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Daniel Johnston

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*Dan Johnston*



# Daniel Johnston

## **BORN:**

Passaic, New Jersey  
December 9, 1947

## **EDUCATION:**

University of Virginia, Charlottesville, BS, Electrical Engineering with Distinction (1970)  
Duke University, Durham, NC, PhD, Biomedical Engineering and Physiology (1974)

## **APPOINTMENTS:**

Postdoctoral Fellow and Instructor, Dept. of Neurology, University of Minnesota, Minneapolis (1973–1975)  
Assistant Professor, Depts. of Neurology and Biomedical Engineering, University of Minnesota (1975–1977)  
Assistant, Associate, and Full Professor, Depts. of Neurology, Neuroscience, and Molecular Physiology and Biophysics, Baylor College of Medicine, Houston, TX (1977–2004)  
Director of the Graduate Program, Division of Neuroscience, Baylor (1988–2004)  
Professor of Neuroscience, University of Texas at Austin (2004–2022)  
Director, Institute for Neuroscience, University of Texas at Austin (2005–2015)  
Founder and Director, Center for Learning and Memory, University of Texas at Austin (2004–2020)  
Chair, Department of Neuroscience, University of Texas at Austin (2011–2015)  
Emeritus Professor of Neuroscience, University of Texas at Austin (2022–present)

## **HONORS AND AWARDS (SELECTED):**

Grass Foundation Fellowship in Neurobiology, Marine Biology Laboratory, Woods Hole, MA (1976)  
Michael E. DeBakey, MD, Excellence in Research Award, Baylor College of Medicine (1997)  
Marc Dresden Excellence in Graduate Education Award, Baylor College of Medicine (1999)  
Barbara and Corbin J. Robertson, Jr., Presidential Award for Excellence in Education, Baylor (2001)  
Dart Foundation Scholar in Learning and Memory, Marine Biology Laboratory (2004–2006)  
Endowed Chair, Karl Folkers Chair in Interdisciplinary Biomedical Research, University of Texas at Austin (2004–2022)  
Gill Center Distinguished Neuroscience Investigator, The Gill Foundation (2009)  
Elected Fellow, American Association for the Advancement of Science (2016)

*Daniel Johnston's work has focused on the use of quantitative, biophysical methods to study cortical neurons and synapses under normal and disease conditions. He made landmark discoveries on the mechanisms of intrinsic burst generation in hippocampal CA3 pyramidal neurons and on the conductance changes associated with long-term synaptic potentiation in hippocampus. Using both experimental and theoretical analyses, he laid the groundwork for the ability to voltage- and space-clamp synapses on neurons with complex dendritic trees.*

*His group was the first to study the properties and distribution of single voltage-gated ion channels in cortical neuron dendrites. He and his team discovered that dendritic ion channels are expressed nonuniformly in dendrites, are activated by synaptic inputs, and undergo activity-dependent changes in their properties and expression patterns in parallel with synaptic plasticity, so-called plasticity of dendritic excitability. Many of the mechanisms for this plasticity of dendritic ion channels were also identified by the Johnston group. Moreover, they demonstrated how these dendritic channels contribute to the information processing and storage of the nervous system. Throughout his career, Johnston applied some of his basic research findings to a better understanding of certain neurological disorders, in particular epilepsy. His landmark findings on the synaptic nature of the electrical discharge in focal epilepsy and on the changes in dendritic ion channels or "channelopathies" that contribute to epileptogenesis have had major impacts on the field. His broad expertise in cellular neurophysiology and biophysics is embedded in the highly regarded textbook with Sam Wu entitled, Foundations of Cellular Neurophysiology.*

# Daniel Johnston

## Prologue

As I try to recall my life from early years to the present, I'd like to use an analogy drawn from all the time I've spent in boats and canoes on moving water to perhaps explain how I ended up being a successful scientist. Think about watching the way things on the surface of water drift from place to place. Sometimes it seems like this drift is purely random, but of course it is not. It is influenced by the tides, winds, bottom structures, and nearby land. In some ways, my journey to becoming a scientist is analogous to this ocean drift. There were many people and events throughout my life that helped determine my ultimate career. I could have been trapped behind a rock or in an eddy, but fortunately I was not. In the sections to follow, I will highlight some of the influencers (people and places) that contributed to my "drift" toward science.

## Early Years

I was born on December 9, 1947, in Passaic, New Jersey to middle-class parents. My father, Vivian Daniel Johnston Jr., was a quality control chemist for Givaudan Corp in Nutley, New Jersey (which was later purchased by Hoffman-La Roche). My mother, Elizabeth Booth Johnston was a secretary who never went to college. I have one sister, Laura, who is two years older than I am. We were very close growing up, but drifted apart over the years. The name given to me at birth was V. Daniel Johnston, III. The V. was for Vivian, but since my father didn't want to name me Vivian, but did want me to be the "Third," he just gave me the initial V. I dropped the V from my name as soon as I could and just used Daniel as my first name with no middle initial.

My parents met in New Jersey and married young. My mother was the youngest of four children born to immigrants from Holland. She was an amazing mother who instilled in me a deep appreciation for the importance of family. My mother's father died when I was very young, but my grandmother, Alida, lived a long life (102 years old). She was a wonderful person whom I saw often throughout my life.

My father was born in Roanoke, Virginia, to a middle-class family. He had one older brother, Fowler. His father was his namesake, Vivian Daniel Johnston, Sr., who passed before I was born. His mother, Laura, was called Mother J, and I visited with her many times when I was young during our frequent trips to Roanoke for Thanksgiving. My father went to

the University of Virginia for college and majored in organic chemistry. As a youth, he was most interested in electronics, so he thought he would major in something related to this. When my father asked his college graduate older brother for advice, Fowler told my father that there was no future in electronics! The future, he said, was in chemistry, not electronics. I suppose the latter piece of advice is still true, but certainly not the former. I still chuckle when I think about him telling me this story. Although my father didn't major in anything related to electronics in college, it was a lifelong hobby for him. He became a ham radio operator and devoted an entire room in our house to ham radio. He also seemed to be able to fix anything electronic in our house. I'm sure his love of electronics ultimately influenced my decision to major in electrical engineering in college.

We lived in Passaic, New Jersey, until I was about five years old, and then we moved to a small town in New Jersey called Little Falls. It is nestled between the better known towns of Montclair and Paterson. The major industry in town was the Little Falls Laundry, which was situated right next to the Passaic River and a "little" falls for which the town got its name.

We had lots of pets as my father really liked animals. Our main pet was a dog named "Boots." Boots was a mutt weighing about 40 lbs. She was brown with white paws (white boots!) and a large white spot on her head. She was a great dog, and I was very devoted to her. She was more my dog than anyone else's. She slept at the foot of my bed until I went to sleep at night and then left my room. She also stayed with me whenever I was sick. She was my best friend, and my love of dogs has continued ever since.

We also had various and sundry other pets, including rabbits, cats, and monkeys. The rabbits were mostly for my sister, the cats for my mom, and the monkeys for my dad. The monkeys were nothing to love or hate but were simply interesting and a learning experience. They were extremely smart, but also unbelievably messy and dirty. We had two, one at a time, and they were each kept in a large cage in the basement. They threw their food and excrement all over the room. The room smelled, was hard to keep clean, and ultimately attracted bugs. I don't think we ever realized just how wild and undomesticated they were. Ultimately, Dad had to get rid of them because one of them bit me rather severely on the thumb and hand.

