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> December 22, 1937

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The Sparks lab used the primate superior colliculus (SC) as a model for studying how sensory signals are transformed into commands for the generation of movements. The lab discovered cells in the SC with high-frequency bursts of activity tightly coupled to the onset of saccades (the quick, high-velocity movements of the eyes), which are involved in the initiation of saccades. The accuracy of saccades results from a combination of the movement tendencies produced by the entire active population of coarsely tuned cells rather than the discharge of a small number of finely tuned cells. The saccadic system does not localize visual targets based solely on information about the region of the retina activated, but also uses information about the current positions of the eyes in the orbits to localize the target in a more abstract spatial frame of reference. The visual, auditory, and somatosensory signals observed in the SC specify the movement required to direct gaze to the location of a stimulus, not the location of the stimulus in external space. Information about the change in eye position used for remapping sensory signals into motor coordinates is still available after extraocular muscle proprioceptive signals are eliminated by surgical sectioning of the afferent pathways. Corollary discharge, a copy of a motor command, must have provided the eye-position information instead. The motor map in the SC represents a command for a change in gaze, not separate eye, or head commands. Correlations between the activity of neurons above the level of the motoneurons and the parameters of the eye movement may be misleading when more than one oculomotor subsystem is active. The collicular signals involved in specifying the direction and amplitude of a movement are separable from those initiating the action.

David L. Sparks

Overview

The manuscript for this autobiography was due November 1, 2021—two months shy of the 17th anniversary of my retirement date. In those 17 years, I have enjoyed extended time with family, and I communed with nature while sailing in French Polynesia, the Strait of Georgia, and along sections of the U.S. coast of the Gulf of Mexico. I renewed my interest in nature photography and photographed birds and other animals on all seven continents. As I learned while writing this article, I also forgot many of the details about the research done in my lab during the 40 years before retirement!

In this autobiography I focus on telling the story of how my interest in neuroscience developed and how I adopted a motor, rather than perceptual, perspective on the processing of sensory signals. The story has a somewhat unusual trajectory. It is a testament to the impact that textbooks and published papers can have on the interests and actions of a reader. I still marvel at the chance encounters that led to, and facilitated, a research career trying to understand how sensory signals are translated into commands for the control of movements.

To allow for grouping of experiments relating to particular topics, sketches of research projects are separated from descriptions of the different faculty positions I held and of the extraprofessional pursuits at each place of employment. Students, postdoctoral fellows, and colleagues are introduced after descriptions of their research projects.

Family Background

I was born in Guntersville, Alabama in 1937, the eldest of the two sons of Lee and Ruth (Mooney) Sparks. During my early childhood, we lived in Alabama, Tennessee, Georgia, Kentucky, and North Carolina while my father worked on many of the dams that the Tennessee Valley Authority (TVA) built on the Tennessee River to provide power, improve navigation, and control periodic flooding. The TVA was part of President Roosevelt's New Deal designed to help the United States recover from the Great Depression.

Both of my parents were born in Alabama. My mother graduated from high school, but my father dropped out of school after the ninth grade. He was a skilled operator of heavy equipment but progressed to the roles of foreman and superintendent on construction projects during the earth-moving phase. Later, when I was in high school and college, he worked on

the construction of a power plant in Kentucky; turnpikes and interstate highways in Ohio, Michigan, Illinois, Indiana, and Pennsylvania; the Lewis Smith Dam in north Alabama; Keystone Dam near Tulsa, Oklahoma; and the nuclear test site in Nevada.

Between 1937 and 1954, when I graduated from high school, my best estimate is that we lived in 18 different towns or cities in seven different states. I do not remember where we lived when I started the first grade, but I was permitted to start at age five. I skipped the fifth grade. The material to be covered in the fifth grade in Florida was mostly a repeat of what I had studied the year before in three different public schools in Georgia, a system that had only 11 grades at that time. I regretted graduating from high school at age 16 because I could have had two more years to play high school basketball, my favorite sport. Needless to say, the peripatetic nature of my father's work resulted in a very spotty educational background. Continuous compensation was required.

I adjusted to the frequent moves by creating my own cognitive world, a space that did not need to be left behind when we changed locations. Happiness, aspirations, feelings of success or failure, and other psychological states occurred within that world and were not dependent on input from individuals who would not make the move with me. I developed a sense of independence that allowed me to follow the path paved with chance encounters that led to a research career in the field of neuroscience.

My father enjoyed fishing and hunting. Fish, quail, and other game were a significant part of our diet. My mother was a homemaker. She managed to keep track of our possessions during all our moves. She strongly encouraged us to be good students and pinched pennies to purchase a *World Book Encyclopedia* and several volumes of Will and Ariel Durant's *The Story of Civilization* and to pay for our piano lessons.

Memories of most of the places we lived when I was a child are sparse. My most vivid childhood memories are from 1948 and 1949 when my father worked on a construction project in Saudi Arabia. My mother, my brother, and I stayed in the United States and lived in a small house close to the home of my maternal grandparents on their small 80-acre farm in northern Alabama. There was a barn for storing hay and maintaining livestock, a potato house, a chicken house, and a smokehouse for preserving the salt-cured or smoked meat of the hogs that were slaughtered after the onset of cold weather. A large garden and orchard provided enough vegetables and fruit for consumption during the growing season and for canning, which preserved them for the remainder of the year. Neither house had running water the first year we lived there. Electricity had only recently become available. A pump was added to the well during the second year, and water lines were run to the small house where we lived. I no longer had to carry buckets of water from the well at my grandparents' house to the house where we lived.

I learned about farm life by helping with the farming activities of my two uncles and my grandparents when I was not in school on weekends, holidays, during the summer, and the annual two-week break from school, a break that allowed students to assist in harvesting crops. In northern Alabama, this was primarily cotton-picking time. I was 11 and 12 years of age during this period. My uncles and grandfather taught me how to manipulate the combination plow and hopper filled with corn seed. As the plow was pulled by the mule (Betsy), seeds dropped into the furrow and were covered by the rear of the planter. The difficult parts for a young boy were making sure the seeds were dispensed in a straight row and getting the planter turned around and headed in the opposite direction at the end of the row. Betsy was very experienced and made the learning process less arduous by being tolerant of the novice that was following behind.

Cotton seeds were spaced such that when they germinated and sprouted, there was a continuous row of plants. When the plants reached a certain height, it was time to "chop" the cotton. This was done manually. A hoe was used to thin the plants so that the space between them would accommodate the mature plants with their branches and bolls. In the process, weeds were removed, and the remaining plants were propped up with a mound of dirt. As I was learning to do this, one of my uncles would be working an adjacent row while checking my work and correcting my errors. But after a couple of days, I could "carry my own row."

A long sack made of heavy cloth and reinforced on the bottom was used for picking cotton. The shoulder strap allowed it to be dragged along the ground while using both hands to remove the cotton from the bolls. Initially, one of my uncles would be on an adjacent row checking to make sure I didn't leave too much cotton in the boll and didn't put too much trash in the sack until I was once again trusted to carry my own row. The most cotton I was able to pick in one day was 150 pounds.

When the first wagon was full of cotton and ready to go to the cotton gin, my grandfather told me to get aboard. He drove the horses the seven miles to the cotton gin on the outskirts of Decatur, Alabama. After the wagon was unloaded and he received his payment, my grandfather took me to the Blue Bird Cafe and bought us ice cream cones. As we sat at a small table in the cafe, he pulled out his book and totaled how much I had earned that year ($3 a day for chopping cotton, planting corn, etc., $3 for each 100 pounds of cotton picked). I don't remember the total, but, psychologically, I was wealthy. Developmentally, these interactions with my grandfather were important. He reinforced hard work and emphasized the importance of education by giving me problems, such as converting feet and yards into acres, furlongs, and hectares. When not doing farm work, I roamed the woods and fields with my brother and with Ralph and Ray, nonidentical twins about my age, who lived a few miles from our house. We swam in the local creeks and fished in all the ponds located on the surrounding farms.

These were the years when I learned to love being outdoors, a passion that carried over to later years when, at various times, activities such as camping, fishing, hiking sections of the Appalachian Trail, sailing, and nature photography became my way of accessing and enjoying nature.

My brother, Gary, earned a bachelor's degree in architecture from Oklahoma State University (OSU) in 1966. He worked for architectural firms in Tulsa after his service in the U.S. Army until he started his own firm in 1986. His most noted architectural projects were the expansion, renovation, and preservation of the historically valued sporting facilities on the OSU campus. In 1995, there were rumors that the once-famed, but now outdated, Gallagher-Iba Arena constructed in 1938 would be replaced by a new off-campus arena. The existing arena was the home to more NCAA Championships than any other facility in America. It was named for Edward Gallagher, the university's first wrestling coach whose teams won 11 NCAA team championships, and the basketball coach, "Hank" Iba, whose teams won national championships in 1945 and 1946. Gary thought it would be a tragedy to destroy the arena with its rich history and the special 1-1/4 inch white maple basketball court. He devised a plan by which the historic building would be preserved and renovated, and seating capacity increased from 6,000 to 13,600 by constructing a new seating bowl and roof structure over the existing arena while continuing to have events during the two-year construction process. He convinced the decision makers that this could be done, and his firm was awarded the contract.

College and Graduate School (1954–1963)

Upon graduating from high school in 1954, encouraged by my parents (devout Southern Baptists), I attended Tennessee Temple University, a four-year private Christian university located in Chattanooga, Tennessee, for two years. Finding the course offerings very limited compared with what I saw in the course catalogs of other universities, I transferred to the University of Alabama in Tuscaloosa. My parents were Alabama residents at that time, and the lower cost of tuition for in-state residents was a determining factor in the choice of an alternative college. My parents assisted with tuition expenses, but I covered much of the cost of attending college with my savings, earned each summer while working on the construction jobs my father acquired for me. The first summer, I worked as a manual laborer, but the next summer I worked as a mechanic helper. Oil changes, lubrication, and minor repairs of the large pieces of equipment occurred during lunch breaks and in the interval between the two 10-hour shifts. While working as a mechanic helper, I learned to operate some of the heavy equipment. In subsequent summers, I worked as an operator of Caterpillar Dozers and the Caterpillar DW21 Scraper. When operating the heavy equipment, I earned a little more than $3 per hour and usually worked 50–60 hours per week.

As I sampled the broader range of courses available at the University of Alabama, I gravitated to those offered by the Department of Psychology. Three of the psychology courses (Experimental Psychology, Physiological Psychology, History and Systems of Psychology) and a course in the Philosophy Department that included a section on the philosophy of science were the ones that most intrigued me. The textbooks in the psychology courses I enjoyed were *Experimental Psychology* (1949) by Benton J. Underwood; *Physiological Psychology* (1950) by Clifford Thomas Morgan and Eliot Stellar; *A History of Experimental Psychology* (1950) by E. G. Boring; and *Experimental Psychology* (1954) by Robert S. Woodworth and Harold Schlosberg. I graduated with a BA in psychology in 1959.

In his *Notes for a Life Story,* S. S. Stevens wrote "Any man's life builds on a succession of accidents and that among the chance encounters, there are some that take effect while others do not." Several of the chance encounters that affected either my choice of a career or facilitated my research efforts are described in this autobiography. The first occurred in my senior year of college. History and Systems of Psychology, a required course for an undergraduate major, was being removed from the undergraduate listing and becoming one of the core courses of the graduate program. In this transition year, most members of the class were graduate students.

