanageable and had to be returned to the enclosures at the Yerkes Laboratories. Pribram, an eminent neurosurgeon, kindly sent me a copy of his book, *Brain and Perception*, in 1991.

Henry Nissen was a gentle, wonderful person with a house right on the St. Johns River. I was invited to visit his place on numerous occasions, and I became a good friend of his daughter, Joanna. Some years later, Henry, who carried out developmental studies, went to remove an infant from a chimp called Helene. The chimp, who turned out not to have been sufficiently tranquilized, attacked him, resulting in serious damage to his back from which Henry never recovered. His health deteriorated, and in 1958 he committed suicide.

Karl Lashley was a most lively individual and quite a jokester. He was an avid sailor like my father. One day I had the honor of sailing with him on his beautiful yawl named *Skidbladnir*. Having learned that I had some sailing experience, he instructed me to take over at the wheel. While sailing against the wind on starboard, he instructed me to come about to port, which is normally achieved by turning the wheel clockwise. When I did this, instead of what I had expected, the boat did the opposite and bore off staying on starboard. I was dumbfounded. Lashley laughed merrily and told me that he had reversed the steering arrangement by twisting the line that connects the wheel to the rudder into a figure eight. I am not sure whether he did this because it was an easy way to tighten up a loose connection or to play games on his friends.

Lashley became world famous for his research achievements, the most controversial of which was his equipotentiality theory according to which all areas of cortex are equally important in learning (Lashley, 1929). This theory by now has been proven to be quite wrong. I sometimes can't help but think that Lashley had proposed it as yet another one of his jokes.

In 1965 the Yerkes Laboratories was moved to Atlanta. I visited there once many years later and was surprised to recognize an old, graying chimp I had known back in Orange Park in 1949.

During the two summers I had spent in Florida I worked two different jobs. One of these was as a caretaker and counselor in a summer camp called Camp Seminole. This camp was quite close to Henry Nissen's house, which was one of the reasons I visited him so often. The camp was fun but nothing much of interest happened there other than my learning how to play baseball. The second summer I worked as a waiter and host at a restaurant called the Rainbow Grill. I remember the owner and his wife fondly; they were very kind people who often allowed me to spend the night at their home right next to the grill when I had worked late hours. At the Rainbow Grill I met up and became friends with a very interesting person by the name of Bobby Byers. He taught me many things about life, mostly about its seamier sides. He was a hunter and instructed me in how to shoot pistols and rifles, reminding me of our weapons collection in Budapest. Mostly everything Bobby and I did ended up in competition. We shot at various targets with his weapons and he beat me regularly, but gradually I got better. We played chess a great deal, which was one of my hobbies at the time. Having read several books on chess, I became fairly good at it and I ended up beating him most of the time. This only propelled him to want to play me more, determined to better me. Bobby also taught me about prostitutes with whom he apparently often dealt. Sometimes he would pick one up at the Rainbow Grill or when we were driving around in the seedier parts of Jacksonville. This was where I drew the line, as I did not want to be educated in this aspect of life.

Bobby had served as a pilot in the U.S. Navy and was eventually dishonorably discharged for repeatedly flying too low. He was often at loose ends. Bobby liked to drink and once he crashed his mother's car and suffered some rather deep cuts on his face. Some years later Bobby got a job as a pilot to fly crop dusters. One day, flying too low, he crashed. The plane blew up and burned him to cinders.

In early 1949 my father spent time carrying out experiments on rats in the laboratory of B. F. Skinner at Harvard. While there, one day he went on a skiing trip to Mt. Washington. As he was heading down at Tuckerman's Ravine, he fell into a crevice near a large boulder and was killed. He was just 41 years old. His name is now listed in the Sherman Adams Summit Building on top of Mt. Washington along with 140 other individuals who have perished on the Presidential Range. The large boulder is now called Schiller's Rock.

After my father died, my stepmother found a position as a teacher at one of the top private schools in Jacksonville, the Bartram School. Since this was a girl's school, I could not join her there. So I ended up in Charleston, South Carolina, where I lived with another friend of my father's, Jim Anliker, a physician who held a position in the Anatomy Department at the Charleston Medical School.

While I lived in Charleston my stepmother and Karl Lashley fell in love and married in 1956. This ended up being a rather short marriage because Lashley died unexpectedly when they took a trip to France in 1958; he was 68 years old. My stepmother died in 1988. Her major scientific contribution was a book she had edited in 1957 entitled *Instinctive Behavior*, which contained an introduction by Lashley and chapters by Konrad Lorenz, Jakob von Üxkull, Nicholas Tinbergen, and my father (Schiller, 1957).

Jim Anliker took great care of me in Charleston. He got me a job in the Anatomy Department where he worked. I had two responsibilities. One was to tend after a group of monkeys housed in the animal quarters. The other was to help out keeping things in order in the department. The least appealing part of this job was to clean up the large room in which the medical students dissected cadavers.

The staff in the Anatomy Department was very friendly and helpful. I got involved in photography and learned how to develop film and make enlargements in the darkroom of the department. I was given a 35mm Leica camera by my stepmother and ended up taking innumerable pictures and spending many hours processing them in this darkroom, which fortunately was otherwise quite unused. How different things are now! With a digital camera one can get an instant view of the pictures taken and erase the unwanted ones. Those selected can be processed without ever going into a dark room.

Jim Anliker is a great pianist and organ player. One of his passions at the time was to explore the sounds and quirks of various organs in the Charleston area. I accompanied him to numerous churches where my task was to record his organ playing on a tape recorder. Many years later Jim moved to Boston. I visited him there once. He had a rather large apartment there in which he had several pianos. I had spent an enchanted evening there listening to him playing various classical pieces and explaining to me how the pianos differed. Some years later I spent another enchanted evening like this when I visited Mickey Goldberg at his home. Mickey is also a superb pianist. He played several classic pieces, which made the experience much like going to a concert.

Jim Anliker had yet another interesting attribute. He was an avid collector of unusual, enigmatic, and profound quotes. He printed these quotes on slips of paper, which he then mounted on his office walls, increasing their number week by week. I loved this hobby of his, so to this day I do the same thing but with a bit more moderation. Worth noting perhaps are three of these which are on the same wall as Andrea's Morse code card: *Knowledge is folly, except grace guide it* (George Herbert). *All predictions are wrong. That is one of the few certainties granted to mankind* (Milan Kundera). Except that I had changed the word *predictions* to *hypotheses*. The third is a cartoon by Barsotti that displays a disheveled, sweating guy who appears to be walking on a road in the direction indicated by an arrow on which the word *truth* is inscribed. Looking down one can see that this guy is actually on a treadmill.

Jim Anliker and I had rented a wonderful apartment on the top floor of a house owned by a Mr. Gibbs, who, as it turned out, was an English teacher at the high school I had attended during the 11th and 12th grades in 1949–1951. Gracefully, he took it upon himself to improve my English and I was proud to receive an A in his class. Mr. Gibbs was color blind, which was the first source of my interest in color vision. He told me one day that he had just gotten a ticket for running a red light in Charleston. This happened at a site where for some obscure reason the green light was on top and the red on the bottom. Since he could not differentiate these colors, he inferred them on the basis of their position. I was surprised, and always being a skeptic, the next day I went to check it out. This was indeed the case; the red light was on the bottom, green on top. I can only presume that this mistake has been corrected by now.

I led a very busy life in Charleston and, once again, made several good friends. Having become a reasonably proficient swimmer in Hungary at an early age, I thought I might be good enough to become a member of the school swimming team. It turned out that I was. To do really well, I swam endless laps on a daily basis at the local YMCA. This effort paid off. I competed in the breast stroke, the free style, and the medley relay at the numerous meets we had and I managed to come in first every time. This was really because these teams were not very strong. One of the rewards of this was that at the senior closing graduation ceremonies I received one of the two trophies that had been given out. The other one went to the star quarterback of the football team who was also a good friend. But we both were big frogs in a small pond. My friend never became a starting quarterback in college.

During my last year in high school I had the good fortune of being mentored by the psychoanalyst David Rapaport, who was yet another friend of my father's. Originally also from Hungary, David Rapaport became a major figure in clinical medicine. He held a position at the Austen Riggs Center in Stockbridge, Massachusetts, where he was a good friend of Erik Erikson's. Rapaport was a remarkable scholar, who had written several books. The two-volume book entitled *Diagnostic Psychological Testing*, which collectively came to more than 1000 pages, was first published in 1946 and went through 15 printings. Another book he had written, entitled *The Organization and Pathology of Thought*, was first published in 1951 and went through four printings.

Rapaport took me under his wing and I spent several years working with him at the Austen Riggs Center in Stockbridge, Massachusetts, which at the time was a psychoanalytically based institution for the treatment of the neurotic youngsters of wealthy families. I worked there through two summers and while in graduate school at Clark I took weekly 1-day trips to Stockbridge. During one of those summers I also served as a tennis instructor in the Austen Riggs athletic center. Erik Erikson's wife was in charge of this program. Tennis had become another of my passions around that time. As a result, I had the privilege of interacting with her as well as with Erik on quite a number of occasions. Surprisingly, by virtue of being involved in tennis, I had met Richard Dyer-Bennet and ended up playing with him many times. I remember that several years later, when I was at MIT, Richard gave a concert at our Kresge Auditorium to a packed audience. In the middle of one of his songs he suddenly went silent, a silence that was broken when he proceeded to tell the audience that he had momentarily forgotten the words of the second verse of the song. Following another brief pause, the words came back to him and he continued. Upon finishing he received a thunderous ovation. Sadly Richard died in 1991 at the age of 78.

During the summers I was at the Austen Riggs Center I received rigorous training in assessing and criticizing the books and articles Rapaport had assigned to me to read. We met daily one on one. He trained me extensively in Freudian theory. I had to read many of Freud's books, most notably among them the *Interpretation of Dreams*. Initially he lent me his copy of the book for me to read in which he had some notes and comments on just about every page. Subsequently I got my own copy, which I still have. In this book, trying to imitate Rapaport, I made notes and comments on many pages.

One of the minor accounts in this book now comes to mind. A patient seen regularly by Freud had challenged his central contention that dreams are wish fulfillments. She told Freud that she had a dream the night before in which she wanted to give a dinner party, but when she went to the store to purchase what was needed for the dinner, she found the store closed. So she asserted that her dream was not a wish fulfillment. Freud did not bat an eye (I am just saying this since I was not there). You just did not want to give a dinner party, he asserted with certainty. In the book he elaborates his reasons fairly convincingly.

Subsequently I often wondered about why dreaming had become so pervasive in mammals. Animals, just like humans, dream regularly and I doubt that they have what can be identified as ids, egos, and superegos. Subsequently, as a result of work I did that involved the immobilization of one eye in rhesus monkeys, as described a little later, I came up with a much less profound idea about why dreaming evolved in the first place. My theory asserts that dreaming came about to induce eye movements during sleep, as in REM (rapid eye movement) sleep, which assures that the eyes remain well rounded and the corneas remain smooth and polished. When the eyes are prevented from moving, they become misshapen and the corneas become ridged. I have learned that animals that hibernate also move their eyes about during hibernation, presumably by virtue of dreaming about something. But then in their dreams maybe they are roaming about freely in warm weather with plenty of food around. Wishes fulfilled.

This training with Rapaport came in very handy. Subsequently I taught a course on personality for a while at MIT as well as sections in other courses on Freudian theory.

Another person I recall during the time I had spent at the Austen Riggs Center is Daniel Kahneman, who had also worked with David Rapaport. Kahneman received the Nobel Prize in Economics in 2002. While at the Austen Riggs Center, we played around with some experiments that subsequently I pursued in more detail. Kahneman is now at Princeton. I met him there recently at the wedding celebration of Charlie Gross and Joyce Carol Oates; it was wonderful to reminisce about our time with Rapaport, whom we both held in awe.