## Early Years: Sports

I have very fond memories of my childhood. My recollection is that I was a very quiet and shy child (and still am). I went to the cleverly named "School No. 1" in Little Falls for elementary school and then to Passaic Valley High School. There was no middle school in the town, just elementary (K-8) school and then high school. My childhood was rather uneventful, I played the trombone in the elementary school band, I got into some minor trouble during my school years (some playground fights and other mischief), and

I did have one serious girlfriend, Donna, but in general I was not particularly interested in girls. I did well in school but was not exceptional. I remember my sixth-grade teacher, who got me interested in math and algebra, but mostly, I was interested in sports, primarily baseball and basketball. All of my closest friends were met through playing sports, which goes to show how important athletics were to me growing up. Actually, sports have been an important part of my entire life. In addition to baseball and basketball, I have played tennis, racquetball, squash, and many other sports. I also took up running later in life and ran in a number of marathons.

My first memories of sports revolve around baseball. I started playing organized baseball at a very early age (perhaps six?), and I think our team was called the Little Falls Laundry because of the sponsorship by the laundry. It was the farm league at that time; I wouldn't enter Little League until around age 10. My parents were actively involved in my teams. I remember dad being the coach of most of my teams and mom being an avid rooter. Over time, I became a pretty good baseball player; eventually alternating between playing first base and pitching.

Although I remember playing basketball in the mornings and at recess in elementary school, I didn't become serious about the game until high school. I went out for basketball in my freshman year and made the team. I had a wonderful coach whom I looked up to, Mr. Dwyer. He helped spark my love of the game. I remember playing pretty badly the first few games of the year, but Mr. Dwyer took a special liking to me and really worked with me on skills. I was tall and skinny and probably pretty uncoordinated. I remember him drilling me in shooting layups, turnaround jump shots, and rebounding. There was a rebounding drill that still sticks in my mind. A lid was put on the basket so that balls could not go through. I remember getting rebounds, putting the ball back up again, and having the ball bounce off this lid to be rebounded again over and over until my legs ached. Mr. Dwyer helped bring out in me a self-discipline and self-determination that has stayed with me ever since.

Basketball in high school was a wonderful experience for me. After Mr. Dwyer, I played for the varsity coach, Mr. Suglia. Mr. Suglia was a good coach who also seemed to have a special liking for me. I had high aspirations for a future in sports. I wanted to get a basketball scholarship to college, my father even promised me a car if I did. Passaic Valley High School was a large school, but we played in a small league because we never played against very good teams. I did well in high school but looking back I don't think we had the competition of other big schools, and I probably wasn't as good as I thought I was.

My experience with football deserves a special section because it had (or more accurately the coach had) a big impact on my life. I went out for football because it was the thing to do. It was totally an ego thing. To be a "real" boy you had to play football. I thought I would be considered a sissy by the

girls if I didn't play football. The truth was though that I hated football. There wasn't anything about it that I liked. I hated being yelled at and told what to do. I didn't like the work involved in running with pads, pushing the sleds, and hitting people. I played end because of my size and I remember catching a few passes for touchdowns. I guess I liked this, but I can't remember anything else that I liked. The head coach was a man named Mr. Gerty. He was an intimidating bully. He was tall, about 6'4", and weighed 250–300 pounds. He liked to scare everyone into playing football. I ultimately quit football after my freshman year, and Mr. Gerty never let me forget it and always called me a coward for doing so. This did have an impact on me for many years. It affected my self-confidence, but at the same time, it was a self-motivating force that pushed me to be the best I could at anything I tried. It also helped me to be more understanding of the feelings of others.

### High School (1961–1965)

High school was fairly easy for me. My favorite subjects in high school were physics and math. I took advanced physics from Mr. Gerty, the football coach. He was actually a pretty good teacher, and the two years I took physics made me think I wanted to study theoretical physics in college. I did hang around some unsavory types of people in high school, but fortunately didn't get too involved with them. Although my time in high school was dominated by sports, I did have some girlfriends, but I was not obsessed with girls. During high school I hung around with Doug Frey quite a bit. He went on to marry my sister and became my brother-in-law.

I worked for my Uncle Jim in the summer as an electrician's helper during high school and into my first few years of college. I learned a great deal from working with my Uncle Jim, and it has helped me throughout my life in the various houses we've owned. I've often said that learning to be an electrician was probably the most valuable skill I ever learned. I enjoyed the work so much that I even half considered becoming a full-time electrician and not going to college. Uncle Jim was a wonderful, no-nonsense man, who died way too early from a heart attack.

One thing worth mentioning about this time is that my father had two weeks of vacation every summer in July. We spent these weeks in many places within driving distance from New Jersey, including Maine and Cape Cod. Thinking back, I don't know how we did this, because the car we had for such trips was a VW bug. Somehow, we squeezed four people, a dog, a small outboard motor, clothes, food, and everything we needed to camp for two weeks. Sometimes we even put a sailfish sailboat on the roof! I have fond memories of many of these vacations, but the ones that stand out, and that perhaps influenced some of my future decisions, were the summers we spent at Nickerson State Park on Cape Cod. Our family continues to spend summers in Cape Cod (Woods Hole), and we now own a house there.

## College (1965–1970)

The high school I attended was a fairly large regional school that was not strong academically. Although I don't know the exact number, I can't imagine that more than 10–20 percent out of a graduating class of approximately 450 went to college. I had my heart set on going to Princeton to major in physics. Our family doctor went to Princeton, and he tried to get me accepted. I applied to their theoretical physics program, which in retrospect was a huge mistake. Only a handful of exceptional students were accepted into this program; although I had good SAT scores, particularly in math, I was not one of them. I might have gotten accepted if I had not requested this particular program. I did visit there once and attended a basketball game. I even met with the great Bill Bradley after the game. He was a junior or senior at the time. It was a thrill of a lifetime.

I visited a number of other colleges, including the University of Virginia (UVa). UVa has a beautiful campus, and perhaps because my father went there, I applied and was accepted. Although I didn't get a basketball scholarship to UVa, I was considered a basketball recruit. I was put in a dorm with some of the players as well as a roommate who wanted to play. He was much taller than I was and a pretty good player, but not everyone in the dorm was a basketball player. There were many others in the dorm with whom I became friends.

I remember many things about college, mostly good. Freshman year was spent as a physics major. However, I discovered that I didn't really like the kind of physics (or math) I was learning. The concepts were too abstract and theoretical, and I was interested in more practical applications. During my freshman year, I decided I didn't want to be a physics major. I took an introductory course in psychology, thinking I might want to be psych major, but I didn't like that either. Toward the end of my freshman year, I took an aptitude test to see what major might fit my interests. This turned out to be incredibly helpful. Interestingly, I had the highest aptitude for being a pilot. Of course, I didn't have the vision to be a pilot, so I turned to the second-highest-ranking aptitude, which was as an engineer. This made a lot of sense to me because applied physics and math seemed much more to my liking. I applied for the engineering school and was accepted. In retrospect, I was lucky because my grades freshman year were not that good. Because I missed all the required engineering courses during freshman year, I assumed it would take me five years to finish. I ultimately chose electrical engineering, maybe because my father was a ham radio operator, or because of the summers I had spent in high school (and later in college) working as an electrician's helper. Whatever the reason, I really enjoyed electrical engineering.