Perhaps that motivated me because I was receiving good grades on the exams. One day the professor, George Passey, stopped me as I was leaving the classroom and asked if I had considered graduate school. I told him I had not. He then asked what I would do if he promised me an assistantship that would pay tuition and provide some funds for living expenses. I told him I would go to graduate school.

I entered graduate school the following fall as a relatively undifferentiated student. I knew my interest was in experimental, rather than clinical, psychology but I did not have a particular area of experimental psychology in mind. The seminar offered by Dempsey Pennington, a visiting professor, was the chance encounter that was decisive in my choice of a career path. The *Organization of Behavior* by D. O. Hebb and *Science and Human Behavior* by B. F. Skinner were among the books and readings selected for discussion. Interestingly, my decision to pursue a career studying the biological bases of behavior was stimulated by Skinner's book, not Hebb's.

I recognized the importance of Hebb's proposed mechanism for increasing synaptic efficacy and his attempt to bridge the gap between neurophysiology and psychology. But, as a first-year graduate student, I was not excited by it. I was unable to envision ways of testing his theoretical formulations experimentally using the methods then available to an investigator.

In contrast, I had very strong negative reactions to many of the statements in Skinner's book. He argued that psychology should engage exclusively in research that would eliminate the type of experimentation that had aroused my interest in the field. According to Skinner, placing an emphasis

on physiological variables obscured attending to external ones, the variables he thought should receive priority. Skinner recognized a "causal chain" with three links: an operation performed on the organism, an inner condition, and a kind of behavior. Skinner did not deny the existence of internal states. "The objection to inner states is not that they do not exist, but that they are not relevant in a functional analysis." Skinner maintained that it was not possible to account for behavior while considering only inner conditions, and that if it was always necessary to go back to variables outside the organism, it would be possible to "avoid many tiresome and exhausting digressions" by simply studying behavior as a function of the external variables.

The strength of my negative reactions to Skinner's assertions was informative. I had not recognized that I felt so strongly about the need to learn about the internal events associated with behaviors. I began thinking about how to counter Skinner's arguments in favor of pursuing a strictly behavioral approach to experimentation. I had "conversations" with Woodworth and Schlosberg by rereading their chapters on vision. Suppose, I asked, we had avoided the "many tiresome and exhausting digressions" of learning about the types of receptors in the retina, the anatomical distribution of rods and cones, and their differential sensitivity to light levels. Would an accurate estimate of the visual sensitivity of the human visual system be available? Not knowing that the receptors were not evenly distributed, those trying to obtain an estimate would not know to control the fixation point of the subject. Lacking information about the sensitivity of the different receptors to various wavelengths, an arbitrary range of wavelengths might have been used for the test stimulus. After a few of these "conversations," I realized that, for me, whether or not my ruminations countered any of Skinner's arguments, I was very much interested in the anatomical and physiological aspects of sensory systems and how they related to the results of psychophysical studies. I was fascinated by how biological information informed the design of behavioral experiments, and the ways that behavior could be used to test hypotheses about underlying biological mechanisms. I was attuned to Woodworth and Schlosberg's point of view: "Research at all levels is important in giving us a full account of vision — no single level is enough. The brilliance, hue, and saturation of a color sensation depend not only on the stimulus but also, to a marked degree, upon the receiving apparatus and on its condition."

These reactions suggested that the biological bases of behavior could be the direction I should pursue as a career. I began spending hours in the library. I discovered the *Journal of Comparative and Physiological Psychology* and the *Journal of Neurophysiology*. I found papers from Vernon Mountcastle's lab and resonated with his effort to quantify neural events at successive stages of the somatic afferent central projections, his expectation of finding lawful transformation between peripheral sensory and central neural events, and his hope of learning "which quantitative aspects of the

neural response tally with psychophysical measurements" (Mountcastle et al. 1963, *Journal of Neurophysiology, 26*: 807–834). Now, instead of just being interested in some area of experimental psychology, I had a goal. I needed to find a way to become involved in studying the three-dimensional correlations between the physical properties of the stimulus, the psychophysical report of the subject, and the intervening neural events. Although there were excellent experimental psychologists on the faculty, none were studying the biological bases of behavior. But I had a lot to learn and needed to address the inadequacies in my knowledge base. I changed my graduate minor to biology and took courses in mammalian anatomy, histology, and genetics and continued my voyages to the library.

A third chance encounter was with a second-year graduate student, Bob Travis. He had worked in Jim Olds's lab at the University of Michigan as a research assistant for several years after his undergraduate degree. He had a small office in the abandoned army barracks building that was being used to house the animals used in experiments conducted by faculty members and students and oversaw the animals. Bob and I had frequent conversations. One day I mentioned reading an interesting article in *Science* about a phenomenon called spreading cortical depression (SD), a depression of brain activity reflected in changed EEG patterns following application of electrical, mechanical, or chemical stimuli to the cortical surface. The paper used SD produced by the application of potassium chloride (KCl) to the cortex as a functional unilateral ablation technique because SD is restricted to a single hemisphere. Bob then told me about the experiment he had been involved in when Jan Bures visited the Olds lab. They studied the effects of SD on the rate of electrical self-stimulation in rat. After further discussion of the article, we designed an experiment that evaluated the effect of prior training under varying degrees of SD on the subsequent performance of the nondepressed organism. We built an avoidance box, obtained 25 percent KCl from a local drugstore, and constructed a trephine of the appropriate size to place an opening in the skull that would allow a two-millimeter-by-two-millimeter piece of filter paper soaked in the KCl solution to be placed on the surface of a rat's dura. This was done by welding a section of a fine-toothed hacksaw blade around a small-diameter welding rod. The relays, photoelectric switches, and electronic timing units necessary to automatically schedule the experimental events were available in the lab.

Not attuned to the fact that we should let someone on the faculty know what we were doing, we conducted the experiment, wrote up our results, and submitted a manuscript to the *Journal of Comparative and Physiological Psychol*ogy. After a few months we received the two reviews. The first sentence of the first review read "the title is a meaningless word salad," and the comments went downhill from there. The cover letter from Eliot Stellar, the editor of the journal and one of the authors of my undergraduate text in Physiological Psychology, stated that despite the harshness of the

criticisms, he believed that if we performed the yoked control suggested by one of the reviewers that the results were interesting and worthy of publication. We did the additional experiments and asked one of the faculty members for assistance in preparing the manuscript, and this became my first original scientific publication (Travis and Sparks 1963).

Many years later, I met Eliot Stellar when interviewing for a position at Penn. Eliot was provost. Of course, he had no memory of his role in the publication of the SD paper when I told him this story 27 years later. Eliot died while I was still working at Penn. In 2001, after I had moved to the Department of Neuroscience at the Baylor College of Medicine, I was honored to accept an invitation to give the Stellar Lecture at Penn.

The textbook for the Sensation and Perception course taught by George Passey was *The Human Senses* (1953) by F. A. Geldard. Too large to be required as a textbook, multiple copies of the *Handbook of Experimental Psychology* (1951) by S. S. Stevens were available in the departmental library. The content of this course reinforced my decision to focus on the biological bases of behavior.

Even though no faculty member was involved in research related to the biological bases of behavior, Bob Travis and I were permitted to conduct research related to our interests for our dissertations. Bob did a series of SD experiments for his thesis, and I studied how radio-frequency lesions in several limbic-system structures affect active and passive avoidance behavior.

The next chance encounter was highly significant for me. The event was the first meeting of the lab component of an upper-level undergraduate course in genetics that I was taking as part of my graduate minor. As students arrived, they were told to pair up as lab partners. The even number of students in the room when I arrived had already formed pairs. For a brief period, I was the only student without a lab partner. A few minutes later, Betty Ellis arrived, and we became lab partners. Our lab exercises involved selecting fruit flies with certain physical features, allowing them to mate, and cataloging the characteristics of the offspring through as many generations as possible. Coffee after class transitioned into study dates, which evolved into a state in which we were considering marriage.

Betty obtained her BS degree before I received my PhD. She graduated in January 1963 and accepted a research assistant position at Southern Research Institute in Birmingham. After Betty began working in Birmingham, I learned that my application for a National Science Foundation (NSF) Postdoctoral Fellowship in the Department of Neurosurgery at the University of Mississippi Medical School in Jackson, Mississippi, had been approved. We needed to decide if we were staying together. The wedding was in Birmingham on the last day of August 1963. The day after the marriage, we drove to Jackson in the 1958 black Chevrolet Impala convertible I had won in a poker game.

Postdoctoral Fellowship (1963–1965)

Betty began work as a research assistant in the lab of Dr. Charles Randall, the chair of the Microbiology Department at the University of Mississippi Medical School. My goal during the two years of the NSF Postdoctoral Fellowship was to increase my knowledge about the nervous system and to learn different research methods. I took courses in neuroanatomy, histology, and medical physiology and volunteered as an assistant in the neuroanatomy labs the second year. I began research projects in the lab of Irwin Powell in the Department of Anatomy. I learned several methods of anatomical tracing that were being used in his lab, and we published a paper on the interaction of evoked potentials in the anterior thalamus of the cat.

Don Foshee (joint appointment in neurosurgery and in physiology and biophysics) and I published a paper describing experiments in which we recorded EEG activity from a variety of subcortical sites to determine whether seizure activity accompanied electrical self-stimulation of hypothalamic structures producing high self-stimulation response rates.

I observed, but did not participate in, the intracellular recordings from rabbit retina performed in the laboratory of Fred Sias. Fred also taught a basic electronics course for graduate students, which I attended. That course was followed by another course about the use of digital logic components in lab instrumentation. The knowledge I acquired from the two courses was invaluable when setting up a lab at the University of Alabama in Birmingham (UAB).

The Neurosurgery Department had a small library adjacent to the departmental office, containing a wonderful assortment of books and journals. I had 24-hour access to the library and spent a lot of nighttime hours there. In my spare time, I taught a physiological psychology course at nearby Millsaps College, a private liberal arts college in Jackson.

In 1964, I was a participant in a special six-week Summer Institute on Behavioral Genetics at the University of California, Berkeley, organized by Gerald McClearn and James McGaugh. In addition to what I learned about behavioral genetics, I was able to sample the knowledge and research experience of participants from other universities and assess where I stood in terms of preparation for a career in behavioral neuroscience. Participants had access to the university's library. I compared the books on reserve for various courses in biology and psychology with the ones I had read and found several, especially ones related to neuroethology, of which I was unaware.

Betty and I enjoyed being tourists on the weekends while in Berkeley. We checked out Carmel, Pebble Beach, Cannery Row, and the tide pools off Monterey where Doc, the main character of John Steinbeck's novel, spent so many hours. One highlight of our tourist activity was freezing in Candlestick Park during a night game between the Dodgers and Giants that lasted four hours and three minutes. Koufax pitched for nine innings; Gaylord Perry

for five. Willie Mays got one hit and had one stolen base. The Giants won in 13 innings.