The crowning influence of Rapaport in my graduate training was my Ph.D. thesis in which several aspects of learning were examined based on a theory Rapaport had developed which was called the *Theory of Attention Cathexis*. Rapaport did not participate in the last phases of this thesis work because he suddenly died of a heart attack in 1960. He was only 49 years old. I had the honor of being one of his pallbearers. Some years later I joined forces with another disciple of Rapaport, Fred Schwartz, to write a monograph on this theory (Schwartz et al., 1970).

The most satisfying project I had carried out at the Austen Riggs Center was actually one that George Klein had inspired me to do. George was a close friend of Rapaport's and visited the Austen Riggs Center frequently. He was a professor at NYU. He was both incisive and generous. In the course of several discussions we had, he brought up the idea of us doing a developmental study using the color-word interference test devised by Stroop. The Stroop test involves the naming and reading of colors when the colors and words are in harmony and when they are in conflict, such as the word *red* printed in blue ink. Klein had carried out such experiments on adults and the idea now was to determine how the interference arises in development. We got permission at two schools to do this work, one in Pittsfield and the other in Newton, Massachusetts, where I now live. The test takes only about 10 minutes per subject. I ran 240 subjects starting with students in the first grade and also tested college students. The experiment was a lot of fun to run, and the results were gratifying, showing a dramatic rise in the interference that occurs in the naming of colors when they are in conflict with the color words during the first, second, and third grades as the kids learned to read. This is followed by a subsequent decline in the magnitude of the interference. George helped me with the data analysis and the writing of the paper, but then he refused to be a coauthor, saying that he wanted this to be my sole work (Schiller, 1966). This was certainly most magnanimous of him. I took this disposition to heart and subsequently had many students who had done independent work in my laboratory, which was then published by them independently as well. George Klein, like David Rapaport, passed away quite young. He died in 1971 at the age of 53.

I spent two summers at the Austen Riggs Center. Before and after that I spent summers as a counselor in a summer camp in Vermont. I came to work in this camp because it was the place where my stepmother and my sister, Christina, spent their summers. My mother was the executive secretary. The camp was founded in 1939 by Kenneth Webb and his wife, Susan Webb. The camp originally had two sections at opposite ends of the lake, one for boys and the other for girls called Camp Timberlake and Camp Indian Brook. Subsequently a third area was added in-between for older kids. I was a canoe instructor for the boys and took them on extended canoe trips to places like Lake Saranac and Lake Memphremagog and the upper Connecticut River. To be able to teach canoeing and to take canoe trips, the first summer before camp started, Webb sent me to a most instructive canoe school in northern Vermont. He paid for this. One wild canoe trip we took once I was back at Camp Timberlake was down the rushing waters of the upper Connecticut River, where we managed to crash up one of the canoes, which terminated all subsequent canoe trips on this river.

Another great attraction at this camp was horseback riding. We had stables and many horses. My sister Christina became deeply involved in this aspect of the camp, to the extent that eventually horses became her profession. She attended Smith College, where she continued to pursue this passion. Christina now has a place in Florida called the Quiet Hill Farm, which specializes in equestrian jumpers. She has trained hundreds of kids there, some of whom, including her daughter, have participated in numerous competitions. Christina often serves as a judge at such events to this day.

The creator of these summer camps, Ken Webb, died in 1984 at the age of 82. His wife, Susan, became active in politics in subsequent years. She wrote a book entitled *The Susan Howard Webb Story: A Memoir*. She celebrated her 100th birthday in 1995.

At the camp I became a close friend of Frank Sieverts, with whom I have had several adventures. One summer Frank and I decided not to go to camp. Instead, we made plans to go to Alaska. We met up at Swarthmore, where Frank was a student at the time. On the way we decided to stop off in Thiensville, Wisconsin, where Frank's parents lived. This is a little town just north of Milwaukee near Lake Michigan. Once we got there, we had a change of heart and decided not to go to Alaska after all. Instead, we both got jobs and spent the entire summer in Thiensville. I found a job with a construction company where I became a dump-truck driver. We worked more than 10 hours a day. My prime job was to cargo gravel from gravel pits to construction sites. Often my task was to lay down gravel smoothly on newly made driveways. This was accomplished by driving the truck slowly forward or backward and gradually raising the truck bed to pour out the gravel evenly. There was a strong motivation to do this well because otherwise I had to do a lot of shoveling to create an even surface.

Another summer, this time after we had worked at Camp Timberlake, Frank and I decided to go to Colorado to do some serious mountain climbing. I had read up on rope climbing and, at considerable expense, purchased a coil of climbing rope along with the appropriate implements that included pitons used to secure the rope to the rocks as we were climbing.

This trip was both exhilarating and disastrous. We went to Estes Park and then, to acclimate, spent several days doing ordinary hiking. One of these hikes was to the top of Longs Peak along a relatively ordinary, if steep trail. We then decided to get into real rope climbing. We hiked up to the east face of Longs Peak that consisted of a virtually sheer cliff of several thousand feet. About halfway up there was a more or less horizontal break in the cliff, which is named Broadway. Broadway is barely a foot or two in width at most places. We had gotten hold of reports describing the layout of the cliff and strategies for scaling it. We made it up to Broadway without incident. It took quite a few relays to get to this point. Due to other climbers, there were numerous pitons nailed into the rock walls, so I only had to hammer in just a few of them along the way. Each end of the rope was tied to our waist. I would climb along until the rope was stretched to its end. I would then secure my position and wait until Frank climbed up to join me; I made sure to keep the rope taut between us by coiling it as Frank got closer. We then walked along Broadway until we got a steep glacier that stretched up to near the peak of the mountain. We took one relay at which point Frank took over the lead because he had boots better suited for the glacier than did I. I secured myself in a good sized crevice between the glacier and the rock formation and Frank proceeded up. I soon lost sight of him as he moved around a rocky protrusion. Then, suddenly, I heard him scream and saw him slide around the protrusion along the glacier gaining speed. This was a terrible moment because I realized that once he slid down to Broadway he would be propelled over the ledge and catapult down toward the base of the mountain more than 1000 feet below. For a moment I thought my only chance to survive was to untie the rope from my waist so that he would not drag both of us to our deaths. But I realized there was not enough time for that. So I quickly pulled as much of the rope as I could toward me. Once he slid past me I threw the rope around my neck and used both hands to try to slow his slide. Miraculously, I managed to bring him to a halt just as he hit Broadway. But this was at a considerable expense. The abrasion of the rope caused welts on my neck as well as on my hands. They were quite deep and some of my fingers began to bleed profusely. I tried to stanch the bleeding with my shirt and handkerchief. After moderate success I climbed down slowly to where Frank was waiting. The hike back down and then to Estes Park seemed like an eternity as we had to take numerous relays with Frank now taking the lead by letting me go first and keeping the rope taut as I descended. Once we got to Estes Park we went to a hospital where they bandaged me up. One of my hands was completely encased and I had extensive bandages also around my neck.

The next day we decided to head home. Running short on money we thought it most advisable to hitchhike back east. In the outskirts of Estes Park we were picked up by two friendly guys who were driving a brand new car. Their friendliness was fueled by the beer they were drinking. As we were driving down along the long and steep downhill road from Estes Park at a moderate speed, a car passed us rather closely. For reasons still unclear to me, this enraged our driver who proceeded to recklessly pass this car right back going around a curve. As soon as he did so, it became evident that the curve was too sharp for him to make it. With the tires screeching, the right side of the car slammed into the sheer rock to the right of the road which then propelled us to the other side where the left side of the car smacked into the retaining guard rail, luckily preventing us from catapulting into the abyss. Eventually we came to a halt. Hanging on for dear life my hands started to bleed again. We were instructed to get out of the car and disappear. We did so with haste, noticing as we did so that this lovely new car had become a total wreck. Two near-death accidents in a row.

We managed other rides, first to Denver and then to Chicago, where Frank and I parted company. He headed back to Thiensville and I back to Duke. Given my grotesque appearance with all the bandages, hitchhiking became difficult, so eventually I took the train from Pittsburgh to Durham, North Carolina, leaving me broke.

Subsequently Frank and I sent letters to each other on several occasions with newspaper clippings of deadly accidents suffered by climbers in the Rocky Mountains. Looking at my right hand now I see that the marks left by the burns from the climbing rope are still in evidence.

Frank and I remained in contact for several years thereafter. I visited him at Swarthmore a few times where his roommate was Michael Dukakis. Subsequently Frank became a specialist in refugee and relief issues at the State Department and then an executive in the Washington office of the International Committee of the Red Cross. He died in 2004 at the age of 70. We were close friends and I mourn his loss.

In the early 1950s my cousin Andrea, her father Andrew, and her mother also immigrated to the United States. They set up residence in Queens, New York, where I visited them on several occasions. I made sure to be well behaved on these occasions. My uncle was a famous newspaper reporter in Hungary, had spent time as a foreign correspondent in Turkey during the war, and in the United States had started a company in the 1950s that provided information of recent news events called Deadline Data. He worked inordinately hard and read numerous newspapers every day. This relentless hard work had created problems with his eyes and subsequently with his heart. He had quadruple bypass surgery, which was declared to be a success. But my uncle died a few days thereafter. In his will he left me a beautiful winter coat which he had purchased shortly before his death. I still wear this coat every now and then to remind me of my uncle.

College Undergraduate Years

Upon my arrival at Duke in the fall of 1951 one of my first tasks was to secure a job because my financial situation was precarious. I landed a fine job in the cafeterias, where my job the first year was to clear tables during and after one of the three meals offered daily. This took up to two hours a day. For this work I was given free meals, which was most generous indeed. In subsequent years I was “promoted” to work at the dishwasher center in the main kitchen area, where my task was to take the clean dishes and silverware as they emerged on a continuous belt from the gigantic dishwasher. The dishes were then stacked on large rolling carts.

Working with me was an interesting character whose nickname was Hooksie. He earned this name by virtue of the fact that when he played basketball—we often played together on pick-up teams—every shot he made was a hook shot yielding a low success rate. I have never seen him take a regular shot. Hooksie was a couple of years ahead of me in school. When time came close to his departure from Duke, one day as we were stacking the dishes I asked him: "Hooksie, aren't you going to miss your friends here?" Hooksie looked at me, raised his hand dismissively in an abortive hook shot and said: "There's friends everywhere."

The athletic department was apparently well aware of my swimming skills and they wanted me to join the Duke swimming team after I won a race among the incoming freshmen in breast stroke. By this time I was sick of swimming and could not face spending several hours a day in the pool taking laps. So I declined. Instead, I joined the soccer team and played varsity soccer for 4 years. This was a lot of fun because we took numerous trips to play matches at various universities. We had some really fine players; two of them became all-Americans, and one year we won the Atlantic Coast championship.

Starting shortly before going to Duke, as already noted, I had become enamored of tennis and very much wanted to make the varsity tennis team. I had become friendly with several members of the team. The coach was supportive and I soon got the job of stringing tennis racquets. Finally, my junior year I made the team, although I never held a position higher than #6. Our number-one player that year was Buzzy Hettleman, an excellent athlete, whose first name was Kalman, a Hungarian name. Originally his grandfather's name, it subsequently became a family name so that most members of his family have this as a middle name. Like me, Buzzy served 2 years in the Army after graduating from Duke as we had a conscription system at that time. He also served in Germany and on one occasion, when I was in Stuttgart, we met up to play tennis. We just hit because I was no match for him. This was a lot of fun for me in spite of the fact that he assured me, after we were done, that I hit the majority of my ground strokes out of bounds. Buzzy went on to an illustrious career and has published a book recently about education in the United States entitled *It's the Classroom, Stupid* (Hettleman, 2010).

Due to the high scores I had gotten on the college entrance exams in chemistry, I was placed into an advanced chemistry course my first year at Duke. By this time my infatuation with chemistry, induced by a remarkable teacher at the Charleston high school, has faded and I ended up not doing well in this course. Instead, I became involved in psychology. Karl Zener was the director of graduate studies at the time I was at Duke and became chair of the Psychology Department in 1961. He was yet another friend of my father's. He and several other members of the department were most supportive of the students and provided opportunities to run little experiments. I spent quite some time examining visual discrimination in fish. This work was done under the supervision of Gregory Kimble who had written an influential book entitled *Principles of General Psychology*.