During freshman year, I rushed different fraternities. I felt most comfortable with ATO, and so I joined. It felt good belonging to something,



and I became very close to my rush class and later with some of the upper-division guys. I ended up quitting the freshman basketball team. Most everyone had a scholarship, and I felt intimidated. After I quit, I was told that I was one of the top picks to stay on the team. I should have had more self-confidence, but I still attributed this to my experience with football in high school.

My sophomore year had its ups and downs. On the upside, I enjoyed engineering and being in ATO. There were lots of road trips to girls schools (UVa at the time was all boys), and party weekends where I drank too much beer while wishing I had dates. The down part was living in an apartment. At UVa, the dorms were mostly for freshman and after that everyone was expected to live in an apartment. I ended up rooming with Doug Frey's ex-roommate, Stoney. He came to UVa for engineering graduate school after graduating from the Citadel with Doug. We did not get along—maybe because of the differences in age or his military training, or maybe because I was too immature. In any event, it was an awful year from that standpoint. As a result, I did spend a lot of time at the fraternity house learning to play bridge and watching TV with the guys. I did very well in all my engineering courses and got mostly As. One of the important things I learned in college and being in a fraternity was how to separate work from play. My motto was to work hard and play hard, a lesson that has stayed with me throughout my life.

Junior year I roomed near the house with one of my fraternity brothers, Sam Young. Sam was a philosophy honors major and quite the talker. We got along well, so living that year was much better than the previous year. Other than my schoolwork, which was going fine, most of the rest of my college life revolved around ATO and my friends. Tom Heffron was my best friend, but he was having trouble in school. He ended up dropping out of school at some point during junior or senior year and joined the Navy. Life revolved around road trips, big weekends, and hanging around the house. I had very few serious girlfriends. I remember one woman I was smitten with from Hollins College with an unforgettable last name, Hellabush. During the summer between my junior and senior years, I worked for an aerospace company on Long Island. As a budding engineer, my job was to calculate the probability of failure for some of the electronic parts on several different space capsules. While it seemed important, I couldn't see how it would be very accurate, but I did as I was told. I think this job, however, soured me from ever working in industry.

Senior year I figured out that I didn't really need five years to graduate. I squeezed in all the courses I needed to graduate on time, or nearly on time. I was trying to decide on graduate school or even medical school. I considered staying at UVa and getting a doctorate in electrical engineering focusing on control theory, but ultimately I decided to pursue biomedical engineering at Duke. I did my senior thesis on eye movement recordings,

and the idea of designing medical equipment was particularly appealing to me. Duke seemed to have an attractive biomedical engineering program as well as a good stipend, but that decision meant I would have to take organic chemistry. I applied and was accepted at Duke. I took organic chemistry in summer school and hated it. Way too much memorization. I had a pretty serious girlfriend my senior year, Robin, but I was incompetent with girls. Girls and relationships just scared me.

### Graduate School (1969–1973)

I left for Durham and graduate school in the fall of 1969. Although I had all the credits I needed to graduate after finishing summer school, I didn't officially graduate until the next year, 1970. I began graduate school working in Fritz Thurston's lab. He was an expert on ultrasound transducers and became world famous for designing the transducers used for imaging babies in the womb. He was a very nice and impressive man, but I was not that interested in the topic. I took a course in physiology and got really enamored by the lectures on neurophysiology, and, in particular, those on the electrical activity of neurons. It seemed like the perfect fit for my background in electrical engineering, and so this is what I decided I wanted to do. I talked to Howard Wachtel, a neurophysiologist, about joining his lab and did so in my second year. Howard had a joint appointment in the Biomedical Engineering and Physiology Departments. Bill Wilson and Ted Carnevale were also in Howard's lab and a few years ahead of me. There were also a few other people in Howard's lab, and in general it was a fun lab to be in. I got friendly with John Moore (see volume 7) and some other faculty members in the physiology department, which was where Howard's lab was located. The Physiology Department was also one of the top departments in the country at the time with some outstanding people. John Moore, of course, was one of the early designers of the voltage clamp for squid axon. Another member of the department whom I interacted with and admired greatly was Toshio Narahashi. He discovered tetrodotoxin, a blocker of sodium channels.

Most everyone in Howard's lab worked on *Aplysia*, which was Howard's main focus, being one of Eric Kandel's first graduate students. At some point, I met with Myron Wolbarsht in ophthalmology, who worked on the eye of the *Limulus*. He had a woman working for him who had a technique for removing the lens and exposing the individual photoreceptors or ommatidia. She showed me this technique and after talking to Howard, I decided to work on the *Limulus* eye. I don't remember how exactly I came up with the project, whether it was all or mostly my idea or whether the ideas were gleaned from Howard's lectures and talking with Wolbarsht and his student. In any event, I decided to try and reproduce the famous Hartline experiments first describing the spread of lateral inhibition, and for which he won a Nobel Prize. Instead of using groups of photoreceptors with the lens intact as they

did, I wanted to measure the spatial spread of lateral inhibition by recording from individual pairs of ommatidia. I designed extracellular electrodes in which I coated the outside with silver paint, put a fiber optic in the barrel of the pipette and filled it with saline so I could record photo-responses. I thought the whole thing was rather clever. I recorded simultaneously from two ommatidia at different distances from each other to map the strength of lateral inhibition. Each ommatidia was stimulated with light through the electrodes with presumably no light scatter between electrodes. It all seems pretty crude today, but at the time was novel. I did find some differences in the spatial spread of lateral inhibition from the original Hartline experiments. I also built a model to suggest that the strength of lateral inhibition was due to the distance of the inhibitory synapses from the photoreceptor spiking trigger zone. Although I didn't have any direct proof of this, it was an interesting idea that made sense from a theoretical standpoint. Toward the end of my studies, I had a scare in which I feared that the light bulbs illuminating the light pipes might have reduced the total light to each bulb (the load) when they were on at the same time compared with when they were on individually. I feared that this could have contributed to the spatial spread of inhibition I measured. I did some control experiments, however, in which I separated the voltage source to each light bulb and didn't find any evidence of such an artifact. This scare was a lesson for me that I never forgot about the importance of controls.

At the end of my thesis work, I talked to Howard about one or more papers that we could publish based on my data. Howard outlined three papers, two of which I would be first author on and one for which he would be first author, which made me really angry. I didn't see any reason why he should be first author on any of them, just senior author. When I went to John Moore about this he was very supportive of me, partly because I was right, but also because he didn't particularly like Howard. In retrospect, this situation probably got blown out of proportion, and in the end, I only published one paper in *Journal of General Physiology*. These events led to a lifetime friendship with John Moore and a deep appreciation for the sensitivities surrounding authorship.