Support from the NSF Postdoctoral Fellowship was for only two years. I needed to find a job. Bob Travis had acquired a position in the Department of Psychiatry in the Medical College at UAB, and there was a possibility that I could join him there. During the interview with Jim Sussex, the chair of the Department of Psychiatry, I learned that S. Richardson Hill, the new dean of the Medical College, had begun evaluating the clinical programs based on research productivity as well as clinical service. Sussex said he looked at the credentials of his faculty and saw that he would need to recruit additional members of the department to generate significant research output. Bob Travis had been added to the faculty two years earlier. Sussex said he was now in the position of having one lovebird. I was offered a position as a second lovebird. I accepted the offer. We moved to Birmingham in June 1965 and lived there for 24 years.

University of Alabama in Birmingham (1965–1989)

Overview of Faculty and Research Positions

Both Betty and I were employees of UAB, and each of our positions changed several times. She worked for Drs. Wayne and Sarah Finley in the Laboratory of Medical Genetics from 1965 until 1970. She taught biology labs part-time at Samford University (a private university in Homewood, Alabama) from 1973 to 1978 to be home when school hours were over for the boys (more about them later). In 1981 and 1982, Betty worked in the lab of Dr. Jimmy Neill, chair, Physiology and Biophysics at UAB. She noticed that biology had changed so much that her degree (1963) was out of date. To compensate, she entered the graduate program in biology and received a MS degree in 1983. She then began working for Dr. Ken Zuckerman, deputy director of the Hematology–Oncology Division of the Department of Medicine. From 1985 until 1989, Betty worked in the laboratory of Dr. John Whittaker, chair of the Department of Neurology.

My initial appointment at UAB was in the Division of Behavioral Science in the Department of Psychiatry, first as an instructor and then as assistant professor. This was a full-time research position, but I did teach the Physiological Psychology course in the Psychology Department in the newly established College of General Studies. George Passey, the professor who offered me the assistantship that enabled me to enter graduate school, was now head of the social sciences division of the College. UAB, located in the largest city in the state, became an autonomous component of the University of Alabama system in 1969 and I moved to the Department of Psychology as chair and associate professor. It was obvious to me that growth in enrollment would be rapid and that graduate programs would

emerge as the faculty grew in size and areas of expertise. Accepting the position as chair allowed me to influence the direction of growth, to recruit faculty with a strong interest in research and teaching, and to make sure the administration provided space and facilities for their research programs. I resigned as chair in 1973 to have more time for research after a proposal for a graduate degree in psychology had been submitted. I remained in the department as a professor until 1981, when I switched back to the medical school component of UAB as Professor of Physiology and Biophysics. While at UAB I was an active participant in two interdisciplinary groups: visual sciences and neuroscience.

Extraprofessional Pursuits While at UAB

Betty was a member of groups that raised funds to support blind and disabled individuals and to support the Birmingham Symphony. She completed the classes and voluntary work required to become a Master Gardener. In the spring, Betty and I would usually go to Sarasota for the annual meeting of the Association for Research in Vision and Ophthalmology. Bob Travis and I walked the Appalachian Trail from Davenport Gap to Clingman's Dome each year for several years.

Our three sons, Steve, Greg, and Scott were born in 1965, 1967, and 1971, respectively. The family spent many summer vacations at Perdido Bay (Pirates Cove) near the pass to the Gulf of Mexico close to the Alabama/Florida border. The boys and I would leave to fish in the gulf in our Boston Whaler boat before sunrise. After fishing, we would go sailing, water skiing, and shrimping. We enjoyed the time at the coast and made an offer on a unit in a planned extension of a condo complex. The building permit for the extension was not granted, and we bought a 27-foot sailboat instead.

In the fall, we would often camp for a week in the Smoky Mountains, enjoying the autumn colors, hiking to the waterfalls, and watching the black bears overturn the garbage cans in the Cades Cove campground. Camping trips over the years included trips to Tuxpan (Mexico), Rocky Mountains, Yellowstone, Tetons, Jasper, and Banff National Parks (Canada), the Oregon coast, and the Florida Keys.

When I was still the lab's computer programmer and the same computer was used for developing programs, training animals, collecting data, and analyzing data, I would often go back to the lab after spending a little time with the family at dinner. Betty was encouraging me to spend more time with the boys. So, in 1978, I bought an Apple II computer, thinking I would be involved with the boys while they were learning to use it. I brought the computer home and the boys gathered around as we set it up and started working through the instruction manual. At some point, I became tired and told the boys we could continue tomorrow. That was the end of my spending time with them with the Apple II computer. By the next

morning, they knew much more about how the Apple II worked than I would ever know.

Greg (11 years old at the time) and his friends Archie Cobbs and Mark Russinovich became Apple II experts. While they were high school students, Greg had a summer job programming for people in the vision research community, and Archie programmed for someone in the chemistry department. Archie and Mark both wrote articles for the Apple II *Nibble* magazine.

Greg graduated from the University of Texas in Austin with a major in computer science. Currently, he is a principal software engineer for Dell EMC. Archie got a BA in mathematics at Princeton, and both an MA in mathematics and a PhD in computer science at the University of California, Berkeley. He is founder and CEO of various software companies specializing in medical applications and has several patents for Java methodologies.

Mark Russinovich also achieved much success and is chief technical official for Microsoft Azure. According to Wikipedia, he "earned his BS degree in computer engineering from Carnegie Mellon University, MS degree in computer engineering from Rensselaer Polytechnic Institute, and PhD in computer engineering from Carnegie Mellon. He was introduced to computers when his friend's father got an Apple II in the 1970s. He was able to reverse engineer its ROM and write programs for it."

University of Pennsylvania (1989–1997)

In 1989, I accepted a position as a trustee professor of behavioral neuroscience in the Department of Psychology. There, I was able to interact with the faculty of the Mahoney Institute of Neurological Sciences and the students in the Neuroscience Graduate Group. I enjoyed team-teaching courses in the neuroscience group and the interactions with students in the psychology and neuroscience programs. Jack Nachmias, who studied small eye movements early in his career, participated in our lab journal club sessions.

When we arrived in Philadelphia, Betty was the occupant of an empty nest. Our sons were all in college. She did not continue working because back problems prevented her from standing for long periods. She arrived in Philadelphia knowing no one, but she adjusted. When we moved to Houston eight years later, Betty was a graduate of a two-year art appreciation course at the Barnes Museum, and a three-year program of horticulture at the Barnes Arboretum in Merion, Pennsylvania. She was on the Nomenclature Committee for the Philadelphia Flower Show; chair of the Botany-Horticulture committee of the Herb Society of America, Philadelphia Unit; and chair of the Long-Range Planning Committee and head of the Salvia/Tender Perennial Special Interest Group of the Philadelphia unit of the Hardy Plant Society. She worked as a volunteer in the Experimental Horticultural Section at Longwood Gardens. Articles about the garden

she constructed in our back yard appeared in two Sunday editions of the *Philadelphia Inquirer*.

The Move

The rumor that the only reason I accepted the job at Penn was so I could sail our (now 30-foot) boat around the Florida Keys and up the east coast to the Chesapeake was not true. But moving the boat was fun. It was a (mostly) family affair. Gary (my brother), Jess (a fishing/sailing friend), Greg (middle son) and I sailed the boat from Mobile Bay to Fort Myers. Steve and Scott (our other sons), Greg, Jess, and I spent a week fishing, snorkeling, and sailing from Fort Myers to Fort Lauderdale. Jess, Greg, and I continued sailing up the east coast until the time allocated for the first stage of moving the boat expired. We left the boat at a marina in Oriental, North Carolina. After the lab equipment was transferred to Penn, Betty and I found a slip at a marina on the eastern shore of the Chesapeake and then sailed the boat from Oriental, North Caroline, to the Chesapeake.

Extraprofessional Pursuits While at Penn

We enjoyed sailing on the Chesapeake and discovered some wonderful anchorages. I also explored the coast of Maine during the summer months. I chartered sailboats in Maine for a couple of weeks for two summers and sailed my boat from the Chesapeake to Maine and back three times.

Betty enjoyed gardening, working in the Philadelphia Flower Show, and visiting gardens in New England with members of the Hardy Plant Society. She and friends obtained U.S. Department of Agriculture permits and made two trips to England to visit gardens and nurseries and returned with lots of new items for their gardens.

Baylor College of Medicine (1997–2004)

After presenting a seminar to the Division of Neuroscience, Baylor College of Medicine in 1996, I called to check on Betty. She asked whether they offered me a job. To my surprise, she became excited when I said yes. With all her gardening friends in Philadelphia and her activities in the gardening societies and art museums, I did not think she would want to leave Philadelphia. Her desire to return to the South was well hidden from me.

Nikos Logothetis and John Maunsell had set up animal surgery, histology, and animal facilities in space close to their labs. Nikos, who had been at Baylor since 1990, had just accepted a position at the Max Planck Institute for Biological Cybernetics. All Nikos's lab equipment would stay at Baylor. I could move in and begin doing experiments immediately because Nikos and I were doing similar experiments. Major attractions included the rapidity

with which I could resume research after a move, the reduction in teaching and administrative responsibilities, and the proximity to the labs of other faculty and their associates engaged in outstanding research in systems neuroscience. During my time at Baylor, my lab adjoined the labs of John Maunsell, Mike Crair, and Fabrizio Gabbiani. Joint journal club meetings were held weekly.

Extraprofessional Pursuits While at Baylor

Betty and I enjoyed the classical music programs available in Houston. Rice University, near Baylor College of Medicine, has an outstanding chamber music series. While we were in Houston, Betty and I attended concerts by the Academy of St. Martin in the Fields and the Pacifica, Emerson, Julliard, American, Shanghai, and Tokyo String Quartets. Another highlight for me was hearing, for the first time, a live performance of Verdi's *Requiem* by the Houston Symphony and Chorus. Using contacts in the Hardy Plant Society, Betty was able to connect with gardeners in the Houston area and very quickly became an active member of several groups. In 2000, Betty began dividing her time between the house we had purchased in Pensacola, Florida, as an eventual retirement home, and our apartment in Houston. An only child, she needed to supervise the medical care of her parents in Mobile, Alabama. I moved the sailboat (now 32 foot) to Pensacola, and we both traveled between Houston and Pensacola frequently. Betty's gardening activities switched to Florida.

Research: Acquiring Equipment, Developing Methods, and Exploratory Data

I arrived at UAB in 1965, eager to begin projects related to the goal I had set in graduate school—exploring the three-dimensional correlations between the physical properties of an external stimulus, the psychophysical report of the subject, and the intervening neural events. I wanted to study these relationships in awake, behaving animals. This seemed ambitious but I was optimistic. Wall, Freeman, and Major had recorded from dorsal horn cells in freely moving rats. O'Keefe and Bouma recorded the activity of amygdala cells in freely moving cats. Hubel had successfully recorded single-unit activity in the lateral geniculate body in unrestrained cats and Jasper, Ricci, and Doane reported studies of single-cell activity during avoidance conditioning in monkeys. I never lost sight of my goal, but, in retrospect, it was seven years before I made any serious progress. In those seven years, we migrated from bulky relay modules to more compact digital logic modules to laboratory computers for controlling experiments.

An issue I had not resolved was which sensory system to study. The visual system was my first choice, but a major concern was whether the

small receptive fields of the cells in most of the visual areas that had been studied could be studied in an alert animal. Even small movements of the eyes could cause the image of a stationary spot to move on the retina over an area larger than the visual receptive fields that had been reported. I planned to explore the properties of visually responsive neurons in the superior colliculus (SC), an area that lesion experiments (Sprague and Meikle 1965, *Experimental Neurology, 11*, 115–146) had implicated in visual functions that might not demand small receptive fields.