An unpleasant incident at Duke occurred as a consequence of one of the despicable practices this institution had at that time: Freshmen were required to wear blue caps called dinks, so everyone they encountered could tell right off that they were just mere frosh. One evening, as I was walking back to my dorm on the campus, I was accosted by three townies. The relationship between the Durham population and Duke was always tense and animosity was rampant. These townies I encountered demanded my dink, which I gave them fearfully. During the following days I walked around the campus dink-less. Soon I was called in front of a judiciary committee whose members were mostly upper classmen. I was told that unless I started to wear my dink right away I would have to wear a yellow dink, which was the mark of students who had committed misdemeanors. I was also told and that unless I obeyed, I would lose my job at the cafeteria. I explained what had happened and accused Duke for being lax in providing student protection on campus. The committee, which I consequently considered a bunch of quislings, did not care. I also told them that as long as they paid for it I would be happy to buy a yellow dink. They refused that too. I then went to the Duke Dope Shop—I do not know where that name came from—as I intended to buy a yellow dink myself. My obstreperousness failed because I was told that they could only sell a yellow dink if I had gotten written approval from the administration. So in the end I was compelled to buy a second blue dink so I would not lose my cafeteria job. As an ineffectual protest, I drew a picture of the famous Duke chapel wearing a yellow dink on its spire.

In spite of this incident, my life at Duke remains memorable. It is at Duke that I had met and fell in love with Ann Howell. We got married shortly after I graduated from Duke. By that time I was in the U.S. Army, a requirement then due to our conscription system at the time.

In the Army

So after getting my B.A. degree at Duke, I had to serve 2 years in the Army. Initially this requirement filled me with deep resentment. This feeling gradually receded as a result of the incredible experiences I had during this period. To the extent, in fact, that now I sometimes feel that having a conscription system has important benefits. It matures individuals and expands their horizons by exposing them to new experiences and new situations. It also serves to bring different factions of our society together and assures that the Armed Services are a part of our nation, not a separate, isolated entity.

In the 8 weeks of basic training I learned how to use a great variety of weapons and how to kill. This was not new to me, having had extensive exposure to war and death during World War II and having done quite a bit of shooting with Bobby Byers. One minor aspect of this training, relevant to my future work on vision, was how to shoot a rifle at night without night goggles. We were instructed to aim by looking off to the side a bit so that the image would impact on perifoveal regions of the retina that contain both rods and cones; rods are absent in the fovea. The existence of two these two kinds of photoreceptors, the rods and cones, was discovered by Max J. S. Schültze in the 1860s when he developed a new procedure to stain neurons in the retina (Schültze, 1866). Initially no one believed him. Now it is a true, basic fact. In trying to figure out what the rods are for, he cleverly noticed that they were absent in the fovea where night vision is quite poor. Noting this he hypothesized, correctly, that rods are for night vision. Had the Nobel Prize been in effect at that time, he would surely have been awarded it.

After basic training I was sent to clerk-typist school where I learned to touch type. I did not realize at the time that in my life I would be spending hours every day in front of a computer banging away on a keyboard. This training alone made my service in the Army worthwhile.

I was then sent to Frankfurt, Germany, where I became a clerk-typist in the medical section of the Fifth Corps Headquarters that was housed in the I.G. Farben Hochhaus, a large building in the outskirts of the city. One curious arrangement in this tall building was that it had continuous elevators with open doors. The cars moved slowly and we had to time carefully the entering and exiting of the elevator. Numerous accidents occurred, mostly minor, making it evident why this elevator design had demised.

For the first few months in Frankfurt I was billeted in a caserne the Germans had used during World War II. It was located in the outskirts of the city, as was the 5th Corps Headquarters which had belonged to a paint conglomerate that manufactured mostly explosives during the war. Neither of these building complexes was damaged much by the relentless bombing raids during the war which had destroyed and leveled large sections of the city, including the opera house.

Shortly after starting my service in the medical section, I was severely reprimanded by the colonel in charge. After firmly standing at attention, as instructed, he berated me for trying to be an individualist soldier. I was mystified. Yelling at me, he then told me that I was wearing my belt backward—something no one had noticed before. Initially I could not fathom what he meant. Turns out that being a lefty, I always put my belt on my pants starting on the left side, so that once the end of the belt came around, its tip emerged to the right of the belt buckle. He made me reverse this right then and there. After leaving the service I have returned to my former evil ways of wearing belt buckles "backward." Our sterling colonel did not seem to notice that I was wearing my watch on my right wrist, which I did, of course, to be an individualist.

One of my fellow clerk typists in the office was quite a character—Corporal Black. His hobby was race-car driving. He raced most weekends at various locations in the area. We became well acquainted and he taught me a great many things about driving. It was like learning this skill all over again. Ever since then I had always purchased stick-shift cars.

During the summer of 1956, my wife, Ann, joined me after having graduated from Duke. The Army was most generous, and we were allowed to live in a rented apartment in the city. We purchased a Volkswagen Beetle—which came with a stick shift—and took many trips visiting places in Switzerland, France, and Italy. Frank Sieverts visited us once and we reminisced about our past exploits, mostly about Longs Peak.

The major occurrence while I served in the Army in Frankfurt was the outbreak of the Hungarian revolution. When this happened I rushed to the intelligence division of the 5th Corps headquarters and told the general in charge, who kindly consented to see me, that I speak fluent Hungarian and therefore could be of some help dealing with this crisis. The general looked me up and down and dismissed my offer. "The Army is always prepared," he told me. "Ever hear of Monterey?" I shook my head. "It's a school in California where selected individuals in the armed forces are taught various languages in 9 months, including Hungarian. After they master a language they do whatever is required. So we have trained people to deal with this situation."

He went on to accuse me of using this as a ruse to get out of the impending field exercise and dismissed me. A few days later we did go on this field exercise in a forest near Frankfurt. One of my jobs was to erect a large tent with several other noncommissioned soldiers. We drove to the site in a large truck, which in addition to the tent had some wooden posts sticking out in the back. I learned from one of the soldiers that these were a part of the four-poster bed for the general. Honest!

The next day a jeep arrived at the site to pick me up. I was driven back to Frankfurt. The Army kept great records and had established from my forms that I spoke Hungarian. I was then sent to Stuttgart for 3 weeks for intelligence training. That is when I met up with Buzzy Hettleman to play tennis as noted earlier.

After this intelligence training I was sent to Munich, which at the time was the prime location to which Hungarian refugees had been sent by train. I worked in a small intelligence outfit in a beautiful villa that, right after the war, had been confiscated from a high-ranking Nazi. My job was to interrogate Hungarian refugees for military information. This was a fascinating job. I met many Hungarians from many walks of life. One of them actually provided us with some rather useful information about Russian fortifications near the Yugoslavian border. We had one other Hungarian enlisted noncommissioned officer in our group, and we also had two trainees from Monterey "ready to do whatever is required." Except they could not do so. Their language skills were dismal, and I ended up having to interrogate many of the refugees that had originally been assigned to them.

My wife joined me from Frankfurt shortly after I had started my intelligence work in Munich. Again, we were allowed to live in a rented apartment, this time in a lovely suburb of Munich, Schwabing. Because of the nature of my service, I was told never to wear an Army uniform. So I blended in well. Luckily, I still spoke German fairly well, so we lived comfortably in the city. We loved living there, visiting the museums of the numerous remarkable sites nearby. We even rented sailboats on several occasions on the Starnberger Lake south of Munich.

During this period I spent a great deal of time studying for the GREs. My wife, an English major, was of great help in expanding my vocabulary. I learned hundreds of new words in preparation for the test. I ended up doing quite well, but still remember one analogy question I could not answer. This question asked something like this: a monkey is to cage as chicken is to—followed by four words. One of the words on this list from which the choice had to be made was *coop*. I made the wrong choice as I had no idea what the word *coop* meant. But I do now!

I was delighted to learn that I was accepted into the graduate program of the Psychology Department at Clark University, which actually was the only place to which I had applied. The chairman at the time was Heinz Werner, yet another acquaintance of my father's. Due to my training with David Rapaport and George Klein, I had developed a strong interest in mental illness and in development. Werner was a developmental psychologist who had written an influential book at the time entitled *Comparative Psychology of Mental Development* (Werner, 1940).

Graduate Training at Clark

In the fall of 1957 my wife and I arrived in Worcester to start my graduate training at Clark University. This was a dramatic change after my 2 years in the U.S. Army. A repeated reminder of our time in Germany was the Volkswagen Beetle, which we had bought there and then had shipped back to the States. We continued to have this car for many years because we were both fond of it.

At Clark I was reminded daily of Rapaport and the research I had been doing with him because as one walked up to the top floor of our building where the Psychology Department resided, one passed by a statue of Freud. The reason for this was that Freud, before he became world famous, was once invited to Clark University to give a presentation back in 1909. This occasion is still heralded there, and a photo depicting Freud with several other prominent individuals is on display. They are Stanley Hall, after whom the building housing the Psychology Department had been named, Carl Jung, A. A. Brill, Ernest Jones, and the Hungarian Sandor Ferenczi. Prominent figures, now largely forgotten.

My supervisor at Clark was Morton Wiener. At that time he had worked on subliminal perception and got me involved in experiments studying this phenomenon. At this time subliminal perception became a popular topic because it was claimed that when at movie houses the word *Drink Coca-Cola* was flashed subliminally between frames, viewers would rush out in droves during the intermission to purchase the product. Based on our research we argued that rather than it being some mysterious, extrasensory event, subliminal perception is actually due to the perception of partial cues. As it turned out, this was the first published research article that had my name on it (Wiener et al., 1960).

While this research on subliminal perception was a fun undertaking, it did not hold my interest long; my interest shifted to examine visual illusions and visual masking. To carry out this new line of research, I designed a five-field stereoscopic tachistoscope, which enabled us to carry out interocular experiments. Stimuli in this device could be flashed on separately for each eye either simultaneously or successively. The department had a nice little shop, which fortunately was little used. I got permission to work there and I was able to do so without anyone else bothering me. Morton Wiener provided funds for the electronic device that could drive the fluorescent lights in the five compartments of the device. Once constructed, I carried out experiments on illusions and visual masking. In both of these types of experiments the question we addressed was to what extent various illusions and masking effects occur before or after the input from the two eyes has converged in various cortical areas. By carrying out the experiments on illusions systematically, we showed that the Ebbinghaus, Poggendroff, Müller-Lyer, and Ponzo illusions occur centrally, not peripherally. This was a debate at the time. Our ability to present stimuli interocularly for brief durations minimized binocular rivalry. The magnitude of the illusory effect was similar for binocular and interocular presentation conditions, which was not the case, as reported in some other studies in which much longer duration presentations were used that did induce binocular rivalry.

Several years later I returned to the study of illusions. In a recent study with Christina Carvey we examined the Hermann Grid illusion, which according to Gunter Baumgartner is attributable to the center-surround organization of retinal ganglion cells. By systematically varying stimulus conditions, we established that this theory is wrong and that the illusory effect is attributable to cortical mechanisms (Schiller et al., 2006).

After the initial work on illusions using the five-field tachistoscope, I turned to the study of visual masking which occupied parts of my research efforts for several subsequent years. This work was inspired by a wonderful series of experiments Heinz Werner had carried out on contour interactions in the 1930s (Werner, 1940). One line of this work had examined temporal interactions generally called metacontrast masking. When a disk and a ring are presented in rapid sequence, with the contours of the inner portion of the ring and the preceding disk shared, the disk is not perceived when the interval between the presentations of the two images is between 60 and 100 milliseconds. The conditions under which this effect occurs have been extensively studied by several investigators. Upon reading this work and carrying out informal little experiments, I became fully aware of the fact that there are several different types of masking. For some of these a monotonic function is obtained with the strongest effect occurring when the two stimuli appear in succession without a temporal interval. Such masking is dramatic when two homogeneous stimuli are presented in the same location but with the second stimulus being bigger and having a higher contrast than the first; this kind of masking earned the name brightness masking. A third effect, also yielding a monotonic function, is pattern masking when, for example, the first stimulus is a letter and the second a crisscross pattern with both having similar contrasts. What I wanted to determine was where in the visual system these masking effects occur. The first step in this effort was to determine whether masking occurs at a peripheral or a central level in the visual system. Using the stereoscopic tachistoscope I had built enabled us to address this question by presenting both stimuli either to the same eye or by presenting them interocularly. This work was carried out in a series of experiments that continued even after I became a postdoctoral fellow at MIT. Our basic finding was that brightness masking occurred only when both of the two successive stimuli were presented to the same eye, whereas pattern masking and metacontrast occurred even under interocular presentation conditions (Schiller, 1969).