I typed my dissertation on an IBM Selectric typewriter using lots of correct type. Howard was very critical of the content, in a good way, and I think I ended up typing some 10-plus versions of my thesis before going final. I also had to make 10–15 copies of the thesis and my future wife Jean helped me with this. I don't remember any particular problems with my thesis defense, at least nothing like my oral qualifying exam. Although I passed my orals, I don't think I did that well. One of the questions was about vacuum tubes! I was not prepared for that one.

For the most part, graduate school was a blast for me, one of the happiest times of my life up to that point. I loved the courses, the research, and the faculty. While in graduate school I made a strong friendship with Mike

Ramsey. He was a medical doctor doing his doctoral work in biomedical engineering; his interests were in cardiology and heart monitoring. He already had a small company that he started in Tampa, which is now a much bigger company and for which he's probably made a lot of money. Mike and I really hit it off. We both had motorcycles and although he was married (Lynn), it didn't seem to cramp his style. We joined the Duke film society and made a silent movie, *Any Old Kind of Day*, based on the music of Harry Chapin. The film society (called the Freewater Film Society) had equipment and film that we could use. They paid for this from the proceeds of their Friday night film series on campus. We started another film, which involved partial nudity, but never finished it. We, mostly Mike, had fun interviewing candidates for the topless scene.

Other than my first year, I lived in a house share with four other guys, three of whom were graduate students in biomedical engineering. One of the guys was a business major whom I had lived with for part of my first year. We all got along pretty well with no major problems until the end of our time in the house when the business guy, who kept track of our shared finances, decided to try and charge us for the use of his TV the past three years. We would have none of it, but I did learn a lesson about finances from this experience.

I didn't have many girlfriends during graduate school and met Jean as a blind date my last year. Wilkie (Bill) Wilson set it up. He knew her because she worked as a nurse for the epilepsy center at the Veterans Administration (VA) that he was involved with. She liked motorcycles! I remember our first date in which she showed up in a short dress of UVa colors. I assume she knew I went to UVa, but I thought it was pretty coincidental. We dated for the rest of my time in Durham.

While I was in graduate school, the Vietnam War was raging, and the army draft was ongoing. I got a low draft number (43), which meant I would be drafted in the army. Rather than go as an enlisted man, I joined ROTC. My first Army experience was boot camp at Fort Knox, Kentucky. It was not pleasant, but I went along as best I could. I did lose weight and get in shape, which were good things. After boot camp, I went to drills and marches on weekends during the year around once a month. The next summer, I went to what was essentially another boot camp at Fort Bragg, North Carolina. I got set up in the barracks and started drills, but early on there were a lot of medical tests and physicals. They found that I had an anal fissure, which sometimes caused bleeding during bowel movements. This condition allowed me to choose whether or not to accept a medical discharge or volunteer to stay in the Army. Needless to say, I chose to take the medical discharge, I didn't like the Army and being told what to do. I guess I was a peacenik at the time, against the war, and essentially a liberal-leaning person. Although I don't regret getting out of the Army, I also feel somewhat guilty about it as I know many people who went to the war and suffered because of it.

Before my defense, I had secured a postdoc in Minneapolis, Minnesota, working with Giovanni Ayala, a neurologist working on epilepsy. After defending my thesis, Jean and I drove all of my things in a U-Hall truck to Minneapolis to start my postdoc. She helped me get set up in a small apartment and then went back to Durham. She definitely wanted to get married, but I was not ready.

### Postdoc (1973–1977)

I stayed in Minneapolis for a total of four years. I was a postdoc for about two of those and then I got a soft-money instructor position in the Neurology and Biomedical Engineering Departments at the University of Minnesota. Working as a postdoc and later as an instructor in Ayala's lab was fine. We got along well, and he had a few other student's and postdocs with whom I also got along fine. Ayala was a neurologist studying epilepsy. He had published a major paper on epilepsy some years earlier using intracellular recordings from a penicillin focus in cats. He characterized what was then called the paroxysmal depolarizing shift (PDS). I had an hypothesis that the PDS was similar in mechanisms to bursting neurons in *Aplysia*. I went to Ayala's lab to explore this in *Aplysia* as well as to learn intracellular recordings from anesthetized cats. Bill Wilson had designed a so-called single-electrode voltage clamp (SEC), which I wanted to build and use on cat cortical neurons during the PDS. While I did build an SEC, I never got to use it in cats. Although Ayala was supposed to be the expert on *in vivo* cat work, it seemed that we had a hard time keeping the cats alive. He was a great guy, but not much of an experimentalist. As a result, most of my work in Ayala's lab was with *Aplysia*. In fact, my first paper from Ayala's lab was in *Science*, in which we tested the actions of Dilantin on *Aplysia* bursting neurons. I published a total of nine papers and three book chapters during my four years with Ayala.

At some point during my time in Minneapolis, I visited Eric Kandel's lab in New York. Ayala knew Kandel fairly well, and at the time, Kandel was on the board of the Klingenstein Foundation, which was originally set up to fund epilepsy research. Arnold Kriegstein, a postdoc in Kandel's lab, was involved in a project trying to raise *Aplysia* in the lab. I think it was partly set up at the Marine Biological Laboratory (MBL) in Woods Hole, Massachusetts, but somehow it was also ongoing in Kandel's lab at Columbia. To get money from the foundation, Kandel needed to have some tie-in with epilepsy. So, after my first paper was published on the effects of Dilantin in *Aplysia*, the idea was born that I would go to Columbia and test the effects of Dilantin on developing *Aplysia*. Anyway, I went there for several weeks, but the project never went too far. There were some very nice people in the lab, including John Koester, Tom Carew, and Vince Castellucci, to name a few. It was an intense environment where I never felt quite comfortable. Eric and I,

however, remained cordial over the years whenever we would occasionally meet at meetings.

A pivotal experience I had while working with Ayala came when he encouraged me to apply for the Grass Summer Fellowship Program at the MBL in Woods Hole. I did apply, was accepted, and credit this with completely changing my career. I had proposed to use the SEC I had built to clamp the squid giant synapse to test the effects of anticonvulsant drugs (mostly Dilantin). When I arrived in Woods Hole and set up my rig in the Grass lab, I had no idea how to even dissect the squid synapse. I went to Rodolfo Llinás's lab to see if I could watch his dissection. The first time I went, I was told by his student, Kari Walton, to come back the next day after she discussed my request with Llinas. I came back the next day, and she told me that "Professor Llinas told me to show you nothing." This was quite a shock to me as the MBL seemed a very open and collegial environment. What I didn't know at the time was that there was an intense competition (rivalry) going on between Llinas's lab and another lab, consisting of a collaboration among Milton Charlton, George Augustine, Steve Smith, and Bob Zucker, to be the first to voltage clamp the squid presynaptic terminal and measure calcium currents. I ended up meeting Milton, and he showed me everything and was extremely helpful and supportive. This was an incredible summer. I met many amazing people, both other Grass Fellows as well as all the scientists who gave informal talks to the Grass Fellows. It was also an eye-opening experience, and although I didn't make any great breakthroughs on the experimental side, the networking with other people was invaluable. It literally changed my life and career. I fell in love with Woods Hole and was determined to return at some point. Although I did return to Woods Hole, it would not be for another 13 years in the summer of 1989.