I worked with Bob Travis on his studies of the neural correlates of discriminative conditioning while setting up a separate area for conducting my own experiments. While discussing the data Bob had obtained recording evoked potentials during conditioning paradigms, we decided to work together to develop a chronic single-unit recording setup. Bob began making microelectrodes. I built a cathode-follower high-impedance probe. Within a couple of days, we were successfully recording extracellular action potentials in anesthetized rats. Next, we needed a way to control the position of an electrode in the brain of the squirrel monkey subjects Bob was studying in his experiments. UAB had a well-equipped machine shop staffed with excellent personnel. With their assistance, we designed and built an 80-threads-per-inch screw-driven electrode carrier (Sparks and Travis 1967). One complete turn of the screw advanced the electrode approximately 300 microns. The electrode carrier, machined for a slip fit with the support rods, was internally threaded so that rotation of the screw advanced the electrode carrier without rotating the electrode.

By 1968, Bob and I were joint authors on six papers that involved recording the activity of single neurons in extrapyramidal and other subcortical areas. These were exploratory studies, for there was little to guide us concerning how individual neurons would respond to the behavioral variables we were manipulating. Mostly unknown to us, several other labs had also become actively engaged in experiments recording the activity of individual neurons in alert, behaving animals. Evarts published a description of his technique for recording the activity of subcortical neurons in moving animals, and Wurtz and colleagues had a series of papers describing single-cell activity in striate cortex in awake monkeys.

The International Congress of Physiological Sciences was held in Washington, D.C., in 1968. Bob and I went to the meeting and arranged to visit the labs of Evarts and Wurtz at the National Institutes of Health (NIH). Evarts very graciously gave us a set of drawings of the microdrive they were using with rhesus monkeys. After observing the rhesus monkeys performing behavioral tasks in the Evarts and Wurtz labs, Bob and I decided to switch from squirrel monkeys to rhesus monkeys.

In 1968, we had noticed unit activity closely related to stereotyped head, neck, and eye movements in the reticular formation, but we could not document it because we were not measuring eye or head movements in

those experiments. We followed up those observations in experiments using rhesus monkeys and the Evarts microdrive, and we determined that the firing patterns of some reticular formation neurons was related to horizontal eye movements (Sparks and Travis 1971).

A number of important chronic single unit recording papers related to the neural control of eye movements appeared in the early 1970s. Fuchs and Luschei recorded the activity of neurons in the abducens nucleus during horizontal eye movement made by alert monkeys. Schiller described the activity of single cells in the oculomotor and abducens nuclei during eye movements of unanesthetized monkeys. Robinson reported on the activity of oculomotor cells in monkeys, and Bizzi and Schiller recorded single-unit activity in the frontal eye fields of unanesthetized monkeys during eye and head movements. Luschei and Fuchs reported on the activity of brainstem neurons during eye movements of alert monkeys. Six papers related to the visual, attentional, and motor properties of neurons in the monkey SC were published by Schiller and Koerner, Schiller and Stryker, Wurtz and Goldberg, and Goldberg and Wurtz. Fuchs and Robinson (1966, *Journal of Applied Physiology, 21*: 1068–1070) published a paper describing a new high-resolution method of recording the horizontal and vertical movement of the eyes in rhesus monkeys. I contacted David Robinson and went to Baltimore to learn more about the technique. Alex Skavenski was finishing his postdoctoral training in Robinson's lab and had made extensive notes about construction of the field coils and electronic circuits for generating the magnetic fields. He generously gave me a copy of his notes, and I used them to replicate Robinson's setup in Birmingham.

In 1967, UAB received a NIH grant to purchase a large central computer system for online acquisition and processing of data from biophysical experiments. Small laboratory computers installed in a few labs were directly connected over long coaxial cables to the large central computer. One of the laboratory computers (a Digital Equipment Corporation [DEC] PDP-8/I with 8 k of 12-bit memory, a Teletype, and an AXO8 interface box with eight channels of a/d conversion [12 bit], two channels d/a conversion [10 bit], eight digital inputs, and four digital output lines) was installed in our lab. A few days before his putative start date, the person we had hired to program the PDP-8/I informed us that he had accepted a position in California and was no longer in Alabama. I used the DEC *Introduction to Programming* book to learn the assembly language instructions and became the lab programmer. A free one-week assembly-language programming course came with the lab computer. After I had written code that met our most immediate needs, I signed up for the course offered in California rather than one on the east coast and modified our Dodge van so it would accommodate our camping gear, Betty, me, and two small boys. We camped in the Rocky Mountains, Yellowstone, Tetons, Jasper, and Banff National Parks in Canada, and along the Oregon coast on our way to Palo Alto.

In 1972, Bob Travis stopped conducting experiments in the lab to focus on clinical research. I inherited his electrically shielded, sound-attenuated, walk-in room with a rhesus monkey restraining chair and computer-controlled HP 1310A large-screen oscilloscope for presentation of targets for visual tracking tasks. I had completed winding the coils and connecting the circuitry used to produce the magnetic fields. The equipment necessary for detecting and recording movements of the eyes was installed and working. The PDP-8/I had been programmed to enable direct experimental control of the monkey's eye position and velocity, along with the measurement of attendant neuronal activity. The system (1) generated and controlled the position and velocity of a visual tracking target presented on an oscilloscope; (2) generated a serial pulse code of target parameters, which was recorded on analog tape; (3) monitored horizontal and vertical eye position; (4) compared horizontal and vertical eye position with target position; (5) delivered reinforcement for appropriate tracking of the visual target; (6) provided online displays of eye positions, target position, and spike activity; and (7) permitted modification of target parameters based on the response properties of each neuron studied. Several offline data-analysis programs also had been written.

I now had the tools to pursue my goal of studying the three-dimensional relationships between stimulus input, psychophysical report, and the intervening neural events. But the scientific environment had changed. Some questions I had about the SC were already answered by the experiments done in the labs of Schiller and Wurtz. The grant application I submitted in September 1972 to study the role of pontine and other brainstem neurons in the control of saccadic and pursuit eye movements did not include experiments relating neural activity to sensory input. The need to obtain funds to keep the lab going was prepotent, and I made a vow to myself to add the sensory component later. The application to the National Eye Institute for funds to support the lab for three years was approved.

Many anxious minutes spread over more than three decades would have been avoided if I could have looked into the future and discovered that this grant would receive continuous funding and still be active when I retired at the end of the year in 2004. If this sounds as if obtaining funds to support research was smooth sledding, it did not seem that way at the time. Initially, I requested three years of additional support on each renewal application. After each submission, there was a long period of uncertainty and anxiety about the outcome of the review process. Nine years later, I began requesting five years of additional funding, and the periods of uncertainty and anxiety were not as frequent. The renewal application requesting funding from 1987 to 1992 was ranked 1 out of 62 applications recommended for approval by the VIS B study section and was selected for a NIH Merit (Method to Extend Research in Time) Award from 1987 to 1997.

Evolution of Ideas Concerning the Role of the SC in the Control of Movements

Recordings from the SC: A Signal for Saccade Initiation

Shortly after beginning to record the activity of neurons in the pontine reticular formation, I deviated from the proposed research plan. The optimal orientation of the microdrive for reaching the pontine target cells was such that the electrodes passed through the SC before reaching the pons. I could not resist observing for myself the important findings that had then been recently reported by Wurtz and Goldberg (1971, *Science, 171*: 82–84; 1972, *Journal of Neurophysiology, 35*: 575–586; 587–596) and by Schiller and Koerner (1971, *Journal of Neurophysiology, 34*: 920–936). Also, I had questions about the activity of collicular neurons, which were not answered in those papers. This diversion was supposed to be short, but it was not.

I was not yet convinced that the SC played a critical role in either the initiation of saccades or the precise specification of the direction and amplitude of a movement. My reasons for skepticism were these: the coarse tuning of the *movement fields* (the range of saccade directions and the amplitudes associated with movement-related activity of a neuron), and the failure of earlier papers to report a tight coupling between saccade-related activity in collicular neurons and the onset of the associated saccade. I thought that if the SC participates in the initiation of saccades, it should be possible to isolate a subpopulation of neurons in which the onset of neuronal activity is tightly coupled to saccade onset. Furthermore, in a situation in which a visual stimulus sometimes elicits a saccade and sometimes fails to do so, the occurrence of the neuronal activity should be highly correlated with saccade occurrence. Computer-generated plots of instantaneous spike frequency (the reciprocal of interspike intervals, ISIs) provided a better view (Sparks and Sides 1974) of the temporal pattern of spike activity on each trial than did the raster plots and cumulative histograms used in earlier papers. These plots revealed saccade-related burst neurons (SRBNs) that generated an initial low-frequency component, followed by a pulse of activity beginning approximately 20 milliseconds (ms) before saccade onset (Sparks 1978).

The probability of saccade occurrence was manipulated by varying target duration in a way that when two successive dots (A and B) were presented, the monkey would sometimes make a saccade to position A (near the center of the movement field of the cell) and then a second saccade (out of the movement field of the cell) to position B. On other trials, with the same duration of target A, only a single saccade (not in the movement field of the cell) to target B was observed.

The probability of a spike burst occurring in SRBNs was perfectly correlated with the occurrence of a saccade into the movement field of the cell. A spike burst always occurred if such a saccade was produced. Some buildup of spike activity might be observed but a discrete high-frequency pulse of

activity never occurred when the animal canceled the saccade or produced a saccade that was not in the movement field of the cell (Sparks 1978). I speculated that the discharge of SRBNs served as a trigger input to the pontine and midbrain circuitry that generates the horizontal and vertical signals required for a saccade.

Saccade Commands: Organized in Nonretinal Coordinates

Preliminary studies of the functional organization of the SC were interpreted as supporting early models of the saccadic system in which a signal of retinal error (RE), the distance and direction of the target image from the fovea, was relayed directly to the oculomotor system, which generated a command to correct for RE. Saccades were assumed to be ballistic because the trajectory of the saccade was determined at saccade onset. The site of neural activity in the retinotopic map of the superficial layers of the SC indicates the position of a visual target relative to the fovea. Schiller and Koerner 1971, *Journal of Neurophysiology, 34*: 920–936) hypothesized that the cells in the superficial layers activated underlying regions of the SC containing neurons that discharge before saccades. Because the motor map of saccadic eye movements is aligned with the retinotopic map (Robinson 1972, *Vision Research, 12*: 1795–1808), the ensuing saccade would direct the foveal projection toward the region of the visual field containing the target. Later models assumed that visual targets for saccadic eye movements are localized with respect to the head or body and not with respect to the retina.

The results of experiments Larry Mays and I conducted strongly supported the view that saccade targets are localized in a non-retinocentric frame of reference (Mays and Sparks 1980b, 1981; Sparks and Mays 1983b). On a typical trial, the fixation target was extinguished, and an eccentric target was illuminated for 50–100 ms. The monkey usually looked to the position of the target with a latency of 160–200 ms. Randomly, on 30 percent of the trials, after the target was extinguished, but before the animal could begin a saccade, the eyes were driven to another position in the orbit by electrical stimulation of the SC. Animals compensated for the stimulation-induced perturbation by looking to the approximate position of where the target had appeared. This happened regardless of the position of the target and regardless of the direction and amplitude of the saccade required to compensate for the stimulation-induced movement. Visual background cues could not be used as an external frame of reference for localizing the targets because, except for the fixation target and the briefly flashed target, the task was performed in total darkness. Also, the target was extinguished before the stimulation-induced saccade and could not provide a visual update of the target position.