Heinz Werner, like Rapaport, died while I was still in graduate school. This was 1964 when he was 74 years old. His position was then taken over by Seymour Wapner.

While carrying out this work on visual masking I decided that it would be beneficial to get a clinical degree in psychology, especially since I had extensive exposure to topics pertaining to mental illness, predominantly as a result of working with David Rapaport. The upshot of this was that I took a clinical internship during my fourth year at the Worcester State Hospital. This ended up being a most interesting and eye-opening experience. After some initial training I saw patients on a daily basis carrying out psychotherapy. I was closely supervised by a wonderful psychiatrist who was willing to spend many hours discussing the cases and instructing me in the conduct of the therapy. He was a very busy person and on several occasions I met up with him at his house in the evening to be supervised. Here I was stunned to find out that his wife was a morbidly depressed individual who spent most of her time in bed. He was working on this problem and was confident that she would overcome this situation. I never learned whether this was indeed the case.

I remember two patients in particular I saw during my internship. One of them was admitted after an acute case of catatonia. She could barely move and her jaws seemed to be locked so she could hardly speak. During the many months I worked with her she improved gradually and was eventually discharged. A little later she sent me a letter thanking me for curing her. I felt most embarrassed about this because I think I really had little to do with her improvement. It is known that often, after such a sudden onset of a psychological disorder, improvement occurs over time with or without psychotherapy. Sadly, what is also known is that when, after the "cured" individuals return to the same setting that precipitated the initial episode, they will often have another breakdown. This is the revolving door phenomenon in mental hospitals.

The second case was one in which the patient had been pulled over on the Massachusetts Turnpike for driving erratically. When the officer approached him, he vociferously announced that he is Jesus Christ. He ended up, of course, in the Worcester State Hospital. He remained Jesus Christ for quite some time while I was "treating" him. We had the most bizarre conversations, I must say, but eventually he relented, calmed down, and a few months later was discharged to return to the situation that precipitated the psychotic episode. I never heard from or about this person again. For all I know, he is now Jesus Christ again.

While my clinical training at the Worcester State Hospital was most interesting and instructive, I realized that this kind of work was not my cup of tea. I wanted to return to research full time.

During the latter part of my stay at Clark I began to look into possible postdoctoral opportunities. In particular, I wanted to learn neurophysiological methods so I could carry out experiments at the single-cell level to explain visual masking. The person I turned to was another friend of my father's, Hans-Lukas Teuber. He held a position in Psychophysiology Laboratory at the New York University-Bellevue Medical Center in New York and lived in Dobbs Ferry. I visited him several times at his house, and we discussed possible research opportunities as a postdoctoral fellow in great detail. We took long walks in the neighboring woods, where he told me about the exciting work of David Hubel and Torsten Wiesel, work that I subsequently read repeatedly in great detail. Teuber had just accepted a position as chair of the Psychology Department at MIT and so my prospect was to join him here. I was delighted to have this opportunity.

Postdoctoral Work

So after graduating from Clark University, I became a postdoctoral fellow at MIT with Hans-Lukas Teuber. This period was not only quite productive but was also central in forming the future directions of my research. Teuber was a remarkably supportive mentor who allowed me to work in several different areas. He provided me with ample space and funds to carry out several lines of research.

When I arrived at MIT, the Department of Psychology, of which Teuber had become the chair, was still largely unformed. It was Teuber's task to organize and build this department. He had an interesting vision. He did not want a department that dealt only with psychological issues. He wanted a much broader representation that included brain science. He did this effectively by making a series of outstanding appointments. Notable among these was Walle Nauta, who was a famous neuroanatomist. One of the students trained in his laboratory is Ann Graybiel, who subsequently became a faculty member of our department, has been inducted in National Academy of Sciences and recently became an Institute Professor at MIT. Walle Nauta was a striking personality with whom I had extensive contact. It turned out that he was also an avid sailor and had a sailboat just like mine (a Thistle). He and I were in the same yacht club in Boston Harbor and during the spring, summer, and fall seasons we sailed races just about every weekend. This club had several outstanding sailors, including Joe Duplin who sailed Stars and won the world Star championship one year. One day, when he was at loose ends at the club, Duplin volunteered to crew for me and provided me with many cues to improve my sailing skills. One of these I still vividly remember. As we were sailing along, one my cleats got jammed temporarily. He firmly instructed me to replace it right away: "Once it jams, it will jam again," he assured me. This is true for most things, so I have learned to take his advice in hand. Whenever something in my laboratory malfunctions, I replace it to prevent it from happening again.

The other outstanding sailor, also in the Thistle class, and the winner of most of our Thistle class races, was Hatch Brown. I mention him because subsequently he became the sailing master at MIT. MIT is situated right along the Charles River and sailing is taken quite seriously here. During the weekends and on most weekdays, the river is festooned with hundreds of sailboats, many of them from the MIT Sailing Pavilion. Some of us in the department take advantage of this luxury and sail out of the pavilion periodically. Sadly, the Charles River is quite polluted in spite of repeated projects to "clean up the Charles." On a rather windy day, some years ago, I shipped in about two feet of water into the boat I was sailing, narrowly missing a capsize. Looking down after the boat had been righted, my shoes under the dark brown turgid water could not be seen. While the ocean waters in Boston Harbor are not exactly clear, they are much less polluted than the Charles. So capsizing there, which had happened to me several times, was not nearly as disconcerting.

Shortly after becoming a postdoc at MIT, I became friendly with Steve Chorover and Charlie Gross. We spent a lot of time together and were often referred to as the three musketeers in the department. I ended up carrying out numerous experimental projects with both of them as will be described later.

The first line of work I did at MIT was a continuation of the examination of visual masking. Teuber provided financial support to build a new five-field tachistoscope in one of the instrument shops at MIT. This turned out to be a real Cadillac in comparison with the one I had built at Clark. The displays in each field could be adjusted with millimeter precision. The base of the device was made of a ¾ inch thick aluminum plate. In collaboration with Marylin Smith and Alan Greenfield, we carried out several experiments to further test masking under both monocular and interocular conditions (Schiller, 1969; Schiller et al., 1966, 1969).

Teuber also strongly encouraged me to learn single-cell recording techniques to enable me to study the neurophysiological underpinnings of visual masking. I carefully read the technique sections of many papers, particularly those of Hubel and Wiesel and of Peter Bishop in Australia. I was given the funds to purchase the necessary equipment, which included optic benches, a Xenon arc lamp, stereotaxic instruments, amplifiers, microdrives, oscilloscopes, and printers. I learned how to operate on animals to enable me to record from single cells in the brain. Particularly difficult for me was to learn how to make good microelectrodes. This was a time before I met David Hubel, but I was friendly with one of his students, Michael, who was the son of Francis Crick; he invited me over to the Hubel laboratory at the Harvard Medical School, and he ran me through the process of making varnish-coated tungsten microelectrodes. These are the ones I then used in the experiments recording from the lateral geniculate nucleus of the cat. I found, perhaps not surprisingly, that brightness masking had its source in the retina. The rapidity with which information is processed through the retina to the retinal ganglion cells is contrast dependent. When visual stimuli have low contrast, the processing takes longer than when they have high contrast. Consequently, the response of the retinal ganglion cell to the dim stimulus is taken over by the response elicited by the subsequent bright masking stimulus. I carried out this work on my own and was consequently the sole author on the resultant paper (Schiller, 1968, 1969).

Concurrently with doing these masking experiments I started a project with Steve Chorover that examined retrograde amnesia, an area Teuber had encouraged us to pursue. We trained rats on several tasks and then administered electroconvulsive shock to induce memory loss. In the first set of experiments we used the Hebb Williams maze. This is a most clever device in which, using partitions, the route from the entrance to the location of the reward the rat was after could be endlessly varied. We brought in numerous hooded rats, which we initially allowed to roam around in large groups to become familiar with this wonderful maze. One day, looking as the ceaseless running around of the cute rats, Steve remarked: "Seething ratmanity." The things one remembers!

Initially these experiments were unsuccessful. Electroconvulsive shock administered after a rat had learned a particular maze pattern did not interfere with what had been learned. So we decided to start something different. Based on the work of some other investigators, we built a one-trial learning apparatus which had a little pedestal in the center of an enclosure and an electric grid below. The natural tendency of all rats, once they were placed on the pedestal, was to step down onto the grid. When they did so they received a mild electric shock. The next time they were placed on the pedestal they did not step down. This exemplified one-trial learning. During the experiments we then took the rat out after the animal had stepped down and we administered electroconvulsive shock. Much to our dismay, these treated animals the next day remained crouched on the pedestal. Their one-trial learning was not interfered with by the electroconvulsive shock.

For a while we were stumped and began to doubt much of the literature on retrograde amnesia. But then Steve had a great idea. Right down the street from our laboratory there was a fastener factory we were always aware of because of the constant humming of the machinery that stamped out the fasteners. Steve suggested that we attach fasteners to the rats' ears so that when they stepped down in the apparatus they could receive electroconvulsive shock instantly. So we went to the factory, where the staff was extremely helpful and friendly. They supplied us with boxes of fasteners for our experiment. We got so many of them that we could still run these experiments today were we so inclined. We then proceeded to administer instant electroconvulsive shock and suddenly got dramatic results. When the shock was administered right after the step-down and up to a 30-second delay, the animals the next day, once placed on the pedestal, stepped down right away as if they had never encountered the situation before. We referred to this as short-term retrograde amnesia and published a paper in *Science* describing the work, which received considerable attention (Chorover et al., 1965).

Steve Chorover and I were quite feverish at this time and we got involved in several other projects. To further pursue the metacontrast effect, Steve and I carried out an experiment in which we collected evoked potential data in the human posterior cortex. As reported in a *Science* paper, we found that even when the masking was optimal, the evoked potential generated by the first stimulus, the disk in the disk-ring sequence, was of the same magnitude as when it was clearly visible, indicating that this effect occurs at higher levels in the visual system (Schiller et al., 1966). These findings were in consonance with a study Marylin Smith and I had carried out examining metacontrast, showing that if a forced-choice discrimination task is used in which two rings are presented to the left and right of the initial fixation, subjects could always specify whether the preceding disk had been presented with the left or the right ring. Furthermore, the response latencies were the same throughout the various temporal intervals used between the appearance of the disk and the ring. The results we obtained in these experiments led me to suggest that the metacontrast effect is linked to apparent motion; when a stimulus like a disk appears successively at two locations, motion is perceived and the initial location is discounted (Schiller, 1969; Schiller et al., 1968).

We also carried out several other experiments examining learning and retrograde amnesia. One of these studies, in rats, examined the effects of spreading depression and callosal sectioning. This work was inspired by Jan Bures, who had done a great deal of work on spreading depression. We also carried out some conditioning experiments in planaria, which we had collected from under the rocks in the waters of nearby lakes in Cambridge. Work using planaria was hot at the time resulting in many publications in *The Worm Runner's Digest*. In one series of studies James V. McConnell reported a cannibalistic experiment in which planaria were fed chopped-up soul mates that had been trained in a conditioning experiment in which the conditioned stimulus was light and the unconditioned stimulus was electric shock. The claim was that as a result of this feeding, planaria learned faster when the planaria fed to them had been conditioned than when they were unconditioned. Our work was simply interested in retrograde amnesia, so we tried to interfere with the conditioning using a variety of means. Nothing of much significance came of this work and we never published anything on the planaria work. But doing the experiments was certainly a lot of fun. What I did learn from these efforts is that you need to keep your nose to the grindstone because the majority of experiments one undertakes to study the brain do not work out at all or yield little of significance.