The last year of my time in Minneapolis was very stressful, but some positives came from it. I had several trainees. One was a medical doctor, Gerald Slater, who got me interested in a different anticonvulsant, Valproate, or Valproic acid. We published one paper and a review on the topic. I also worked with another faculty member, J. Sheppard, on reaggregate cultures along with a student, Carl Stafstrom. Carl was a great guy who went on to have a very successful career as a medical doctor/doctor in the field of epilepsy.

During my time with Ayala, he was recruited by Stan Appel, who had recently moved from Duke to Baylor College of Medicine (BCM), to establish a new department of neurology. Ayala asked me to come with him, and so Appel offered me a position as an assistant professor of neurology, which I accepted, starting at BCM in 1977.

Jean and I ended up getting married in December 1973 only months after I had moved to Minneapolis. I had taken her to meet my parents and my sister Laura, and they liked her. We got married in the chapel

at UVa by a minister of Jean's choosing on December 21. Only immediate family members were invited to the wedding and reception. We held a small reception and spent our wedding night at the Bohr's Head Inn near Charlottesville. I refused to wear anything formal, just a camel hair sport's jacket and brown turtleneck. We also played the Moody Blues for wedding music. I was quite the nonconformist.

Jean moved to Minneapolis to live with me shortly after getting married. We rented another U-Haul truck, this time filled with all of Jean's things, and drove it from Durham to Minneapolis. It was in the middle of winter, so it was not a pleasant experience. We had rented a house on the south side of Minneapolis; however, we only stayed there a bit less than a year. We bought a house across from Lake Hiawatha on East 43rd Street and 26th Avenue. It was a small house, but it was all we needed. We met a neighbor's golden retriever named Rufus while living at the rental house. We loved him and decided to get a golden retriever puppy of our own. We found someone with a new litter either in or on the way to Wisconsin and went to visit. The mom had around 10–12 puppies. We played with them and chose the one who kept wanting to play with us and chew my sock. The puppies were so cute! I think it was the first night that we had the puppy that he chewed an extension cord and got shocked in the mouth. He was lifeless, and we didn't think he would live. We drove him to the vet who looked at him and thought he might survive. On the way home Jean was crying and saying that he didn't even have a name. I suggested Coulomb. She asked, "What the hell is a coulomb?" I explained that it was a unit of electrical charge, so she said okay, at least it was appropriate. I slept with Coulomb on the floor of the bathroom during the night hoping that he would live, and he eventually came to. Although he had a serious scar on his tongue and lips, he seemed fine. He was a great dog. We fell in love with Golden Retrievers, and up to now have had five (two females and three males). They are great pets.

There were lots of things I remember about Minneapolis: walking to basketball games in 30-below temperatures and getting ice cream on the way, Leonard Slatkin and rug concerts by the symphony in the summers, cross-country skiing with Coulomb, and of course, our friends Wendy and Muff. They both were great friends whom Jean met at a bridge class. We played bridge with them often, especially in the winter. We also went on a few canoe/camping trips with them. We have mostly lost touch with Wendy, but Muff, now calling herself Meg, has remained close. She got married and moved to Oregon some years after we left Minneapolis. She has come to visit us in Woods Hole and has come to both our girls' weddings in Texas.

While I was a Grass Fellow at the MBL in Woods Hole, Jean stayed in Minneapolis most of the summer, but came to visit a few times. Our dog, Coulomb, however, was shipped several times and stayed in a kennel so I could see him more frequently. He, of course, had a great time and I was glad to see him more than I otherwise would have if he had stayed with

Jean at home for the entire summer. In retrospect, our separation for most of that summer was not a good thing for our marriage, but I was ignorant to this at the time.

Jean had been working with Bob Gumnit, a neurologist, as an epilepsy nurse in his epilepsy center. She had a similar job at Duke working for Tony Escueda in his epilepsy clinic at the VA. There were a number of epilepsy conferences during the year that she had gone to while at Duke, and she attended one, I think, in the fall of 1976. When she came back from the conference, she didn't want anything to do with me, and we separated shortly thereafter. It looked like we were headed for a divorce. However, we ultimately both agreed to have individual counseling. While separated, I decided to do what I had always wanted to do, get a pilot's license! (I flew quite often after getting my license, and even later bought an old Cessna 182, but in 1980, I had a crash with six people on board. Fortunately, no one was injured.) I don't actually remember how long we were separated, but it was at least several months. We later had some joint counseling sessions and decided to get back together. We have now been married for 50 years. In retrospect, I had paid too much attention to my career and not enough to my marriage. My take-home message from this experience is that the stresses of two careers can be significant, but one should not give up on a marriage too easily. The later rewards from being with someone and ultimately having a family together are enormous and far outweigh any difficulties along the way.

I was recruited to BCM in February, and we moved in August. February in Houston seemed like heaven coming from Minnesota, but August was a wake-up call. Clearly, this was a different climate than we had been used to for the past four years in Minnesota.

## First Real Academic Job: Baylor College of Medicine in Houston

I have lots of memories, mostly good, about my first job in Houston. At Baylor, my electrophysiology rig was in Ayala's lab, which was set up in the new Neurosensory Center, a building Peter Kellaway helped establish. Peter was an electroencephalogram (EEG) expert. In fact, he was the first one to bring the EEG technique to the Houston area. He was an impressive man who was head of the Epilepsy Research Center (ERC) at the Methodist Hospital. Peter welcomed me into the ERC, and I was part of the center throughout my time at Baylor. Peter was a doctor, but he knew how to function in the medical world. I think he recognized my ability as a scientist right away and how I was essentially most of what was good in the Ayala lab. Others in the ERC I interacted with were Jim Frost, an EEG expert more on the technology side, and of course, John Hablitz. Hablitz and I hit it off right away, and we started collaborating as soon as my lab was set up. John and I wanted to use the SEC to record from neurons in brain slices.



Bob Thalmann, a neuroscientist in the Cell Biology Department, had done a short sabbatical with Carl Cotman and Gary Lynch, who were early adopters of the brain slice technique. Bob showed John and I how to do brain slices. John had more experience with animal dissections than I did, so he did most of the surgeries while we were experimenting with the technique. I don't remember it taking us very long before we had live healthy slices and were recording from neurons. These were fun and exciting times. Although Ayala was not really that involved in the experiments per se, he was in the lab often enough to kibitz about experiments. He was very supportive and never tried to tell us what to do. Although technically I had an independent (assistant professor) position, Ayala was the head of the lab. He never dictated anything, however, and often had some good ideas. He and Bob Thalmann also did some projects together in the early days.

The switch from *Aplysia* to brain slices was a natural outgrowth of the feedback I had received from one of my first National Institutes of Health (NIH) grant applications that I submitted while in Minneapolis in which one of the reviewers suggested that until *Aplysia* have seizures he/she could not support an application with *Aplysia* being used as a model system to study epilepsy. That review really hit home for me. My first grant at BCM was a project associated with the ERC and was indeed on brain slices. John Hablitz and I published a paper in *Nature* using the SEC on CA3 neurons in slices. I think it was one of the first, if not the first, papers in which neurons in a brain slice had been voltage clamped. That paper was a springboard for me that led to many papers and projects, some epilepsy related and others just basic research. Funding was not really a problem as I had both ERC-related project grants and independent NIH and foundation grants. We had a number of trainees in the lab, mostly postdocs at first until my first graduate student, Bill Hopkins, joined the lab. Frank Lebeda was one of my first postdocs along with Doug Baxter. I also worked and published with Warren Strittmatter and Nick Bryan. Warren was a neurologist interested in protease inhibitors, and Nick was a neuroradiologist interested in contrast agents. It was a productive time for me.