Retinocentric models predict that the animal will produce a saccade with a predetermined distance and direction—a saccade that will direct gaze to

a point in space that differs from the target location by an amount equal to the direction and amplitude of the stimulation-induced saccade. The result predicted by retinocentric models was never observed. In spatial models, RE signals will be combined with information about the change in eye position produced by collicular stimulation. They predict that the animal will look to the actual position of the target in space. This was the result we observed.

The eye movement that compensated for the change in eye position produced by stimulation was *not* a passive, low-velocity movement to an orbital position of mechanical equilibrium established by a tonic pattern of motoneuron activation specified by the visual target. It was a saccade. A new saccade command, based on stored information about the location of the retinal image and information about the new position of the eyes, had been issued.

Larry Mays and I are joint authors on 17 publications. The chance encounter that was the basis of our collaboration happened in 1976 while recruiting Joan Lorden to the Department of Psychology. I learned that her husband, Larry Mays, had a PhD and was also looking for a research/ teaching position. Larry had recorded unit activity from hippocampus in awake rats in his dissertation research, and he had measured eye movements using the magnetic search coil while working with Jim McElligott at Temple University. I secured a postdoctoral position on a training grant for Larry, and Joan and Larry came to UAB. Joan is now provost and vice chancellor for Academic Affairs at the University of North Carolina (UNC) at Charlotte. Larry is professor and chair, Department of Bioinformatics and Genomics, UNC at Charlotte.

Activity of SC Neurons Preceding Compensatory Saccades

John Porter and I did follow-up experiments to determine whether neurons in the SC discharging before visually triggered saccades also discharge before saccades compensating for stimulation-induced perturbations in eye position (Sparks and Porter 1983). Target coordinates were arranged so that the vector of the compensatory movement was in the movement field of the cell under investigation. Forty-nine of the 50 cells studied discharged before compensatory saccades in their movement field. The only neuron that did not was shown to require prior activation by a visual stimulus within its movement field. This finding provided additional support for the hypothesis that the SC contains a spatial map of motor error (ME), the difference between current eye position and desired eye position.

Population Coding of Motor Commands

Spatially, the movement fields of most SC neurons are large and coarsely tuned (Sparks 1975). Each neuron fires before a broad range of saccades. Thus,

a large population of neurons is active before each saccade. The discharge of individual SC neurons is ambiguous with respect to saccade direction or amplitude because identical discharges precede many saccades with different directions and amplitudes (Sparks and Mays 1980). It is the location of active neurons within the topographical map of movement fields, not their frequency of firing, that must specify saccade direction and amplitude.

How are the signals needed to precisely control the direction and amplitude of a saccade extracted from the activity of this large population of coarsely tuned cells? We tested predictions of a population coding scheme in which each member of the active population contributes to the movement, and the exact trajectory of a saccade is determined by the average or sum of the population response (McIlwain 1975, *Journal of Neurophysiology, 38*: 219–230; Sparks et al. 1976).

An insulated, silver-coated glass pipette designed by Malpeli and Schiller (1979, *Journal of Neuroscience Methods, 1*: 143–151) was used to record extracellular unit activity, for microstimulation, and for pressure injection of various agents into the SC. If, as we proposed, the direction and amplitude of a saccade is the result of a weighted average of each neuron's vector contribution, deactivation of a small region of collicular neurons may produce saccades with amplitudes that are either too large or too small. Which one occurs depends on the location of the deactivated neurons within the population of cells active before and during a saccade. For example, if the inactivated cells are "voting for" relatively small amplitude movements, the amplitude of the saccade specified by the remaining active neurons would be larger than the one specified by the full complement of cells. A smaller movement would occur if a different movement (involving a different subset of SC cells) was made in which the same inactivated cells were ones contributing to relatively large amplitude movements.

As predicted by the vector-averaging hypothesis, a systematic pattern of errors in direction and amplitude was observed (Lee et al. 1988; Sparks et al. 1990). Movements to targets requiring a saccade smaller in amplitude than the "best saccade" (the movement produced by passing small-current pulses through the recording/injection probe) were too small; saccades to targets requiring a movement larger than the "best saccade" were too large. The direction and amplitude of movements similar to the "best saccade" were not altered noticeably after the injection. But the velocity of visually guided movements corresponding to the "best saccade" was slower, and the duration was prolonged so that the amplitude of the movement was about the same. The findings of our experiment were important for first demonstrating that saccadic accuracy results from the movement tendencies produced by the entire active population rather than by the discharge of a small number of finely tuned cells. A "News and Views" article written by Terry Sejnowski (1988, *Nature, 332*: 308) highlighted the findings of the experiment in the issue of *Nature* in which our paper appeared.

Choongkil Lee did his PhD research under the supervision of Joseph Malpeli at the University of Illinois and had experience with the Malpeli and Schiller technique for reversible activation or inactivation of small regions of brain tissue. Choongkil is now professor emeritus, Department of Psychology, Seoul National University.

Bill Rohrer obtained his PhD from the University of Notre Dame. Bill worked with Choongkil on the population coding experiment and conducted experiments using express saccades that increased our knowledge about the motor commands found in the SC. He is now a senior professor of Biology and Allied Health Technology, Union County College, Cranford, New Jersey.

Influences of the Site, Duration, and Level of Collicular Activity

Early papers reported that the properties of movements evoked by SC stimulation in monkeys were not influenced by varying stimulation parameters. This led to the conclusion that, within the SC, information relating to the properties of a saccade are encoded solely by the spatial distribution of activity and that neither the level nor the duration of activity plays a role in determining the properties of the movement. However, in various nonprimate species, varying the parameters of microstimulation has large effects on stimulation-evoked orienting movements. Incidental observations in recent (at that time) primate studies were not consistent with the hypothesis that the activity of SC neurons plays no role in the control of saccade velocity or duration. It seemed prudent to check the validity of these conclusions before launching experiments based on the assumption that they were correct.

Thus, we repeated the early primate microstimulation experiments but systematically varied the duration and frequency of the stimulation trains over a wider range than used in the early experiments (Stanford et al. 1996). In contrast to the results of the earlier studies that varied current strength but not train duration, we found that both the site of stimulation and the parameters of stimulation are important factors in determining the properties of stimulation-induced eye movements.

As early studies reported, the site of stimulation within the collicular motor map determined the largest stimulation-induced movement that we could generate. But varying the duration and frequency of the stimulation train produced dramatic effects. For any stimulation site, movement amplitude depends on the duration of the stimulation train: As train duration increases, movement amplitude increases monotonically until it reaches the site-specific limit. Within the range over which amplitude can be modulated, the end of the movement is tightly linked to the offset of the stimulation train. The frequency of stimulation influences the peak velocity of an evoked movement: Higher frequencies produce movements with higher velocities. The parameters of collicular stimulation can be adjusted to

provide independent control over saccade amplitude and saccade velocity. Movements that have comparable amplitudes, but different dynamic characteristics can be produced by varying train duration and frequency. Collicular activity must be sustained throughout the execution of the movement if the site-specific maximal amplitude is to be achieved, and the peak velocity of a saccade is determined, at least in part, by the level of collicular activity.

Terry Stanford received his PhD from the University of Connecticut Health Center in 1989. He developed a method for studying the responses of neurons in the inferior colliculus in the unanesthetized rabbit to auditory stimuli in the lab of Shigeyuki Kuwada and decided to spend some time in my lab to learn more about chronic single unit recording techniques. Terry is now professor, Neurobiology and Anatomy, Wake Forest School of Medicine.

Movement-Related Activity in the SC: A Command for a Change in Gaze

Microstimulation of the optic tectum/SC in several nonprimate species produces coordinated movements of the eyes, head, pinnae, vibrissae, and body. Early experiments in which the parameters of stimulation were not varied systematically failed to observe coordinated movements of the eyes and head following microstimulation of the SC in monkeys. But coordinated eye–head gaze shifts were evoked by electrical stimulation of the SC in rhesus monkeys in a preliminary report by Seagraves and Goldberg (*The Head–Neck Sensory Motor System*, eds. Berthoz, Graf, and Vidal, 1992, 292–295). For his dissertation research, Ed Freedman performed three experiments related to this unresolved issue. The first provided a comprehensive description of the visually guided gaze shifts that occur when the head is completely unrestrained. The second involved a reexamination of the effects of microstimulation of different regions of the SC, and the third examined the pattern of activity of individual neurons before and during the execution of large visually guided gaze shifts involving combined eye–head movements.

Several general rules about the coordination of the eyes and head during large rapid visually guided gaze shifts emerged from the first experiment (Freedman and Sparks 1997a, 2000). These general rules were used as the basis for comparison with movements evoked during microstimulation of the primate SC, and to develop a strategy for determining whether the activity of individual cells in the SC was correlated with the overall change in gaze or with the eye and/or head components of the gaze shift.

The site and parameters of microstimulation of the SC of rhesus monkeys was varied systematically when the head was completely unrestrained (Freedman et al. 1996). Collicular stimulation produces high-velocity, combined eye–head gaze shifts that are remarkably similar to naturally occurring visually guided gaze shifts of comparable amplitude and

direction. The amplitude and velocity of stimulation-induced gaze shifts depend on the parameters (frequency, current level, and duration of the stimulation train) of stimulation and the site of stimulation. Increasing the duration of the stimulation train systematically increases the amplitude of evoked gaze shifts until a site-specific maximal amplitude is reached. The frequency of stimulation affects the velocity of evoked gaze shifts: Higher frequencies result in higher peak velocities.

As is true for visually guided gaze shifts, the head contribution to stimulation-induced gaze shifts depends on the position of the eyes relative to the head at the onset of stimulation. When the eyes are deviated in the direction of the ensuing gaze shift, the head contribution increases and the latency to head movement onset decreases. The head contribution to stimulation-induced gaze shifts also depends on the direction of the gaze shift. The head contribution decreases as the gaze shift becomes more vertical.

Gaze shifts with relatively constant amplitudes and directions occur when stimulating a particular site using constant stimulation parameters. But these gaze shifts of similar directions and amplitudes are accomplished with many combinations of eye and head components, depending on the initial positions of the eyes in the orbits and the direction of the gaze shift. These data are inconsistent with the hypothesis that the SC generates separate eye and head displacement commands. Instead, the findings indicate that a unitary signal of desired gaze displacement is derived from the locus of collicular activity. This signal is separated into eye and head components below the level of the SC. But the level of collicular activity can influence the velocity of gaze shifts without affecting the gaze displacement signal.

The activity of single neurons in the intermediate and deep layers of the monkey SC was recorded during combined eye–head gaze shifts (Freedman and Sparks 1997b). The cells were studied in conditions in which (1) the amplitude and direction of gaze movements was relatively constant, but the eye and head components varied over a wide range; and (2) either the eye or head contribution was fixed but the direction and amplitude of gaze changed over a large range. This allowed the activity of collicular neurons to be recorded under conditions in which gaze and the eye and head contributions to gaze were dissociable.