So to keep my nose to the grindstone, I also became involved in research with Charles Gross and George Gerstein, which examined the functions of inferotemporal cortex using single-cell recording methods. One of my jobs was to make the microelectrodes for the recording since I had some experience with this. At that time a great article had come out in *Science* by Myron Wolbarsht, describing a new platinum-iridium electrode coated with molten glass (Wolbarsht et al., 1960). Not only do these electrodes record well, they are extremely sturdy and can penetrate the dura, making it possible to record neuronal activity in trained, alert monkeys with ease and without discomfort. I learned how to make these electrodes and I still use them extensively to this day. The ones I make, at least in my opinion, are superior to the ones one can buy. Myron is presently a professor of psychology at Duke.

Working with George Gerstein was most instructive. He is a gifted neuroscientist with excellent computer skills. He instituted the poststimulus time histograms which we use to this day to present single-cell recording results.

At the time this work was under way, Charlie was offered a position at Harvard, which he accepted. There he continued the work on inferotemporal cortex that has made a major impact in the field. His autobiography appears in Volume 6 of this series. Charlie, like me, is a canoeist and frequently vacationed on Lake George. This is a beautiful, clear lake in New York State ideally suited for canoeing. It has a great many islands with camp sites. My wife and my children joined Charlie at Lake George on several occasions. I had bought a canoe shortly after working at Camp Timberlake which we took along for these excursions. We also took numerous canoe trips exploring lakes and rivers in New England. On some of these trips we were joined by the people who worked in my laboratory.

For many summers my family and I rented a house on an island called Sutton just off Mount Desert Island in Maine. Quite a few young children vacationed there, and I instituted the Number War game I as described earlier. Charlie Gross joined us there once and we had a great time playing this game. On another occasion David Hubel came for a visit and he too thoroughly enjoyed the game. To the extent that once when he invited me to give a talk at Harvard, most of his introduction consisted of an engaging and funny description of this game.

Another memorable occasion I spent with David Hubel was at a winter conference in Teton Village. He, Marge Livingstone, Ralph Freeman, and I rented a lovely condominium. We did a lot of skiing together and in the evenings had extensive discussions, much of it centering on binocular vision and stereoscopic depth perception, which have been extensively studied by Marge, David, and Ralph. These discussions were one of the early sources of my interest in this area of research which I am still pursuing as described in the next section.

Shortly after I had become an Assistant Professor in the department, Emilio Bizzi came to MIT. We soon got to know each other and began a series of experiments in my laboratory working with alert monkeys. This was a major advance in my training. Emilio had worked at the NIH with Ed Evarts, who had devised techniques to record from behaving, alert monkeys. I soon learned these procedures from Emilio and use them to this day. Ed Evarts was the Chief of the Laboratory of Neurophysiology at the National Institute of Mental Health and in 1974–1975 was president of the Society for Neuroscience. He was always in excellent shape and did a lot of running daily. Quite unexpectedly, Ed died in his office in 1985 from a myocardial infarction. He was just 59 years old.

At the NIH Emilio did recordings in the frontal eye fields of alert monkeys that yielded major new discoveries about the neural mechanisms underlying eye-movement control. In the work we did after he came to MIT, we recorded from the frontal eye fields examining the role of this area in head movements and smooth pursuit eye movements. We found cells specifically involved in both of these motor acts in addition to the cells Emilio had discovered earlier that discharged in association with saccadic eye movements (Bizzi et al., 1970). Emilio went on to a brilliant career. He is a member of the National Academy of Sciences and the President of the American Academy of Arts and Sciences. He was chairman of our department from 1986 to 1998. His autobiography appears in Volume 6 of this series.

In 1964 I became an Assistant Professor at MIT. The first three students who obtained their Ph.D.s in my laboratory were Marylin Smith, Larry Squire, and Michael Stryker. All three carried out independent research in this undertaking.

Research from 1970 until the Present

The research I carried out with Emilio Bizzi opened up the floodgates in my laboratory. In the following six subsections I summarize this body of work, which can also be viewed on our Web site (http://web.mit.edu/bcs/schillerlab/).

The Neural Control of Eye Movements

After the studies Emilio Bizzi and I carried out on the frontal eye field, I wanted to examine the role of various subcortical areas in eye-movement control. The first set of experiments I carried out on my own, recording from single neurons in the oculomotor, trochlear, and abducens nuclei whose axons innervate the eye muscles. This was rewarding work yielding straightforward results, thanks in part to the fact that the extraocular muscles are not segmented; the fibers in each muscle run the entire length of the muscle. Consequently, the activity of a single neuron that innervates a fiber corresponds directly to the movement of the eye. The rate of maintained activity in these neurons defines the positional angular deviation of the eye in orbit. When quantified, this reveals a linear relationship between the neuronal activity and the angular deviation of the eye in orbit. These same cells produce saccadic eye movements by virtue of high-frequency bursts that rapidly contract the muscle; the duration of the burst defines the amplitude of the saccade generated (Schiller, 1970).

While doing this work, David Robinson visited MIT and we were both surprised to learn that he and I were doing highly similar experiments that involved recording in the brainstem oculomotor centers. Our findings were in complete agreement. David suggested that we publish this work concurrently in two different journals, which we did. I have gotten together with David, who has an engineering background, many times since then. David is a brilliant, wonderful individual who has made seminal contributions to our understanding of eye-movement control (Robinson, 1975).

After the work on the brainstem oculomotor centers we moved on to study the superior colliculus. To initiate this work I first developed a surgical procedure to immobilize one eye in monkeys which would allow us to map visual receptive fields and hence establish the relationship between the location of the receptive fields of neurons in the superior colliculus and the physical dimensions of the eye movements that monkeys make with their intact eye. I dissected numerous brains and eventually succeeded in this quest. In the ensuing work we both recorded and electrically stimulated the superior colliculus. I was joined in this effort by Fritz Koerner, Michael Stryker, Sean True, and Julie Sandell. We succeeded in deriving the basic operational characteristics of this structure for the generation of saccadic eye movements (Schiller, 1984; Schiller et al., 1971, 1972). On the basis of our work we concluded that the superior colliculus carries a vector code: When cells in the intermediate and deep layers of the colliculus discharge vigorously, a saccadic eye movement is generated that shifts the center of gaze into the receptive fields of the active neurons. In a similar fashion, electrical stimulation of collicular neurons generates saccades that shift the center of gaze into the receptive fields of the stimulated neurons. What is computed then is the location of the receptive fields of these neurons relative to the fovea. The signal generated is sent down to the brainstem oculomotor centers to produce the desired eye movement that shifts the center of gaze into the receptive field of the activated neurons. Since the visual field is laid out in a neat topographic order in the superior colliculus, different subregions in this structure code different vector saccades. Concurrent work by Wurtz and Goldberg as well as by Robinson were largely in agreement with this view (Robinson, 1972; Wurtz et al., 1971).

An unexpected reward subsequent to the submission of our first paper on the superior colliculus work was an invitation to a conference in Canberra, Australia, that I received, actually before the paper made it to print. This happened because Peter Bishop, who had organized this meeting, had been the referee and was, luckily, impressed by the work. David Hubel, Ann Graybiel, and I joined forces to take this long trip. We were advised to travel with stopovers and decided to visit Tahiti for a few days. There we rented a car and explored the island, taking hikes to scale some of the steep mountains and walking the black sand beaches.

The meeting in Canberra was certainly an august occasion. It began with brief speeches by the prime minister of Australia and the American ambassador. Bob Wurtz and I presented our findings about the collicular control of eye movements. Among the numerous other outstanding presentations, I particularly remember those that dealt with the various classes of retinal ganglion cells initially identified by Enroth-Cugell and Robson and named the X, Y, and W cells (Enroth-Cugell et al., 1966). The extensive research carried out on this topic in Canberra was reported by several investigators (Bishop et al., 1972). This work was of great interest to me, and subsequently I carried out numerous studies examining the parallel channels that originate in the retina as described later.

An interesting aspect of our visit was encountering native Australian animals, such as the kangaroo, koala, wombat, wallaby, and the emu bird. Upon seeing the emu I thought it might be fun to come to Australia for a bit to study emu eye movements. David Hubel and I took numerous photographs during our excursions. On one occasion David, who by the way is also left-handed, spotted a koala sleeping in a tree squeezed between two adjoining branches that had the shape of the letter Y. Subsequently he allowed me to add this picture to a collage of more than 100 neuroscientists, which was published in an article I was asked to write for the 1986 jubilee issue of *Vision Research* (Schiller, 1986). The task was to describe the advances that had been made during the preceding 25 years in visual neuroscience—which was a lot more than what had been made since the beginning of times until 1960. The inscription to the sleeping koala picture in the paper says: *The koala bear, whose visual system has not been studied, suggesting yet another hypothesis for Y cell function.* I am not sure that the participants of this symposium much appreciated this flippancy—if they have ever noted it. The original photos from this paper are mounted in the hallway next to my office for everyone to view. Recently I did something on the morbid side: I marked those in the collage who are now dead by attaching small red labels next to their photos. Several people in our department have asked what these labels mean. I find it dismaying that of the 114 individuals whose portraits appear in this collage 16 are now dead; among them are Stephen Kuffler, Robert Rodieck, Gian Poggio, David Marr, Otto Creutzfeldt, Irving Diamond, James Sprague, Richard Young, and Roger Sperry.

Perhaps the most memorable occasion during this visit to Australia arose when David Hubel, Ann Graybiel, and I went to visit an observatory in Canberra. David, like me, had quite an interest in the constellations. In particular, we wanted to get a good view of the Southern Cross. David had made an appointment with one of the astronomers at the observatory. He was a most friendly, kind person who set up two telescopes through which we could view stars and a planet. This astronomer, however, had the worst stutter we had ever encountered. Pointing to one of the telescopes for us to look through, he tried to explain that it was pointing at the planet M . . . M . . . M . . . M . . . Mars. So everything he told us—we had asked about the major constellations in the Southern Hemisphere—took just about forever to get out. Yet this was a remarkable evening that satisfied our curiosity about the Southern Constellations.

After returning from this trip, in the next set of experiments we went on to examine the visual inputs to the superior colliculus by antidromically activating neurons in the retina, by reversibly inactivating area V1 with cooling, and by selectively blocking the midget and parasol systems in the lateral geniculate nucleus. In this effort I was joined by Joseph Malpeli, Carol Colby, Susan Volman, Julie Sandell, Max Cynader, Nancy Berman, Michael Stryker, and Stan Schein. This work established that the direct retinal input to the superior colliculus, which connects to the superficial gray layer of this structure, comes predominantly from small retinal ganglion cells that fall in the category of W cells as initially identified by Enroth-Cugell and Robson (1966). The input from area V1 to the superior colliculus comes from complex cells that reside in layer 5 and are driven exclusively by input from the parasol system, which I will describe in more detail in the next section. We also showed that when area V1 is inactivated, neurons below the superficial gray layer of the superior colliculus can no longer be driven by visual stimuli, indicating that in higher mammals this structure is under the control of the cortex. When tested, even many months after removal of area V1, these cells cannot be activated with visual stimuli (Schiller et al., 1974).