During the course of the voltage clamp study of CA3 neurons that I did with John Hablitz, I became interested in the question of how well one could voltage clamp a neuron with a complex dendritic tree. The seeds for this interest were planted in me thanks to the influence of John Moore while I was a graduate student at Duke. He, of course, was a stickler for the requirement of having an adequate space clamp based on his and others' work on the squid axon. I read many, if not all, of the works of the great Wilfred Rall. Cable theory was right up my alley given my background in electrical engineering. I also used cable theory as a part of my doctoral thesis. Based on Rall's work and a bit of novelty on my part, I built a theoretical model of a CA3 neuron. I presented this work at a Winter Conference on Brain Research (WCBR) meeting at a ski resort in Colorado. It was an

annual meeting I tried to attend each year, not only because it was an interesting meeting but also because I liked to ski. After my presentation at the meeting, a man named Tom Brown came up to me and said he was building similar cable models and seemed quite excited by my presentation. We really hit it off, and we spent much of the rest of the meeting talking science and skiing. We ultimately arranged to meet again both in Houston and at the City of Hope where he had just taken a position and agreed to maybe even collaborate on some projects.

I later published my paper on the cable properties of CA3 neurons in what was then a new journal. In retrospect, that was a big mistake. It should have gone into a more established journal where it would have been more widely read. I thought I had some novel math in this study that I wanted more people to appreciate. In addition to this paper, I began collaborating with Ted Carnevale. I knew Ted from graduate student days at Duke, and we continued to interact in the subsequent years. We put together what I thought then (and still do) was one of my most important and innovative papers on the theory of current and voltage flow to and from the soma and a remote synapse on a dendritic tree. In some ways, it was a bit ahead of its time, but it laid down some fairly simple and straightforward principles, such as the asymmetry in the spread of voltage and current between dendrites and soma, the effect that a voltage clamp applied to the soma has on voltage and current distribution, and the charge transfer between dendrites and soma. These were extremely important ideas and principles, especially because the voltage clamp was being more widely applied to complex neurons.

The cable properties paper and the paper with Carnevale helped lay the ground work for the collaboration I had with Tom Brown. Although I did visit him at the City of Hope several times, all of our active collaborations took place in Houston. Tom was brilliant, with a different but complementary background to mine, and we really meshed scientifically. We were incredibly productive. Tom would come for weeks at a time, and we would do intense daily experiments. Most of our work was directed toward understanding synaptic transmission using the mossy fiber synapse as a model synapse. We focused on this synapse because of its proximity to the cell body where we thought we would have the best chance for an adequate space clamp. This was probably the first voltage clamp study of a mammalian synapse in a brain slice. We also built a model to determine the degree of error because of the lack of a space clamp. I remember while writing one of the papers that Tom came up with the phrase “electrotonically compact” to describe a CA3 neuron and our ability to adequately describe the biophysical properties of mossy fiber synaptic transmission. Tom was very clever with words, and I really liked this description. We both later regretted this phrase, however, because it ended up being used by everyone to justify their use of the voltage clamp to analyze all synapses on hippocampal pyramidal

neurons, although that was never our intent. In fact, our results showed that the mossy fiber synapse was probably the only excitatory synapse on a pyramidal neuron for which a reasonable space clamp was possible. Tom and I published a number of other papers and reviews, but I believe that our voltage clamp studies of the mossy fiber synapse were one of the two major contributions from our collaboration. After Tom moved from City of Hope to Yale, our interactions declined considerably. (As an aside, the Brown and Johnston, 1983, paper was my first and only peer-reviewed paper sent to a major journal in which the reviews came back without a single suggestion for revision! Nothing but over the top compliments. One of the reviewers turned out to be Chuck Stevens.)

In addition to our work on synaptic transmission, we made what was considered by many in the epilepsy field another major contribution. At the time, there was a raging controversy surrounding the PDS in focal epilepsy. This had been recorded intracellularly, extracellularly, and with EEG recordings. Some believed that the PDS was due to intrinsic burst mechanisms in a single pyramidal neuron, and I had favored this idea based on my previous work with *Aplysia* bursting neurons and CA3 neuron intrinsic bursts. Others, however, thought that the PDS was the result of a hyperexcitable network of interconnected neurons. These were competing camps, but the tide was shifting toward the former idea favored by David Prince and his collaborators who described the PDS as a single cell or voltage-dependent burst. Again, using the voltage clamp technique, Tom and I unequivocally showed that the PDS was due instead to a large, network-driven synaptic input. We did this by clamping a neuron to different potentials in a slice made "epileptic" with a convulsant drug and then showing that the frequency of the PDS discharge did not change with membrane potential. Then, most convincingly, we showed that the PDS could be reversed in amplitude when sufficiently depolarized beyond the synaptic reversal potential. We published these findings in *Science*, and the results completely changed the focus of the field from single neurons to network behavior. Because I had initially favored the idea of the PDS being an intrinsic burst, I ended up being completely wrong. I have said throughout my career that nothing makes me happier or more excited by science than to be the one to disprove my own hypothesis! Tom was much more interested in synaptic plasticity so this was more of a side project for him, but I remain very proud of that work.

I ultimately did become more interested in synaptic transmission and plasticity thanks to Tom's influence. I remember one day while doing experiments Tom asking me if I had ever heard of Hebb's postulate. Not having had much psychology training, I had not. He, of course, went on to test Hebb's postulate in one of his more seminal papers using some of the techniques we had developed together. I also remember us being among the first to use internal cesium in our intracellular pipettes and remarking about

what we called “hyperspace” when we tried to hyperpolarize cells. This, of course, turned out to be due to a block of HCN channels, which I ended up studying intensely later in my career. We continued to collaborate more independently on a few projects related to mossy fiber synaptic transmission, but eventually we went our separate ways.

## Personal Life in Houston

I never really wanted to have children. I thought it would ruin my career, but of course Jean did. She became pregnant in 1978. I remember vividly when she told me. We were lying in bed one night watching TV. She snuggled up to me and whispered in my ear, “I have a surprise, I’m pregnant.” At that moment the TV at the foot of our bed simply died. It was an old picture tube TV in which the screen shrinks to a small circle of light until it goes black. I looked at that TV and thought that I was looking at my career. It was over! Getting used to the idea of becoming a father took some time, and this was not an easy pregnancy for Jean. She ended up in the hospital with preeclampsia and delivered by C-section several weeks early in May 1979. I remember seeing my daughter for the first time. She weighed 4 pounds, 5 ounces and fit in the palm of my hand. I had never really seen a newborn before and was amazed by how, even being so small, she had all the correct wrinkles on the knuckles of her fingers. It took a while for me to connect with my new daughter, Lisa Danielle, but by six months, I was completely overcome with the joy of having this new person in my life. For someone not wanting children at all, I was now ready to have a dozen!