For all the cells for which these analyses could be performed, motor-related activity was best correlated with the amplitude and direction of the gaze shift and was only weakly correlated with eye or head components of gaze. Gaze shifts having similar amplitudes and directions were associated with similar motor-related bursts. These findings supported the hypothesis that a desired gaze-displacement signal is derived from the locus of collicular activity and is decomposed into separate eye and head signals downstream from the SC.

I hired Ed Freedman as a research assistant because of his previous research experience at Brown University and Cornell. Later, he was accepted

into the graduate program in neuroscience and did his dissertation research in my lab. Ed received the 1997 Lindsley Prize in Behavioral Neuroscience awarded by the Grass Foundation and the Society for Neuroscience. He also won the Flexner Award for outstanding dissertation research in the Institute of Neurological Sciences at Penn. Ed spent two years as a post-doctoral fellow in the lab of Albert Fuchs at the University of Washington in Seattle and then accepted a position in the Department of Neuroscience, University of Rochester Medical Center, where he is currently an associate professor.

Evolution of Ideas Concerning the Coordinates of Sensory Signals in the SC

Visual Maps in the Primate SC: What Is Represented?

Visually responsive neurons in the superficial layers of the SC are activated by stimulation of a particular region of the retina. They respond only to the appearance of a visual stimulus in their receptive field, and the location of the receptive field shifts with each change in gaze. Thus, the site of neuronal activity in the retinotopic map of the superficial layers represents a map of RE, the distance and direction of the image from the fovea (Goldberg and Wurtz 1972, *Journal of Neurophysiology, 35*: 542–559; Mays and Sparks 1980a). The deeper layers of SC contain visually responsive cells with activity that represents ME, the difference between current eye position and desired eye position. We labeled these as quasi-visual or QV cells. They discharge whenever a saccade with a particular direction and amplitude is appropriate, regardless of whether the movement becomes appropriate because of the onset of a visual stimulus or because of an eye movement occurring after the disappearance of the target (Mays and Sparks 1980a).

Monkeys were trained to make saccades in response to a single target in one half of the visual field or to two brief targets usually in the other hemifield. On single-saccade trials, after subjects maintained fixation of a target (O) at the center of the oscilloscope screen for a variable period, target C appeared in the receptive or movement field of the neuron under observation. On double-saccade trials, the offset of the center fixation target (O) was followed by successive presentations of targets A and B, neither of which were in the neuron's receptive or movement field. The total duration of targets A and B was less than the reaction time of the monkey. Nevertheless, we programmed the computer to make reward contingent upon a saccade to position A followed by a saccade to position B. A critical feature of this paradigm is that a saccade from position A to position B has the same amplitude and angle as a saccade from the fixation point to C. Only the origins of the movements differ.

On the single-saccade trials, when the animal is maintaining a single fixation position, QV cells appear to be visually responsive, to have visual receptive fields and to respond to targets in their receptive field whether or not a saccade is made toward the target. But on double-saccade trials requiring a change in fixation, QV cells begin to fire only after the eye has reached position A, and they continue to fire until after the saccade from A to B. The cells firing in this case are not those whose receptive field contained the original target B, but the cells whose receptive field would contain target B if the target were flashed again in the same spatial location after the eyes reached position A. Unlike neurons in the superficial layers, which are activated if, and only if, a particular region of the retina is stimulated, QV cells are activated by stimulation of any region of the retina if, after a subsequent movement of the eye, a saccade with a particular trajectory is required to look to the target. No component of the discharge of the QV cells appeared to be motor in the usual sense. Instead, the activity of QV cells reflects eye-position error (the difference between actual and desired eye position) and holds this information in spatial register until a saccade occurs or is canceled.

Note that the presumed linkage, implied in earlier versions of the foveation hypothesis, between the superficial layers (receiving direct retinal inputs) and the deeper layers of the SC is not necessary for the activation of neurons with saccade-related activity. In this experiment, the discharge of overlying visual cells was neither necessary nor sufficient to activate most cells with saccade-related activity.

Auditory Maps in the Primate SC: What Is Represented?

Experiments studying saccades to auditory targets also indicated that the responses of sensory cells in the deeper layers of the SC are encoded in motor, rather than sensory, coordinates (Jay and Sparks 1984, 1987a, 1987b, 1990). Monkeys trained to look to either visual or auditory targets in a completely darkened room were placed with their heads fixed in the center of a semicircular track. Movement of a speaker (with a light-emitting diode attached) along the track and rotation of the track allowed targets to be presented at most locations on an imaginary sphere surrounding the animal. Three fixation lights separated by 24 degrees were placed along the horizontal meridian. At the beginning of each trial, one of the three fixation lights was randomly activated. After a variable interval, an auditory (broad-band noise burst) or visual target was presented, and the animal was required to look to the target location to receive a liquid reward. A delayed saccade task was used to separate, temporally, sensory and motor activity.

The major objective of the experiment was to plot the receptive fields of sound-sensitive cells in the SC of alert monkeys while varying the direction

of visual fixation. If the receptive fields of auditory neurons in the SC are based on interaural cues and are organized in head-centered coordinates, the direction of fixation would have no effect. But, if the response of auditory neurons is organized in ME coordinates, then the response should depend on both speaker position and fixation direction. We found that the position of the eye in the orbit had a distinct effect upon the response of sound-sensitive cells in the SC. When the magnitude of the neural response was plotted as a function of the stimulus location in space, the receptive fields of the neurons shifted with the position of the eye in the orbit. But when the magnitude of the neural response was plotted as a function of the direction and amplitude of the movement required to look to the auditory target, the plots obtained with the different fixation positions were closely aligned. Thus, the discharge of sound-sensitive neurons in the SC is not determined solely by the position of the auditory stimulus in space, but rather depends upon ME, the trajectory of the saccade required to look to the target.

We also monitored the activity of cells that generated a burst of activity before saccades to visual targets while monkeys made saccadic eye movements to auditory targets. Most neurons generating bursts before saccades to visual targets also burst before saccades to auditory targets. Visual and auditory signals, originally encoded in retinal and head-centered coordinates, respectively, have undergone a transformation that allows them to share a common efferent pathway for the generation of saccadic eye movements.

The sound delivery system we used in these experiments was constructed by the technical staff at Cal Tech. It was a duplicate of the system used by Knudsen and Konishi (1979, *Journal of Comparative Physiol*ogy, *133*: 13–21) in their studies of auditory localization by the barn owl. John Pettigrew (1984, *Nature*, *309*: 307–308) wrote a "News and Views" article in *Nature* about the use of the hoop in the "revelations" of Knudsen and Konishi finding a computational map of auditory space in the brain of the barn owl and the "surprising" finding that the coordinate frame of the map of sound space in the monkey SC shifts when the monkey's eyes change positions.

Sometime in the early 1980s, I received a letter from Albert Fuchs inquiring about the possibility of transferring a graduate student, Martha Jay, from the University of Washington to UAB. Martha's husband had accepted a faculty position in the Department of English at the University of Alabama in Tuscaloosa. Martha was in the MD/PhD program at the University of Washington and her thesis for the MS degree involved studies of the auditory system. The timing was perfect. I had just completed installing the sound delivery system described previously. After she received her PhD, Martha's husband accepted faculty positions in South Carolina and then Wisconsin. Martha received her MD from the University of South Carolina School of Medicine and did her residency in Ophthalmology at Northwestern University. She was the first eye surgeon in the Milwaukee area to perform laser refractive surgery and remains at the forefront of the field.

Somatosensory Maps in the Primate SC: What Is Represented?

The saccadic eye movements directing gaze to the source of a tactile stimulus cannot be based solely on information about the region of the body surface that is activated. Information about the current direction of gaze also must be considered. Jennifer Groh's dissertation research at the University of Pennsylvania addressed this issue. Her thesis combined behavioral, electrophysiological, and computational methods. The computational component demonstrated that the required sensorimotor transformations could be performed using conventional neural circuits and neurons with typical biophysical properties (Groh and Sparks 1992).

Animals (with the head fixed) were trained to look to the source of visual or somatosensory stimuli (Groh and Sparks 1996a, 1996b, 1996c). Behavioral data were used to compare the accuracy and other characteristics of saccades to visual targets with those of saccades directed to vibratory stimuli. Somatosensory saccades were less accurate than visual saccades, and the peak velocities of somatosensory saccades were lower than those of visual saccades of the same amplitude.

Primary objectives of neurophysiological experiments were to determine whether cellular responses to somatosensory stimuli are affected by the positions of the eyes in the orbits and to determine whether cells that discharged before saccades to visual targets also discharged before saccades to somatosensory stimuli.

All but one of the 86 cells with saccade-related activity studied discharged before saccades to both visual and somatosensory targets. The remaining cell was active only for visual saccades. This result indicates that visual and somatosensory signals, originally encoded in quite different coordinate frameworks, have been translated into a common frame of reference and are sharing premotor neural elements.

Nearly all cells responding to somatosensory stimuli also responded to visual targets. Eye position significantly affected the responses to both somatosensory and visual stimuli in a similar manner. The cells responded to visual and somatosensory targets located at approximately the same direction in space with respect to the eyes. The activity of these cells exhibited both sensory and motor qualities. The discharge was more closely linked in time to stimulus onset than to the movement. Nonetheless, the activity of collicular cells was related to the change in eye position necessary to bring the target onto the fovea, rather than the location of the stimulus on the body surface. Somatosensory signals in the SC, like auditory ones, appear to be encoding the metrics of a movement to a stimulus rather than the location of that stimulus in space.

Jennifer Groh learned about my research in a graduate course at the University of Michigan, and she had heard rumors that I was moving to Penn, where she had also been accepted into their graduate program after she applied the year before. She wanted to know if I moved to Penn, would it

be possible for her to transfer and to do her dissertation research in my lab. Jennifer flew to Birmingham to discuss a possible transfer before actually doing so. She recently told me I met her at the gate in the airport holding up a copy of the *Journal of Neurophysiology* so she would recognize me. After receiving a PhD from Penn, Jennifer spent three years as a postdoctoral fellow in Bill Newsome's lab at Stanford University. She is currently professor in the Departments of Psychology and Neuroscience, Neurobiology, and the Center for Cognitive Neuroscience at Duke University.

The Importance of the Findings of the Experiments Conducted by Jay, Groh, and Mays and Sparks

The research of most sensory neurophysiologists is devoted to understanding how neural representations of external and internal events are related to cognitive factors, especially perception. But sensory processing is also required to initiate and guide action. Indeed, perception and cognition have no adaptive value in the absence of action. Action is usually directed to the spatial location of objects, but the localization of a stimulus in space requires complex neural computations. Visual stimuli activate receptors in specific regions of the retina, but there is not a one-to-one correspondence between which region of the retina is activated and the location of the visual object in space. Which region of the retina is activated by a stationary visual stimulus depends on the positions of the eyes in the orbits, the position of the head, and the position of the body.

Information about the region of retinal activation must be combined with information about eye, head, and body position to compute the location of the visual stimulus. It is not possible to know the location of a visual stimulus in space by processing only information that arrives over the optic nerve. The localization of somatosensory and auditory stimuli also requires complex neural computations. The raw sensory data must be combined with information about the positions of the eyes in the orbits, the position of the head on the body, and other sources of information to compute the location of the target and the trajectory of a movement to the target. Results of experiments by Mays and Sparks (1980a), Jay and Sparks (1984, 1987b), and Groh and Sparks (1996c) provided early examples of cases in which sensory stimuli were coding information in a motor frame of reference. They also provided examples of the types of experimental manipulations required to demonstrate coding in motor coordinates.