We then proceeded to expand our effort by examining the role of various cortical areas in the generation of saccadic eye movements. In our initial effort to study the cortex we electrically stimulated various regions using microelectrodes to determine from which areas saccadic eye movements can be generated. This work revealed, as did the work of many other investigators, that quite a few cortical areas contribute to eye-movement generation. Notable in our work were areas V1, V2, LIP, the FEF, and the MEF. In this effort I was joined by Edward Tehovnik who has the distinction of having spent the longest time in my laboratory, more than 20 years. Ed was extremely productive during this time period and published more than 40 papers, many of them independently. He made a major contribution to establishing the functional characteristics of the MEF. This structure, unlike most others we had studied in the cortex, carries a place code; electrical stimulation shifts the eye to a particular orbital position and keeps the eye there. Different subregions of this structure shift the eye to different orbital positions. The other areas, V1, V2, LIP, and the FEF, when stimulated, produce saccades similar to those obtained in the superior colliculus; a constant vector saccade is generated, the amplitude and direction of which depends on the subregion stimulated within each area. As in the superior colliculus, in area V1 the stimulation generates a saccade that shifts the center of gaze into the receptive field of the stimulated neurons. Prolonged stimulation in V1, V2, and the FEF produces a staircase of identical saccades (Schiller, 1998).

The next question we posed is how the activity in these cortical areas reaches the brainstem. We discovered that after the superior colliculus has been removed, electrical stimulation still evoked saccadic eye movements from the FEF and MEF, but failed to do so from the posterior cortex, even many months after collicular removal. These findings suggested, as supported by anatomical studies, that the frontal cortex has connections that reach the brainstem oculomotor centers directly (Schiller, 1977, 1998).

We then proceeded to examine what kinds of deficits arise in eye-movement generation when the superior colliculus and various cortical areas are removed. At this time we were also engaged in studying express saccade generation. Initially we were greatly surprised to obtain a bimodal distribution of saccadic latencies when monkeys made eye movements to singly appearing visual targets. I am ashamed to say that I first accused my postdoctoral collaborator at the time, a gifted computer programmer, John Maunsell, of having made a mistake in his program that collected eye-movement records. After a careful examination of his program he assured me that the effect was a real one. Shortly thereafter a paper came out by Fischer and Boch documenting this effect and naming the first phase of the bimodal distribution express saccades (Fischer et al., 1983). This discovery triggered hundreds of experiments. We have also published numerous papers on the topic. As an aside, Fischer once told me that the first time he saw the bimodal distribution of saccadic latencies he too thought it was due to a computer programming error.

Our lesion studies showed that after collicular removal express saccades are eliminated and after FEF lesions monkeys have difficulties in target selection. However, after each of these lesions, as long as they were made bilaterally, monkeys continued to make eye movements quite well, even when tested just 4 or 5 days after the lesions. This was not the case, however, after unilateral collicular lesions, which induce extreme deviations of the eye toward the side of the lesions as well as circling behavior. These deficits persist for many months and have been noted in other studies as well that denoted severe deficits after unilateral brain infarcts (Schiller, 1998; Schiller, et al., 1979, 1980).

The most significant finding in these lesion studies was that after bilateral removal of both the superior colliculi and the frontal eye fields, monkeys became incapable of making visually guided eye movements at all; their eyes appeared fixed in orbit looking straight ahead. We have documented these effects, from which there was practically no recovery, by filming the animals, films I had shown at a great many presentations.

In an elegant set of experiments around this time Wurtz and Hikosaka established that the generation of each eye movement involves a complex interaction between excitatory and inhibitory processes (Hikosaka et al., 1985). They showed that when a GABA agonist is injected into the colliculus, which increases inhibition, monkeys have major difficulties in generating saccadic eye movements with the vectors represented by the affected neurons. Conversely, they showed that when a GABA antagonist was infused, thereby reducing inhibition, the monkeys could not help generating saccades with the vectors represented by the disinhibited neurons. Subsequent work identified some of the complex circuitry involved in the generation of saccadic eye movements (e.g. Schiller et al., 2005). We expanded on this work by carrying out similar experiments in the cortex, showing that in the FEF the effects obtained were just like those in the superior colliculus. We have furthermore shown that infusion of both of these substances into area V1 eliminated the generation of saccades with vectors that would have shifted the center of gaze into the receptive field of the affected neurons (Schiller et al., 2005). We presume this happened because visual processing in area V1 is disrupted by both of these agents.

The upshot of all of these experiments was our proposition that visually guided saccadic eye movements are controlled by two parallel systems, which we called the anterior and the posterior. The posterior system gains access to the brainstem through the superior colliculus and plays a central role in the rapid and accurate execution of saccadic eye movements, whereas the anterior system plays an important role in the process of selecting visual targets in the visual scene to which saccadic eye movements are to be made. Humans make about three saccades per second, some 170,000 saccades a day. With each shift in gaze, a decision has to be made as to where to shift the eye next, except in situations when only single stimulus appears on a homogeneous background, as would be the case when a bird materializes in the blue sky. We carry out most of these calculations without being aware of them.

Further work examining the role of cortical areas in visually guided eye movements has been carried out in my laboratory independently by Jeff Schall. After leaving my laboratory Jeff became a professor in the Department of Psychology at Vanderbilt University, where he continues his outstanding work studying the functions of the frontal lobe.

The Midget and Parasol Systems of the Retina

Two major retinal ganglion systems that originate in the retinae of higher mammals are the midget and parasol. As several studies have established, including the ones Joe Malpeli and I carried out, the midget and parasol retinal ganglion cells project to different sublamina of the lateral geniculate nucleus of the thalamus; the midget cells project into the parvocellular layers and the parasol cells into the magnocellular layers (Schiller et al., 1978). Joe Malpeli came to my laboratory as a postdoctoral fellow in 1974 right after obtaining his Ph.D. at Johns Hopkins. He received his undergraduate degree at MIT in 1967, so joining my laboratory was like coming home. Joe is a most innovative individual with outstanding manual skills. He created several types of hardware for our work, including a metal-coated glass microelectrode that could be used to both record and inject various pharmacological agents into various brain regions (Malpeli et al., 1979). We used these electrodes in several experiments in our efforts to learn about the functions of the midget and parasol systems. Joe Malpeli and I were joined by several other students and collaborators in this effort. They included Carol Colby, Stan Schein, John Maunsell, Eliot Charles, and Nikos Logothetis.

In the first set of experiments we set out to determine the extent to which inputs to area V1 from the midget and parasol systems remain separate or converge on single cells. To accomplish this, thanks to Joe Malpeli's skills, we reversibly inactivated either the midget system or the parasol system while recording from individual neurons in area V1. The inactivation was achieved predominantly by infusing lidocaine into either the parvocellular layers or magnocellular layers of the lateral geniculate nucleus (LGN), thereby blocking the input to V1 from either the midget or parasol systems. This was difficult and time-consuming work as it required us to place our electrodes in the LGN and in area V1 at sites where the neurons in these two areas had overlapping receptive fields, thereby assuring us that the small injections in the LGN affected those cells that connected with the cortical neurons we were studying. The results obtained with this work showed that more than 30% of V1 cells receive convergent input from the midget and parasol systems. However, as already noted, the layer V complex cells that project to the superior colliculus are driven exclusively by the parasol system. Subsequently John Maunsell's group examined the projections of the midget and parasol systems to areas V4 and MT and showed in an elegant series of studies that area MT is driven predominantly by the parasol system, whereas V4 receives input from both systems (Ferrera et al., 1992; Maunsell et al., 1990).

We next turned to the question of what the functions are of the midget and parasol systems. To answer this question, we carried out a long series of experiments in which we used psychophysical procedures to assess several visual functions after either the midget or parasol systems had been blocked as a result of small lesions made in the magnocellular or parvocellular layers of the LGN. These experiments revealed that the midget system processes color, fine pattern detail, and stereopsis, whereas the parasol system plays a central role in the processing of motion and motion parallax for depth perception. The conclusion we came to is that these two systems have emerged in the course of evolution to extend the range of vision, with the midget system extending it into the high spatial frequency domain and in wavelength analysis for color vision, and the parasol system extending it into the high temporal frequency domain (Schiller, 1993; Schiller et al., 1990).

Our ability to carry out this work was greatly aided by developing a set of computerized systems to collect quantitative data using randomized sequences of stimulus presentations. In the initial work, the computer programs were created by Andreas Polit and Sean True using a PDP 11/20 computer. Visual stimuli were presented first using optic benches I had put together with stepping motors that allowed randomized presentations of bar orientations and lengths, directions of movement, and varied spatial frequency gratings that could be moved across the receptive fields of neurons in recording experiments. Subsequently we used color monitors whose resolution to this day does not come close to the resolution one can get with optic benches.

The new computer system was then used in several experiments. With Susan Volman and Barbara Finlay, we made a detailed quantitative study of neurons in area V1 following in the footsteps of Hubel and Wiesel. We did this work during the time we examined the cortico-tectal projections. When we started that work and identified the cortical neurons that projected their axons to the colliculus, we did not realize how low the probability was of finding such neurons using antidromic stimulation methods. As we were advancing the electrodes in the cortex, we kept obtaining beautiful responses from one neuron after another; having such a neat system to study the receptive field organization of neurons, we could not resist examining every well-isolated cell. We ended up obtaining detailed data from more than 200 cells, 45 of which projected to the superior colliculus. Our quantitative work confirmed Hubel and Wiesel's remarkable discovery of the simple and complex cells in V1. We furthermore identified several subclasses of simple cells, some of which received input only from the ON system, some from the OFF system, and some from both. The ON and OFF systems will be discussed in the next section. We found that virtually all simple cells were directionally selective. The majority of complex cells were also direction selective. What we failed to show, however, is that the third category of cells Hubel and Wiesel had identified, the hypercomplex cells, form a separate, distinct category. The prime definition of these cells was that they are "end-stopped," which meant that they responded much more vigorously to short bars presented in their receptive fields than to long bars. Quantitative analysis of the length tuning curves we obtained revealed that the degree of end stopping varies over a broad range in both simple and complex cells, indicating thereby that the attribute of end-stopping does not yield a distinct third population of cells in area V1.

We published our findings on this recording work in area V1 in five successive papers in the *Journal of Neurophysiology* in 1976. Shortly after it was published I received a letter from Vernon Mountcastle in which he complimented us profusely, especially for the quantitative methods we had used. He went on, however, to point out two errors in the figure legends—there were a total of 75 figures with legends in the five papers—errors which no one, including of course myself, had previously spotted. What a scholar! Vernon Mountcastle's autobiography appears in Volume 6 of this series.

A second line of work utilizing our computer system constituted Michael Stryker and Helen Sherk's thesis at this time. They decided to examine quantitatively the claim made by Colin Blakemore that in kittens that had been reared in a restricted environment during the first 3 months of their lives, by exposing them daily to either only horizontal or vertical gratings, most neurons acquired the orientation specificity corresponding to the conditions under which they had been raised. The data Helen and Michael collected were carried out without them knowing how the animal had been reared. Each cell's orientation selectivity tuning was obtained with the automated computer system (Stryker et al., 1975). This work, which created quite a stir at the time, failed to replicate the initial findings by Blakemore and Van Sluyters (1974). On the lighter side, when Michael Stryker presented these findings at a neuroscience meeting, he wore a custom-made striped shirt that had vertical stripes in front and horizontal stripes in the back.

A significant additional fact that arose pertaining to this work came about when Helen Sherk had the idea of determining just how the stripes on the walls of the circular chamber, in which the kittens were placed daily, impinged on the retina. She did this by taking photographs from the cat's eye point of view. This revealed something quite unexpected. The projections of both the horizontal and vertical stripes formed many different orientations on the retinal surface. So no wonder that in area V1 of these animals neurons with many different orientations were found. On the whole, however, the orientation tuning properties of cells in these specially reared cats were not nearly as sharp as in normally reared animals.

In 1977 a major disaster struck our department at MIT. While Hans-Lukas Teuber was vacationing with his wife, Marianne, in the British Virgin Islands, they took a swim and the strong tide there swept Lukas out to sea. In his effort to swim back, he became exhausted and had a fatal heart attack. He was just 60 years old. Dick Held took over ably as the Department Chair, a position he held until 1986 at which time Emilio Bizzi took over followed by our present chairman, Mriganka Sur in 1998. Since its inception in 1961, our department has grown by leaps and bounds. We now have 47 faculty members, 95 graduate students, and 180 postdocs and research investigators. The department, since its inception, has awarded 329 Ph.D. degrees. Eight of our faculty have been inducted into the National Academy of Sciences: Edward Adelson, Emilio Bizzi, Robert Desimone, Ann Graybiel, Richard Held, Nancy Kanwisher, Susumu Tonegawa, and myself. A more detailed description of our department is provided on our Web site (http://bcs.mit.edu). The autobiographies of Richard Held and Emilio Bizzi appear in Volume 6 of this series.