Our second child, a daughter named Lauren, was born in 1982. She was quite a handful from the beginning and required much of our time. Thinking back years later, we always regretted not having spent more time with Danielle. Fortunately, however, both daughters have turned out to be wonderful adults with their own children, so maybe we did something right. Our third child, David, was unexpected. When we found out we were pregnant, I was hoping for another girl. I had gotten so attached to Danielle and Lauren that I couldn’t image having a boy. David, however, was delightful and such an easy child to raise. He was born in 1984 and now has two of his own children. We are now blessed with seven grandchildren, with maybe more on the way.

Raising three children was so much fun, but also quite challenging. Jean was a nurse who worked full time until David was two years old. At that point, we decided that we were paying so much in childcare that it almost wasn’t worth it financially for Jean to work. Thankfully, Jean was willing to become a full-time mom, and she was good at it! Although I still spent as much time as I could with all three children, this change did allow me to devote more time to my work. I thoroughly enjoyed all the family time together both in Houston and on vacations. As important as my career had

been to me, I would have traded it for my family in a heartbeat if I had had to. I have so many wonderful memories of swim meets, soccer games, daddy-daughter dances, and of course our summers in Woods Hole beginning in 1989. The one dark spot, and it's a big one, from our time in Woods Hole is David's bike accident and head injury at Nickerson State Park. It is painful to even think about, so I'll instead end this personal-life section on an upbeat note with the fact that David recovered and now has a wonderful family and career of his own.

### New Division of Neuroscience (1989)

I continued working in the Neurology Department at Baylor, rising through the ranks from assistant to associate and then to full professor during the years from 1977 to 1986. These were happy and productive times, but neuroscience at Baylor and throughout the country was growing, and many independent departments of neuroscience were being created. In 1989, Baylor recruited Jim Patrick from the Salk Institute to be head of a new Division of Neuroscience at Baylor. It was an independent academic department in everything but its name. For some complicated political reasons, it had to be called a division rather than a department, but it really made no difference to anyone what it was called. I had been the director of the Graduate Program in Neuroscience for several years, and while it was to remain interdepartmental, the graduate program was now to be based within the new department. Jim offered me the first academic appointment in the division, so I moved my primary appointment (and lab) from the Neurology Department to the new department and to a new building. Although I did receive a bit of startup money for this move, it was still mostly a soft-money position. The joke at Baylor was that tenure meant that you had a guaranteed job, just not a salary. I remained as director of the Graduate Program. I loved working with graduate students and helping to develop a rigorous training environment for them. This remained a joy of mine throughout the rest of my career. As part of Jim's recruitment package, he had many positions to fill, and much of my time was spent helping in these recruitment efforts. We hired many outstanding faculty, including David Sweatt, Peter Saggau, Paul Pfaffinger, Michael Crair, John Dani, Fabrizio Gabbiani, Rob Gereau, Nikos Logothetis, David Sparks, John Maunsell, Read Montague, Mark Perin, Sarah Pallas, and Dan Ts'o. Many of these people have become household names in the field of neuroscience. I learned a great deal in working with Jim to help develop this new department. Jim had very high standards and was uncompromising in hiring only the very best people. He also was honest, open, and interacted well with all the faculty in the department. These were lessons I took with me for later in my career.

I had many outstanding graduate students during this time, one of whom was Nelson Spruston. After graduating from Baylor, Nelson went

to Germany to do a postdoc with Bert Sakmann at the Max Planck in Heidelberg. After being there for a few years, Nelson invited me for a visit to give a talk and to see some of the techniques in the Sakmann lab for recording from dendrites. I was extremely impressed with not only the methods but also the people in the lab who were using them (e.g., Greg Stuart, Michael Hausser, Jackie Schiller, among others). Everyone, including Bert, was extremely open and collegial. I learned as much as I could, and when I returned to Houston, I set up several rigs using the methods from the Sakmann lab. Jeff Magee had already been in the lab for a short time and was struggling to record mossy fiber synaptic responses, but he immediately appreciated the power of these new methods. Also, given our more channel-oriented interests, we decided to begin studying ion channels in dendrites. Some of this interest in ion channels was inspired by the work I had done during several summers at the MBL in Woods Hole with John Lisman and Bill Ross. I will take a brief detour here to reminisce about my MBL/Woods Hole experiences.

## The Marine Biological Laboratory

It would be hard for me to write a scientific autobiography of my career without including some description of my many summers at the MBL. As I mentioned earlier, being a Grass Fellow in 1976 was a career-changing experience for me. I vowed then to somehow try and get back to the MBL for more summer research. Because at the time, there was no way to use rodents for experiments at the MBL and all my work was with brain slices, my hopes for doing research at the MBL were slim. I had met John Lisman during the summer of my Grass Fellowship, and we remained cordial whenever we saw each other at various scientific conferences. In 1988, he told me that the MBL was going to establish a small vivarium above the old Marine Resources Center. He had become interested in the neurophysiology of brain slices and wondered if I would be interested in collaborating with him at the MBL and whether I would teach him brain slice recording techniques. I, of course, jumped at the chance. He was a regular each summer at the MBL so he made all the arrangements for the lab, whereas David Jaffe, a graduate student of mine at the time, and I packed up our equipment and shipped it to Woods Hole for the summer of 1989. We actually shared a lab that summer with Bill Ross and Ann Stuart who were doing a calcium imaging project together on barnacle photoreceptors. Everything was going fine, but at some point during the summer, John, Bill, and I decided to try to image calcium in the dendrites of CA1 pyramidal neurons from brain slices. This turned out to be incredibly successful and led to several summers of collaborations, as well as several landmark papers on both calcium and sodium signaling in dendrites. Bill was the imaging expert, John was the idea man, and I guess I was more of the experimentalist. Anyway, we all meshed extremely well.

I continued to spend each summer at the MBL in either collaborative projects with John, Bill, and others or with the small group of people I brought with me from Texas. I cannot imagine what my career would have been if not for the summer research at the MBL. Not only were the collaborations fruitful, but just interacting with all the amazing scientists who came to the MBL each summer either to do research or to teach in one of the courses was quite inspiring for me. I am always amazed at how many neuroscientists have had some MBL experience. It is truly a special place.

On a more personal level, all three of my children essentially grew up in Woods Hole, spending each summer there well into college. We drove to Woods Hole from Texas each year in a minivan packed with dogs, rabbits, birds, food, and clothes. I guess the summer trips to Cape Cod in a VW bug when I was a kid prepared me for this! All of my children took classes at The Children's School of Science when they were young, had summer jobs in and around Woods Hole when they got a bit older, and looked forward to spending each summer in Woods Hole. They still have many friends from Woods Hole with whom they have remained close throughout the years. Our oldest, Danielle, learned to scuba dive near Woods Hole, and I went diving with her many times at different locations on the Cape. Actually, all of my children learned to dive, and a number of my business trips were combined with family scuba diving excursions. Unfortunately, I had a diving accident on Curacao in 2018 at one of the many Winter Conferences on Neural Plasticity I attended and ended up spending eight days in a hyperbaric chamber. I haven't dived since.