Extraocular Muscle Proprioception: Essential for the Spatial Localization of Saccade Targets?

Localizing visual stimuli in spatial coordinates requires that retinal and eye-position information be combined. The two possible sources of the

eye-position signal are extraocular muscle afferents and a neural copy of the command to move the eye. Bart Guthrie, John Porter, and I (Guthrie et al. 1983) investigated the role of extraocular muscle afferents and, by exclusion, the contribution of a copy of the central motor command to the eye-position signal used in target localization.

We did anatomical studies to determine whether, in the monkey, extraocular muscle afferents reach the central nervous system exclusively through the ophthalmic branch of the trigeminal nerve, as they do in the cat. Injections of horseradish peroxidase into individual extraocular muscles of monkeys, labeled pseudounipolar neurons, localized only within the ipsilateral semilunar ganglion (Porter et al. 1983). Intracranial transection of the ophthalmic nerve before muscle injection eliminated all labeling within the ganglion. Thus, the extraocular muscles can be selectively deafferented to examine the role of proprioception in the control of eye movements.

Bart Guthrie developed a surgical procedure for reliably sectioning the ophthalmic branch of the trigeminal nerve. After surgical elimination of extraocular muscle proprioception, we tested animals on a stimulate/compensate task (Mays and Sparks 1980b; Sparks and Mays 1983b), a task requiring rapid and accurate feedback about eye position. If extraocular muscle proprioception is an essential source of eye-position information, without it, the oculomotor system would not be capable of generating an accurate compensatory saccade. In contrast, if corollary discharge is used as an accurate eye-position signal, the animals would continue to compensate in the absence of extraocular muscle proprioception.

After initial testing of animals on the stimulate/compensate task, the ophthalmic nerves were transected bilaterally at their junction with the trigeminal ganglion, eliminating extraocular muscle proprioception. Complete transection was determined postoperatively by loss of the corneal blink reflex and confirmed postmortem by the absence of labeling of trigeminal ganglion sensory neurons after injection of horseradish peroxidase into the extraocular muscles. Postoperatively, animals were still able to compensate for stimulation-induced perturbations in eye position and look to the approximate position of the targets in space (Guthrie et al. 1983). This is possible only if information about the stimulation-induced eye movement is still available. This information could not be provided by retinal stimulation. Experiments were conducted in total darkness, and the visual target was not present during or after the stimulation-induced saccade. Because transection of the ophthalmic nerves eliminated extraocular muscle proprioception, the eye-position information must have been provided by a centrally generated corollary discharge.

Bart Guthrie was in the MD/PhD program at UAB, had finished medical school and a one-year internship, and was working to finish his PhD before beginning a residency in the Neurosurgery Department at the Mayo Clinic in Minnesota. After completing his neurosurgery training at the Mayo Clinic

and a fellowship at Stanford University, Bart was on the faculty at George Washington University. He returned to UAB in 1993 and currently serves as the director of Computer-Assisted Neurosurgery (CANS) at UAB.

John Porter received his PhD in Anatomy from the Medical College of Virginia in 1980. He worked with Robert Spencer studying the morphology and innervation of extraocular muscle fiber types and the destination of extraocular muscle afferents. After a successful research career, John left his position at the Case Western Reserve University School of Medicine to become program director, Neuromuscular Disease at the National Institute of Neurological Disorders and Stroke.

The overlap of Bart's and John's time in the lab was fortuitous. John's anatomical expertise allowed us to perform the experiments needed to see whether the anatomical data about the location of cell bodies of extraocular muscle afferents in cats could be extended to primates.

Single-Cell Signals

Gradual Development of Signals Specifying Saccade Direction and Amplitude

Stimulation of a discrete region of SC produces a sequence of neural events that specifies the horizontal and vertical amplitude of a saccade (*specification*) and provides the signals necessary to initiate that movement (*initiation*). As discussed earlier, the high-frequency burst of SRBNs that precedes saccade onset by 18–20 ms is a collicular signal probably involved in the initiation of saccades. What is the evidence that other types of collicular signals are involved in the specification of saccade direction and amplitude?

While testing the ability of rhesus monkeys to compensate for perturbations in eye position produced by microstimulation of the paramedian pontine reticular formation (PPRF; Sparks et al. 1987), we accidentally discovered that pontine stimulation sometimes triggered, prematurely, a component of the impending saccade to a visual target. The speed of the movements observed after stimulation could be used to distinguish (1) pontine stimulation-evoked low-velocity movements from (2) saccades made to acquire the visual target. This premature saccade was considered a component of the impending movement to the visual target because both its direction (up or down) and amplitude depended on target position.

The amplitude of the prematurely triggered saccade increased as the time of stimulation approached the point at which a normal, visually triggered saccade would have occurred. This suggests that, for normal visually directed saccades, during the presaccadic interval, the input to the saccadic generator circuits gradually develops over at least a 100-ms period. We accidentally discovered that pontine stimulation could be used to sample, at various intervals, the status of this latent signal.

Glimcher and Sparks (1993) tested the effects of low-frequency stimulation, subthreshold for movement initiation, on spontaneous and visually guided saccades. Subthreshold stimuli biased the direction and amplitude of spontaneous and visually guided eye movements in the direction and amplitude of movements evoked by suprathreshold stimulation of the same collicular location without affecting the time at which the movements were initiated. Movement specification is separable from initiation.

The low-frequency signals of (1) the QV cells that encode ME (Mays and Sparks 1980) and (2) those that become active when a target is selected as the goal of an impending saccade (Glimcher and Sparks 1992) are signals that could be involved in the specification of saccade direction and amplitude.

Paul Glimcher received his PhD in neuroscience at the University of Pennsylvania in 1989. His dissertation research was directed by Randy Gallistel. Paul was interested in the neural bases of attention and the processes involved in selecting targets as goals for action. He pursued this line of research after accepting his initial faculty position as an assistant professor in neural science at New York University in 1994. He is now the Julius Silver Professor of Neural Science and professor of neuroscience and physiology at New York University.

Single-Cell Signals: Sometimes Seductive Saboteurs

We encountered two situations in which, for neurons above the level of the motoneurons, correlations between the saccade-related activity of neurons and the properties of the movement are misleading. The first case occurs when recording the activity of excitatory burst neurons (EBNs) in the pontine reticular formation during coordinated eye–head movements. In animals with the head in a fixed position, the number of spikes in the saccade-related burst is highly correlated with saccade amplitude, and the peak velocity of the movement is tightly coupled to the peak frequency of the burst. EBNs have monosynaptic connections with motoneurons innervating extraocular muscles. Early papers viewed the activity of EBNs as a command for a saccadic eye movement. Later experiments found that during coordinated eye–head movements, the spike count of EBNs was better correlated with gaze amplitude than with the amplitude of the eye component (Ling et al. 1999, *Journal of Neurophysiology, 82*: 2808–2811). An explanation for this discrepancy in findings is presented below.

Neeraj Gandhi and I tried to resolve this discrepancy by stimulating the omnipause neurons (OPNs) before and during a gaze shift (Gandhi and Sparks 2007). OPNs, a discrete collection of cells found along the midline of the PPRF, discharge tonically during fixation and are silent during saccades. They inhibit, monosynaptically, the EBNs and, thus, gate the activity of cells presumably generating a command for an eye movement. OPNs are clustered together in a small nucleus that contains only OPNs, and it is

possible to selectively activate OPNs with electrical stimulation. When this is done in animals with the head restrained, OPN stimulation interrupts ongoing saccades for the duration of the stimulation train. The saccade is resumed when the stimulation train ends.

If the EBNs are generating a command only for moving the eyes, then OPN stimulation should perturb only movements of the eyes. If, however, as the correlation between the number of spikes in the EBN burst and gaze amplitude implies, the output of EBNs is sent to both eye and neck motoneurons, the inhibition of EBN activity produced by stimulation of the OPNs should affect both the eye and the head components of the gaze shift.

Stimulation of the OPNs synced to the onset of large, combined eye–head movements interrupted the ongoing gaze shift but not the movement of the head. The interruption of gaze occurred because the saccadic component of the eye movement was halted. Gaze was constant during the interruption period because the eyes counterrotated and completely compensated for the continuing movement of the head. The gaze shift was resumed shortly after the offset of the stimulation train.

We concluded that stimulation of the OPN region gates the neural pathway involved in the production of the saccadic eye component of the gaze shift. The EBN signal is not necessary for the initiation of the head component of a gaze shift or for the continued execution of an ongoing head movement. Having a separate gate for the onset of saccadic movements allows eye and head movements to begin at different times. Also, the separate gate can prevent saccadic disruptions of smooth pursuit eye movements tracking a target moving in a single-depth plane or disruptions of vergence eye movements when tracking a target that is moving through different depth planes. Inhibition of saccade initiation also occurs when the vestibulo-ocular reflex (VOR) allows fixation of a stationary target to be maintained by a counterrotation of the eyes during movements of the body and/or the head.

Why, then, in head-unrestrained animals, is the number of spikes generated by pontine burst neurons more highly correlated with the amplitude of the gaze shift than it is with the amplitude of the eye movement? My suggestion (Sparks 1999) was that during combined eye–head gaze shifts, the eye movements that are executed are not the movements requested by the EBNs. Because the head was moving and the VOR was active and producing a counterrotation of the eyes, the executed eye movements had amplitudes smaller than the movements that would have occurred if the head had not been moving.

In experiments with the head restrained, measures of executed eye movements provide accurate estimates of the saccadic commands transmitted to the extraocular motoneurons. The estimates are accurate because the motoneurons receive no additional inputs from other oculomotor subsystems (e.g., vergence, pursuit, vestibular) during the time

when the saccade command is being implemented. Under these conditions, the amplitude of the movement is tightly correlated with the number of spikes in the saccade-related burst of pontine EBNs, and the peak velocity of the movement is tightly coupled to the peak frequency of the burst. However, when the motoneurons are receiving inputs from parallel oculomotor subsystems while a saccade is being generated, measures of the amplitude, direction, or velocity of the executed saccade provide unreliable and potentially misleading estimates of the saccadic command sent to the motoneurons. In the absence of precise information about other influences on motoneuron activity, correlations of the activity of neurons above the level of motoneurons with various movement parameters cannot be interpreted accurately when more than one oculomotor subsystem is active. I concluded (Sparks 1999) that "advances in understanding the neuronal bases of eye–head coordination and saccadic–vergence interactions will be impeded until we find a way to cope with this neural uncertainty problem—namely, the problem of not being able to determine whether or not the eye movement that was executed is the one that was requested by the subsystem under investigation." See Sparks and Gandhi (2003) for a longer discussion of this issue.