The ON and OFF Channels of the Retina

As a result of the work on the midget and parasol systems, we developed a strong interest in the retina, especially in the origin and functions of the ON and OFF systems as well as the midget and parasol systems.

The basic response characteristics of the retinal ganglion cells were first established by Haldan Keffer Hartline who had recorded from isolated retinal ganglion cell axons and studied their characteristics by shining beams of light into the eye (Hartline, 1938). He found that some cells responded when the light was turned on, some when the light was turned off, and some responded to both events. He called them the ON, OFF, and ON/OFF cells, names used to this day. He received the Nobel Prize for this work in 1967. The initial idea that has emerged from this work was that the function of the ON and OFF cells was to signal, respectively, the appearance and the termination of a visual stimulus. Subsequently several different hypotheses have been advanced as to why there are ON and OFF ganglion cells in living organisms. Two subsequent discoveries played a central role in the formulation of these hypotheses. The first, largely attributable to Kuffler, was that retinal ganglion cells, as well as cells in the lateral geniculate nucleus, have antagonistic center/surround organization; small spots of light presented in the center of the receptive fields of neurons—the small region in the visual field to which these cells responded—produced vigorous responses, whereas large spots barely activated the cell (Kuffler, 1953). The second set of discoveries was made by Hubel and Wiesel, which showed that in the visual cortex neurons are selective to the orientation of edges and to the direction of motion of visual stimuli (Hubel et al., 2005). Hubel and Wiesel received the Nobel Prize in 1981 for their remarkable discoveries. Taking all of these new findings into account, theories have been advanced proposing that the ON and OFF systems originating in the retina evolved to produce the center/surround organization in these cells and to produce orientation and direction selectivities in the cortex.

One of the central features of visual processing is to analyze information in the visual scene based both on the perception of lightness and darkness. Due to the composition of their surfaces, some objects absorb light and some reflect it and typically do so selectively for different wavelengths, thereby giving rise to the perception of color. Living organisms need to and are capable of processing information based on both increases and decreases in the number of photons that enter the eye. Consequently, another idea about the ON and OFF systems has been that they emerged in the course of evolution so that both light increment and decrement could be processed rapidly in the visual system (Schiller, 1995).

Critical examination of these ideas became possible when several additional discoveries had been made about the workings of the retina. Werblin and Dowling developed procedures that enabled them to record intracellularly in the retina (Werblin et al., 1969). This work, carried out in the mudpuppy (*Necturus maculosus*), yielded remarkable and unexpected discoveries. Werblin and Dowling found that all photoreceptors hyperpolarize to light. The neurotransmitter of all photoreceptors is glutamate as has been established in several laboratories. The ON and OFF systems arise at the level of the bipolar cells. The ON and OFF bipolar cells have different neurotransmitter receptor sites. Those of the OFF bipolars are sign conserving and therefore respond in a similar fashion to the incoming light as do the photoreceptors. The ON bipolars on the other hand have a unique metabotropic receptor mGluR6 that inverts the incoming signal from the photoreceptors. Thus, in the course of evolution a double-ended system has been created from the single-ended one seen in the photoreceptors, thereby creating a situation that makes it possible to send excitatory signals into the central nervous system for both light incremental and light decremental information. Dowling and Werblin also established that the photoreceptors, horizontal cells, and bipolar cells only generate graded potentials. Action potentials are produced in all ganglion cells and in some of the amacrine cells. As a result of these remarkable achievements, Dowling was inducted into the National Academy of Sciences, which now has about 2500 elected members from all sciences, with about 50 in section 28 named *Systems Neuroscience*. Dowling's autobiography appears in Volume 4 of this series.

In 1981 a remarkable paper was published in *Science* by Slaughter and Miller, who also carried out their work in the mudpuppy. They applied a glutamate neurotransmitter analog, 2-amino-4-phonobutyrate (APB) to the retina, which had been created by Watkins and Evans in England, and found that it silenced the ON system by blocking the responses of the ON bipolar cells (Slaughter et al., 1981). The OFF system was unaffected. This work opened up the floodgates for carrying out research aimed at determining why the ON and OFF systems have emerged in the course of evolution.

I became greatly interested in this work and began an extensive series of experiments to study the ON and OFF channels of the visual system. As a first step in this effort I wanted to determine whether the discoveries made by Slaughter and Miller also apply to mammals. To accomplish this we proceeded to develop methods that enabled us to infuse APB into the eye of monkeys while recording in the lateral geniculate nucleus and various cortical areas.

I carried out this work in collaboration with several students in my laboratory who included Michael Stryker, John Maunsell and Julie Sandell, Andrew Knapp, and Robert Dolan. Our procedures took awhile to develop. We decided to infuse solutions into the eye through a fine tube and also placed a larger tube at a lower location that allowed the infused solution to escape from the eye. Well, when we first did this, due to the viscosity of the vitreous, the solution could not escape from the eye, thereby increasing the intraocular pressure to a level that terminated the activity of neurons in the retina. We then tried several procedures to overcome this problem. One was to apply hyaluronic acid that breaks up and liquefies the vitreous. This worked, but it caused some mild discoloration. So instead, we turned to a method that sounds terrible but has been commonly used by ophthalmologists. We used the equivalent of an eggbeater, a miniature one, that could be inserted into the vitreous through the larger tube. Twirling it around gently broke up the vitreous effectively without causing any discoloration or damage to the retina. So we ended up using this procedure but then ran into another unexpected problem. Once we started to infuse saline into the eye, thinking it was the appropriate control solution, the neurons again became unresponsive in short order. Looking into this problem, we learned that the composition of the vitreous is complex and that one needs to create a solution which has electrolytes akin to those in the vitreous. Fortunately, Cunningham and Miller (1976) created a perfusate that is similar in composition to the vitreous. Once we had succeeded in concocting this rather complex solution to be appropriate for the monkey, we had a major success: infusion of this substance into the eye did not alter the responses of neurons when their receptive fields were stimulated with light spots. We were then able, through another container, to infuse this solution with APB added and to then wash it out subsequently. Thereby we could assess neuronal responses before, during, and after the administration of APB.

This work has established several facts: First, the ON cells in the LGN were silenced in the monkey when low concentrations of APB were infused into the eye; OFF cells were largely unaffected, showing that the neurotransmitter system is similar in the monkey to that seen in the mudpuppy. Second, we found that while ON-center cells in the LGN were totally silenced by the APB, the responses and the center-surround organization of OFF cells was unaffected. Thirdly, in the cortex cells that normally respond to both light increment and light decrement stopped responding to light edges when APB was infused into the eye without affecting the responses made to dark edges. Fourth, the orientation, direction, and spatial frequency selectivity of cortical cells was unaffected by the APB infusion. These findings established that the ON and OFF systems did not arise for the purpose of creating center/surround organization in the retinal ganglion cells and the lateral geniculate nucleus and also did not arise for the purpose of creating orientation, direction, and spatial-frequency selectivity in the cortex.

We then proceeded to examine how visual perception is affected by the selective blocking of the ON system. We did this in monkeys trained to make a variety of visual discriminations. In this phase of the work APB was injected into the eye with a fine-gauge hypodermic needle while the animal was briefly anesthetized. This effectively blocked the ON system in the injected eye for a few hours. The prime effect of blocking the ON system using this procedure was that monkeys had difficulties detecting light increment, such as a light spot on a gray background, but did not have any problem detecting light decremental cues such as a dark spot on the same background. Furthermore, any residual response made to light incremental stimuli had very long latencies.

These findings pertain to conditions under daylight viewing when the cone photoreceptors are operative. The rod photoreceptors that process information under dark-adapted conditions are organized in a different fashion. In monkeys and in other primates there are only depolarizing rod bipolars as had been established in several studies, including one I had carried out in collaboration with Robert Dolan who obtained his Ph.D. working in my lab in 1992 (Dolan et al., 1989; Wassle et al., 1991). The rod bipolars, like the ON cone bipolars, have mGluR6 neurotransmitter receptor sites whose responses to light are blocked by APB. We showed that monkeys lose the ability to process any visual information under dark adapted conditions after APB is infused into the eye; in other words the monkeys became night blind. All effects produced by APB infusion into the retina with these procedures were temporary. After the APB was broken down by natural processes in the retina, normal vision returned.

Our studies using APB led to the affirmation of the following inferences: In the course of evolution a double-ended system emerged from the single-ended system of the cone photoreceptors by creating the mGluR6 neurotransmitter receptors in ON bipolar cells, which makes it possible to process both light incremental and light decremental information in the retina rapidly and effectively. Objects in the visual scene reflect some wavelengths and absorb others. Consequently, as we move our eyes about, we perceive objects in the visual scene by virtue of either increases or decreases in the number of photons entering the eye. Thus, a fish in the ocean can respond rapidly both to a predator that swoops up from below and is lit up by the reflection of the incoming sunlight from its body and to a dark bird in the sky, like an osprey, that is about to swoop down to catch the fish. Thus, light incremental and light decremental information can be effectively and rapidly processed by virtue of the ON and OFF systems in diurnal animals. This can also be readily seen in humans; we can effectively read dark letters on a white background as well as light letters on a dark background. The former is much more common, of course, as it is a lot cheaper to produce books and newspapers with black letters on white paper rather than the other way around. So when we read books, magazines, and newspapers, the OFF system does most of the work. An overview of these findings is published in *Progress in Retinal and Eye Research*, Volume 15 (Schiller, 1995).

Andy Knapp, who was then a graduate student working in my lab and had participated in some of this work, went on to carry out an independent set of experiments with APB. In a set of elegant studies it was established that there is yet another type of ganglion cells in the retina, the directionally selective cells of Dogiel that project into the accessory optic system. These cells, in concert with the vestibular system, play a central role in stabilizing the retina with respect to the visual scene to prevent blurring when the body or the visual scene is in motion. These cells play a central role in the generation of optokinetic nystagmus that can be seen when a grating is moved across the visual field, resulting in pursuit eye movements interrupted by resetting saccadic eye movements. Simpson and his collaborators discovered that in the rabbit these cells receive input only from ON bipolar cells (Simpson et al., 1979). What Andy Knapp then showed is that when APB was infused into the eye to block the responses of these cells, the optokinetic response was eliminated. Similar work in monkeys, however, did not create this deficit, suggesting that in this species the cells of Dogiel receive input from both the ON and OFF systems (Knapp et al., 1984).

Julie Sandell, who had also participated in several of our studies, went on to carry out an entirely independent project for her Ph.D. thesis. Her work examined the distribution of NADPH diaphorase in the rat brain. This thesis has the distinction of being the longest among the ones that have come from my laboratory, 97 pages.

Studies of Extrastriate Cortex

In the 1980s we began yet another series of experiments examining the functions of area V4 in the monkey. Thanks to a remarkable group of collaborators, we have made considerable progress in this quest. The investigators who have taken a major role in this effort, which has also produced several Ph.D. theses, included Paul Haenny, Karl Zipser, Kyoungmin Lee, Victor Lamme, John Maunsell, Andreas Tolias, Eliot Charles, Nikos Logothetis, Rufin Vogels, and Yoshihisa Osada. This work was carried out on two fronts: single-cell recordings and lesion studies examining the effects of removing areas V4 and MT on visual processing. In agreement with the outstanding work in Bob Desimone's laboratory, at that time at the NIH and who now is the head of the McGovern Institute here at MIT, this work established that area V4 is far more complex than had been thought (Moran and Desimone, 1985). Before these studies it was believed that area V4 specializes in the processing of wavelength information for color vision (Zeki, 1980).