The second case we encountered in which correlations between the saccade-related activity of neurons and the properties of the movement are misleading happens when saccades are made to the remembered location of a target. "Remembered saccades" are characterized by an "upward bias,"—that is, overshooting upward targets and undershooting downward targets (White et al. 1994). We recorded the movement fields of the same SRBN for movements to visual and remembered targets (Stanford and Sparks 1994). In each case, we observed an upward shift of the movement field to remembered targets relative to that observed for movements to visual targets. The most parsimonious explanation for this result is that the signal responsible for the observed upward bias is added at a site downstream to the SC. Because of the dissociation between SC commands and the movements that are observed on memory trials, saccades to remembered targets cannot be used to study the relationship between neuronal activity and the metrics or velocity of the executed movement. Perhaps it is more appropriate to talk about a "collicular request" rather than a "collicular command."

Janis White was the first author of the first of two papers in the volume of *Vision Research* describing our findings about saccades to remembered target locations. Janis has OD and PhD degrees and is currently director of the Low Vision Service of the East Orange VA Medical Center in New Jersey. She did a postdoc in the lab after she finished her PhD in physiological optics at the University of Houston, College of Optometry.

Neeraj Gandhi did his dissertation under the supervision of Ed Keller and obtained his PhD in bioengineering in 1997 from the bioengineering

graduate group offered jointly by the University of California, San Francisco, and the University of California, Berkeley. He is now professor and graduate program director, Department of Bioengineering at the University of Pittsburgh.

The Reproducibility of Motor Command Signals Carried by Individual Neurons

The responses of visual neurons are highly reproducible when the same time-varying luminance patterns are presented repeatedly (e.g., Reinagel and Reid, 2002, *Journal of Neuroscience, 22*: 6837–6841). Xintian Hu and I wanted to perform the motor equivalent of these sensory experiments by measuring the reliability of motor commands for saccadic eye movements generated by single premotor neurons.

We recorded the activity of the EBNs in the PPRF while subjects made repeated saccades from the same initial fixation target to the same eccentric target. Although considerable variability in the amplitude, duration, and velocity of movements was observed, software was used to identify subsets of movements with similar amplitudes and velocity profiles.

We (Hu et al. 2007) found that the ISIs of the high-frequency component of the bursts are very similar during movements having similar amplitudes and velocity profiles. Except for jitter in the duration of the first interval and variability in the last few intervals of the burst, most of the ISIs are similar, at a submillisecond timescale, from movement to movement. This is true despite the facts that (1) the movements selected for having similar amplitudes and velocity profiles occurred over a relatively long period and (2) movements of other directions and amplitudes and velocities were interspersed. Thus, each time the cell's burst has a particular temporal pattern, a saccade with a particular velocity profile will occur. Such a relationship between the activity of a single pontine burst cell and the velocity profile of a subset of movements would not be observed if (1) other members of the large active population of pontine burst cells had quite different temporal profiles of burst activity or (2) if, in general, the burst profiles were heterogeneous and uncorrelated. Thus, these findings indicate that variability in the discharge of a single pontine burst cell is not independent of, but, instead, must be strongly correlated with the activity of other active pontine cells generating saccade-related bursts.

Xintian Hu graduated from the University of Science and Technology of China in 1988. He received his PhD degree from Princeton University in 2000 performing his dissertation research in the lab of Charles Gross. In 2005, he was awarded the One Hundred Persons Project of the Chinese Academy of Sciences and took his current position at the Kunming Institute of Zoology as a full professor.

Other Research

By focusing on experiments related to the format of the motor commands and the frame of reference of sensory signals found in the SC, I have neglected research conducted in the lab on other topics and the individuals performing those experiments. To partially compensate, the neglected individuals, their current positions, if known, and the papers they contributed to are listed here.

Additional Collaborators

Terry Hickey is now retired after resigning as provost of the University of Central Florida in 2010. Terry and I were co–principal investigators on a National Eye Institute grant to study the effects of short-term monocular visual deprivation on oculomotor function.

Mike Gurski was a postdoc in Terry's lab.

Jon Nelson is currently professor of physical therapy at College of Saint Scholastica in Duluth, Minnesota.

Rosemarie "Rosi" Hartwich-Young (deceased) worked for Alcon Laboratories in Fort Worth, Texas, until retirement. Rosi wrote the anatomy section of our chapter in the book *The Neurobiology of Saccadic Eye Movements*, edited by Wurtz and Goldberg.

Laurel Carney received her bachelor's degree in electrical engineering from MIT and her master's and doctoral degrees, also in electrical engineering, from the University of Wisconsin at Madison. She published several papers related to auditory physiology with Tom Yin while at Madison. While a postdoctoral fellow in my lab, Laurel and Terry Stanford devised a behavioral paradigm that revealed a gradual build-up of the signals specifying the amplitude of a saccade to a single visual goal in human subjects. Laurel is currently the Marylou Ingram Professor of Biomedical Engineering and professor of neuroscience at the University of Rochester.

Ellen Barton is now teaching in the Oklahoma State University system. Ellen entered the neuroscience graduate program at Penn after receiving an MSEE degree from Rensselaer Polytechnic Institute.

Jamie Nichols did a postdoctoral fellowship in Bill Newsome's lab at Stanford and later decided not to pursue a career in neuroscience.

Rimas Kalesnykas is the first author of our review of the role of the SC in the control of saccadic eye movement which appeared in *The Neuroscientist*. Yihong Zhang did his dissertation research in Larry Mays's lab at UAB. He worked in my lab at Penn for a short while before I moved to Houston.

Longteng Chen continued the experiments he began in my lab when he moved to the Department of Otolaryngology at the University of Texas Medical Branch in Galveston. He was examining the effects of stimulation of the frontal eye fields and supplementary eye fields on movements of the eyes and head.

Laurent Goffart is currently a member of the Institut de Neurosciences de la Timone in Marseille, France. In my lab, he was able to delineate the time in which activity in the caudal fastigial nucleus can modify the trajectory of a saccade.

Mark Walton is currently a senior scientist at the University of Washington Seattle. He received his PhD in behavioral neuroscience working with Larry Mays. His time in the lab was shortened by my retirement.

Kathy Pearson became the lab programmer in 1980, and, except for three or four years when she was employed elsewhere, she was an integral part of the laboratory until I retired in 2004. For part of the time when the lab was at Penn, Kathy lived in Virginia and worked remotely. When I accepted the position at the Baylor College of Medicine, Kathy stayed in Virginia but moved, virtually, from Philadelphia to Houston.

Papers by the Additional Collaborators

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Committees, Editorial Boards, Review Articles

I felt an obligation to contribute to the rapidly growing community of neuroscientists and the organizations that supported and published my research, including the following:

- Member, Bio-Psychology Study Section, NIH
- Chair, Bio-Psychology Study Section, NIH
- Member, Program Committee, Society for Neuroscience

- Member, National Advisory Eye Council, National Eye Institute
- Member, National Task Force on the NIH Strategic Plan
- Ad-Hoc Member, Board of Scientific Counselors, National Eye Institute
- Motor Commission, International Union of Physiological Sciences
- Board of Trustees for the Society for the Neural Control of Movement
- Board of Scientific Advisors, Regional Primate Research Center, University of Washington
- Editorial Board: *Behavioural Brain Research, Reviews of Oculomotor Research, Journal of Neuroscience, Vision Research, Visual Neuroscience, Behavioral Neuroscience, Journal of Vision, Journal of Neurophysiology*

In addition, Ron Harris-Warrick and I were occasional section editors of the motor control issue of *Current Opinions in Neurobiology*. Several review articles, not cited in previous sections of this document, are listed in the Selected Bibliography.

Retirement (December 31, 2004–present)

After I announced my retirement, Jennifer Groh and Neeraj Gandhi organized my Roast at a combined meeting of the Vision and Oculomotor social groups at the 2004 meeting of the Society for Neuroscience in San Diego. Jennifer chaired the session and did the initial searing before introducing the main Roasters: Kathleen Cullen, Bill Newsome, and Ed Keller. I felt well done when I gave a short, humorous (hopefully), and intellectually light response. At the end, there was a long standing ovation. I was most appreciative.

Xintian Hu's experiments were still in progress when I retired. The National Eye Institute approved an arrangement in which John Maunsell became PI on my active grant (funding had been approved through July 31, 2007) and supervised Xintian's research until he finished collecting data.

Xintian had a position awaiting him at the Kunming Institute of Zoology in China. The Institute purchased the equipment in my lab and would have it shipped to China after Xintian finished his current project. I spent a month in China in 2006 and five weeks in 2007 working with Xintian on the analysis of data he had collected after I retired and preparing the manuscript (Hu et al. 2007).

I was invited to give the keynote address at a Gordon Research Conference (Oculomotor System Biology) in Maine in 2005. Betty went to the meeting so she could visit with participants who had worked in my lab. The last scientific meeting I attended was the 2007 Oculomotor Gordon Conference. Xintian and I had a poster displaying the results of the experiments concerning the reliability of motor-command signals.

Florida was battered by four major hurricanes within a six-week period during the 2004 hurricane season. Hurricane Ivan made a direct

hit on Pensacola four months before I retired in December 2004. My boat (*En Passant*) survived with no damage. All the marinas in the area suffered serious damage and the cost of slip rentals increased significantly after the marinas were rebuilt. Insurance for boats the size of mine was difficult to obtain in Florida and became almost prohibitively expensive. The cost–enjoyment ratio was not working for me. I sold *En Passant* and nature photography became my primary retirement hobby.

Nature photography, especially bird photography, combines birdwatching, being outdoors, photography, travel, messing about with computers, and learning new skills and concepts—all things I enjoy. Much of my time in retirement has been devoted to this activity. My goal has been to capture, in an unobtrusive manner, the beauty and uniqueness of birds, and some of the characteristic behaviors displayed in their natural habitat. I have self-published several photo books to preserve images that I think were successful in achieving this goal in a format that will be durable and accessible to family and friends when I am no longer around.

Since the Gordon Conference in 2007, almost all my in-person contact with neuroscientists has been related to sailing or photography. I helped Ken Britten and Sandra Aamodt sail their new (for them) boat from the Straits of San Juan de Fuca to San Francisco in 2006. Ken, Sandra, and Paul Gamlin came to Pensacola, and we spent a few days sailing in the nearby bays and sounds in 2007. In 2010, I spent a few days photographing the California wildflowers with Bill Newsome and his son David. In 2011, I met Bill Newsome and Brie Linkenhoker in New Mexico, and we photographed the migrating sandhill cranes and snow geese at the Bosque del Apache National Wildlife Preserve. In 2018, Bill Newsome and I went on a South Georgia–Falklands Expedition led by four well-known nature photographers.

In Pensacola, Betty continued her gardening activities, enjoyed the monthly meetings of a literary study group, and spent a lot of time doing genealogical research. She spent two weeks in Kunming in 2006 while Xintian and I were analyzing the data collected in Houston. In 2007, Betty, Sadie (one of our granddaughters), and I met Xintian in Beijing. Xintian was our guide to many of his favorite places in the area for a week. Then Betty and Sadie returned to the United States. Xintian and I went to Kunming. I stayed for four weeks while we finished the data analysis and preparation of the manuscript that we submitted for publication.

We sold our house in Pensacola in 2015 and bought a condo in Colorado to be near our sons and grandkids. Initially, we spent half our time in Colorado and half in Florida, but we moved to Colorado full time in 2017.

During the COVID-19 lockdown, I have been occupied by putting together photo books for family and friends, compiling a book about Betty after her sudden and unexpected death in 2019, and preparing this manuscript.

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watching our two youngest grandchildren develop is something we missed with the older ones because of geographical distance.

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