The single-cell recording studies we and Desimone's lab carried out revealed that area V4 processes several dynamic aspects of visual information processing (Desimone and Schein, 1987; Moran and Desimone, 1985). Most likely, because of extensive interconnections with other cortical areas, the activity of neurons in V4 is greatly influenced by the decision processes made in stimulus selection and in pattern analysis. When monkeys are trained to either ignore or pay attention to the same visual stimulus, V4 neurons respond quite differently. Furthermore, the responses of neurons are modulated by contextual stimuli that impinge in regions outside their classically defined receptive fields as well as by the eye movements monkeys make (Haenny et al., 1988; Schiller et al., 1991; Tolias et al., 2001).

Our psychophysical studies showed that when area V4 is removed, relatively minor deficits occur in color vision, but a major deficit arises in the ability of monkeys to select target stimuli in the visual scene that are smaller or have less contrast than the other stimuli with which they appear. One of the tasks in vision is to be able to ferret out subtle stimuli in the visual scene, as is especially important in the animal kingdom in defeating camouflage. It appears that area V4 plays a central role in this process.

In one set of related experiments we also examined how visual processing is affected in monkeys by the removal of both areas V4 and MT. We were surprised to find that many basic visual capacities, such as perception of color, shape, motion, and stereoscopic depth were only moderately compromised. This suggested to us that area V1 sends projections to several areas in addition to V4 and MT, areas which are also involved in multiple aspects of visual processing (Schiller, 1993).

After working on these projects, most of the collaborators in my lab moved on to fine careers. Yoshihisa Osada, who was a visiting professor, returned to Japan, where he runs a busy laboratory at Rikkyo University. He invited me twice to meetings there and was a most gracious host. I stayed with him and he took me to visit many interesting sites in Japan, including the Japanese Alps, where we took a wonderful hike. Paul Haenny returned to Switzerland to his medical practice. He also was a gracious host when I visited him once and I stayed at his home. After Nikos Logothetis moved to the Max Planck, as already noted, I visited him several times as we continued our collaborations. John Maunsell is now an eminent professor at the Harvard Medical School, where he runs a busy laboratory; we meet up occasionally.

Visual Prosthetics

Largely as a result of the extensive electrical stimulation work Ed Tehovnik carried out in my laboratory (Tehovnik et al., 2009), we moved on recently to examine the feasibility of creating a prosthetic device for the blind based on electrical stimulation of area V1. We have published an article entitled "Visual Prosthesis," in which we advocate that this is kind of work be carried out in animals as had been done in the highly successful creation of the cochlear implant (Schiller et al., 2008). We were both surprised and delighted that this paper has created considerable interest and controversy.

Depth Work

Some years ago, as a result of discussions with David Hubel, Marge Livingstone, Ralph Freeman, Bela Julesz, Gian Poggio, and several other investigators, I became interested in several aspects of depth processing and carried out quite a few experiments on the topic. Part of this work has examined which brain areas are involved in the processing of various depth cues and where the information provided by these cues is integrated. We have studied stereopsis, motion parallax, and shading. In this effort, recording work, which constituted the Ph.D. thesis of An Cao, showed that already in area V1 there are neurons that process information about differential velocity which provides the essential motion parallax information for depth (Cao and Schiller, 2003).

Recently we devised a display system based on the Bela Julesz random-dot stereograms that allows us to present disparity, shading, and differential velocity cues for motion parallax separately and in various combinations.

A new direction that has emerged from this effort is the examination of brain organization in normal, stereo-deficient and stereo-blind humans with various etiologies using functional magnetic resonance imaging. Stereo-deficient and stereo-blind individuals comprise 5% to 10% of the population in the United States. I am aided in this ongoing effort by a team of collaborators that includes Steve Shannon, Geoffrey Kendall, Michelle Kwak, Nikos Logothetis, Johannes Haushofer, and Warren Slocum. Warren has been working in my laboratory since 1991. Since that time he has written most of the computer programs we use in our research and has done extensive data analysis. He is coauthor on many of our published research articles (Tehovnik, et al., 2009).

Collaborators

In my research career I have had more than 50 students, postdoctoral fellows, and associates join my laboratory, which has produced 21 Ph.D. theses and publications with 62 different coauthors. I have been most fortunate in attracting so many remarkable and brilliant individuals. Many of them have gone on to outstanding careers in neuroscience. I am proud of the fact that three of them have been elected into the National Academy of Sciences and into the American Academy of Arts and Sciences: Larry Squire, Nikos Logothetis, and Michael Stryker. Nikos, after leaving my laboratory, moved to the Max Planck Institute in Tübingen, Germany, where he created one of the largest neuroscience labs in the world and became one of the most outstanding experts in functional magnetic resonance imaging research. Larry is now a professor of psychiatry, neurosciences, and psychology at the University of California, San Diego, where he has done outstanding work examining learning and memory; he was president of the of the Society for Neuroscience in 1993–1994. Michael is now at the University of California, San Francisco, where he served as department chair of the Physiology Department from 1994 to 2005.

Here I now provide an alphabetical list of those who have worked in my laboratory over the 49 years of its existence. The asterisks denote those who earned their Ph.D.s based on the research carried out in my laboratory. Much of the Ph.D. work, as stipulated, was carried out independently by these students as reflected in the fact that on many of the ensuing publications I do not appear as a coauthor.

Karl Arrington	Geoffrey Kendall	Jacob Richter
*Nancy Berman	Jennifer Kendall	*Julie Sandell
*An Cao	*Andrew Knapp	Jeffrey Schall
Christina Carvey	Fritz Koerner	Stan Schein

*Eliot Charles	*Michael Kuperstein	*Helen Sherk
*Ron Chase	Michelle Kwak	Warren Slocum
*I-han Chou	Victor Lamme	Stelios Smirnakis
*Carol Colby	*Kyoungmin Lee	*Marylin Smith
*Janet Conway	Tai Sing Lee	*Marc Sommer
Denice Couch-Helwig	Audie Leventhal	*Larry Squire
*Max Cynader	Nikos Logothetis	Renata Stebbins
*Robert Dolan	Joe Malpeli	*Michael Stryker
Barbara Finlay	Scott Mann	Edward Tehovnik
Alan Greenfield	John Maunsell	Robert Thau
Paul Haenny	Jamie Mazer	*Andreas Tolias
Johannes Haushofer	Robert.M. McPeek	Sean True
Shaul Hochstein	Tirin Moore	Rufin Vogels
Anya Hurlbert	Marilee Ogren	Veronica Weiner
*Ron Kalil	Yoshihisa Osada	Ying Zhang
		*Karl Zipser

Family

While I was in graduate school at Clark University in Worcester, Massachusetts, my wife Ann worked at the Worcester State Hospital assisting a psychiatrist in research. After we moved to Cambridge, Massachusetts, upon my becoming a postdoctoral fellow, she secured a job with Hans-Lukas Teuber that involved testing patients with brain injuries, mostly at the Boston VA hospital. Ann was an English major at Duke University with excellent writing skills. In the 1970s she became interested in the history of architecture, which has resulted in her writing a biography about Charles F. McKim, who was the head of the architectural firm McKim, Mead, and White; at the turn of the 19th and 20th centuries, this was the largest architectural firm in the world. In the Boston area they are perhaps best known for building Boston Symphony Hall and the Boston Public Library. Ann's biography is a scholarly piece of work that comes to 411 pages, but it never got published because in 1999 she died of leukemia.

We have three children, David, Kyle, and Sarah. Ann was a devoted mother who took prime responsibility raising the kids. She stopped working to spend all her time raising them. The kids were trained in sports from an early age. David became a fine swimmer, skier, and lacrosse player, to the extent that after college he played professional lacrosse in Australia for a year and then spent one winter as a ski instructor. All three kids earned MBA degrees. David is now employed by Blackrock and Kyle is Director of

Business Management for the GEO Group, Inc. Kyle is a gifted guitarist and plays professionally with a band he has put together. My daughter Sarah took on an entirely different line of work; she is now employed by a radio station in Philadelphia, where she has a daily radio show.

I now have five grandchildren ranging in age from 4 to 21. David and his wife Michelle have two young girls, Madeline and Chloe; Kyle and his wife Gaby have three children, Andrea, Monica, and Nicole. The oldest, Andrea, is a junior at Princeton.

I still have family in Hungary and we have been in contact with each other on quite a few occasions. Because of the Cold War and the Iron Curtain, after immigrating to the United States in 1948, I did not return for a visit to Budapest until 1968. Although we had kept in contact by mail, I had not laid eyes on my mother during these 20 intervening years, so it was quite an experience to meet up with her. We talked endlessly and soon closed this great time gap. Most recently, I visited in Budapest when I was asked to give a presentation in honor of being inducted into the Hungarian Academy of Sciences. I stayed with my cousin Paul Rudas, who runs a computer company. They now spend much of their time in England where his wife, Klara Breuer-Rudas is Deputy Head of Mission at the Hungarian Embassy in London. Their young son, who is attending school there, has become quite the Englishman.

On another occasion, some years ago, after Michael Stryker and I had attended a conference in Turkey, we visited in Budapest and spent a memorable evening with my family at the house of Paul Rudas' twin brother, Peter. His wife, Márti, has made an extensive study of Hungarian folk music and has written about it. We spent much of the evening singing Hungarian folk songs. Sadly, a few years ago my cousin Peter Rudas died in a car accident. Their two children, Anna and Klári, are about to earn their Ph.D. degrees.

My cousin Andrea, about whom I wrote at the beginning of this chapter, still lives in Beirut, Lebanon. I have not seen her in several years because she does not like to travel and because I have not had the opportunity to go to Beirut.

Hobbies

I pursue several hobbies. I have learned to play a number of musical instruments, none of them well. First the piano, then the recorder that is well suited for playing Hungarian folk songs, the guitar, and lastly the banjo, which in spite of a great many hours of effort I have never managed to play even half decently. Initially, my piano playing centered on classical music and involved memorizing most of Bach's two- and three-part inventions and Béla Bartók's folk songs. Later on in life I have turned to improvisations and put together several medleys in which, intermingled with well-known folk tunes and popular melodies, I play some of my own compositions.

After coming to the United States, another hobby I pursued for a while was to translate Hungarian short stories. I remember one of these in particular by the great satirist Karinthy Frigyes. In this short story, entitled "Barabbas," the crowd at the Passover feast that has chosen to commute the death sentence of Barabbas is given a second chance. Each individual now vehemently screams, "Jesus, Jesus, Jesus." But the collective sound Pontius Pilate hears through the airwaves is, "Barabbas, Barabbas, Barabbas." So Jesus is crucified again.

These translations inspired me to write short stories which are based largely on my life experiences. I have written many of them, and each starts with a full-page abstract drawing relevant to the story with the title in the center. At this stage these are private and few people have read them. Perhaps one of these days I will have the temerity to put them together into a book. In one of these stories a grandmother becomes victim of a bombing raid during World War II. Her body is found by her grandson after a long search by recognizing the Triskelion pendant on the neck of her decomposed body. The grandson carts her home and with his grandfather buries her in a full-sized coffin they constructed from dining room furniture at a time when due to short wood supply most of the dead were buried in foreshortened coffins. The initial page is a drawing which in the center has the title, *The Pendant* with the *Triskelion* and a full-sized coffin below. Surrounding this display is an array of foreshortened coffins as described in the War Years section of this chapter.

Another hobby I actively pursue now is artwork that has several forms. I make sculptures, suncatchers, a variety of hangings, abstract pictures generated on the computer, and photographs. I have created several hundreds of them. My office area and my home are overwhelmed by these productions. Recently, with the help of Christina Carvey, we have created a new Web site on which some of my artwork can be viewed (www.richfieldstudios.com).

At this time in my life, undeniably, retirement is looming on the horizon. When I reach that stage and if still healthy, I will continue my busy existence. I have a contract to write a book on *Vision and the Visual System*, which I shall start working on at that time. I also plan to spend more time with my hobbies. After retiring, I will most likely have to sell my house in Newton, MA, where I now live and move into a retirement home—one that has a well-equipped shop. When I get to this point, I can only hope that my friend from our Duke days, Hooksie, was right: "There's friends everywhere."

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