After spending many years living in the MBL cabins, my wife and I eventually bought a house on Wilson Road, which we later sold to Bill and Nechama Ross, and then we bought another house on Fern Lane. We continue to spend part of each summer in Woods Hole. Some of the things we are "famous" for are the backyard Texas barbeques we had for many summers. We invited as many people as we could, which sometimes numbered as many as 150. The other "event" we had one summer, which attracted some attention by the MBL community, was a litter of golden retriever puppies. It seemed as if almost everyone in Woods Hole at some point came to play with them in our backyard.

Another, nonscientific but life-changing experience for me that I attribute to (or blame on!) MBL and Woods Hole is my love for fishing. All the labs I worked in at the MBL were in the Whitman (now called Rowe) building. Although most of our work at the MBL was using imaging methods requiring blacking out the windows, occasionally I'd look out the window to see all the boats in Woods Hole harbor with people fishing. It was so mesmerizing that I decided I had to give it a try. During the winter of 2000, I got on the internet and found a used boat in Martha's Vineyard that I had surveyed and ultimately purchased. It was waiting for me at a marina in Falmouth Harbor when we got to Woods Hole in the summer of 2001. I didn't know

much about handling a boat so it was all very new to me. I bought some fishing gear from Eastman's tackle shop and Andreas Frick, a postdoc of mine who had come with me to the MBL, and I took the boat out into Vineyard Sound, dropped our lines into the water, and just waited for the fish to bite. Needless to say, we came up empty-handed. I decided I needed some help. There was a flyer in Eastman's for a charter captain who would take you out on your boat. This seemed ideal for me because I also wanted to learn how to run my boat. His name was Eric Stapelfeld, who was one of the best striped bass fishermen on the Cape. During the next 10 years or so, I did a lot of fishing with Eric, many times as his deckhand. I learned a great deal from Eric and became a pretty good fisherman in the lower Cape area. Our downfall came when we went into the charter fishing business together with a used lobster boat that Eric refurbished as a fishing boat. The business never really went anywhere, so after a few years, I sold the boat. Unfortunately, Eric and I hardly speak anymore, but I do give Eric a great deal of credit for teaching me how to fish in the area and generally for feeding what became quite an addiction for me.

I often think about how fishing is like doing electrophysiology experiments. You are constantly making adjustments in real time, trying different things, and of course being superstitious when one of them might actually work! In psychology, it's called intermittent reinforcement. Two of my good friends, Steve Redman and Bill Spain, both electrophysiologists and avid fishermen, would agree with me on this. They came to fish with me in Woods Hole for some 15 straight years until Covid hit. When the fish weren't biting, we would always talk science. I ended up buying five different boats in the Falmouth/Woods Hole area. I now regret having sold some of them, but the old saying that "a boat is a hole in the water that you pour money into" is quite appropriate for my fishing/boating experiences.

## Dendrites

Now back to science. The 10-plus years from around 1992 until I left Baylor for the University of Texas in 2004 were quite magical for me scientifically. I had some truly outstanding postdocs and graduate students whose work became focused on neuronal dendrites. In particular, we were interested in the voltage-gated ion channels expressed in dendrites, their plasticity, and how they contributed to the information processing and storage of the nervous system. Jeff Magee started these studies with cell-attached patch clamp recordings of single sodium and calcium channels. Then there was Dax Hoffman with recordings of single potassium channels and, of course, Costa Colbert with both experiments and modeling. There were many talented people in the lab at the time studying various aspects of dendritic function, including outstanding biophysicists, experimentalists, theorists, and disease translationalists. The lab space was designed with a conference



table in the center with many small rig rooms around the periphery. People would go into their rig rooms to do experiments and then come out into the conference table area to talk with whomever was around. The discussions at that table were intense and groundbreaking. I don't think my lab ever experienced such an exciting and productive period. We were truly at the forefront of an emerging field. We had mostly left behind the field of synaptic plasticity, and basically started our own field. There were many groundbreaking and highly cited publications during this period, and most of the people in the group ultimately took independent positions at leading institutions. When we would subsequently get together at neuroscience meetings, everyone acknowledged that this period of time in my lab was indeed magical and was never really duplicated again in my or in anyone else's lab.

### The “Book”: *Foundations of Cellular Neurophysiology*

As part of the Graduate Program in Neuroscience, I taught a course in cellular neurophysiology with Sam Wu. Sam was a faculty member in the Department of Ophthalmology. He was a wonderful electrophysiologist studying retinal neurons from salamanders. Sam and I became very close while I was still in the Neurology Department. Our labs were on adjacent floors in the Neurosensory Center, and we would get together and talk science all the time. We both had engineering backgrounds and felt that neurophysiology should be taught at a fundamental and mathematical level. So, we decided we would teach a rigorous course to first-year graduate students and provide everyone with some background in the functional properties of neurons. Sam wanted to teach the more biophysical parts—for example, the statistics of ion channel opening and closing, theories of ion channel permeability, and Hodgkin Huxley equations—while I would teach cable theory, synaptic transmission, including quantal analysis of transmitter release, and synaptic plasticity. The course began in the late 1980s and continued until I left Baylor in 2004. It was a required course, so all the graduate students at Baylor during that time were “subjected” to the course. Many did not want to take it, but most said they were glad they did and learned a great deal. We had extensive notes that we made for the course and, after a few years, we decided to see if it would be possible to convert our notes into a textbook. We contacted several publishers, but it was Fiona Stevens from the MIT Press who landed the contract. Of course, we discovered that converting course notes into a textbook was much more difficult than we thought it would be, and it ended up being a multiyear project. Rick Gray, a special person in my lab who I will discuss in some detail at the end, was instrumental in the process, in part because MIT wanted the book to be typeset using LaTeX. Although I was somewhat familiar with LaTeX, Sam was not. Fortunately, Rick was an expert. Also, all the figures had to be put into a form suitable for LaTeX. Rick did all of this. Overall, it

was a monumental project. If we had known ahead of time how much work it would be, I don't think any of us would have considered it.

One of the unique aspects of the book was the inclusion of extensive homework problems at the end of each chapter along with the answers to these problems in appendices. One appendix had short answers to each problem, while another appendix had the complete solutions. This way the student could check to see if they were on the right track by looking only at the short answer before looking at the complete solution. Including so many homework problems presented an editing challenge in and of itself because it was time-consuming to ensure that all the problems and answers were correct and typeset properly. The first printing of the book, unfortunately, had numerous errors, but many of these were corrected by the second printing. Sam, Rick, and I are extremely proud of the book. It has been through tens of printings and has sold nearly 10,000 copies. It is a unique book and has been used mostly as a reference but also as a textbook. We always intended to come out with a second edition, but we could never overcome the effort involved in doing so.

### The Move to the University of Texas at Austin (2004–2022)

The Division of Neuroscience at Baylor was a fun and exciting place to be during the 1990s. We had a great department with many wonderful faculty and staff. The science was outstanding, the faculty was collegial, and everyone was focused on what was most important: research and education. Although I never actively sought positions elsewhere, occasionally I would be contacted by other institutions to see if I might be interested in moving as either a full professor or as a department chair. Some opportunities sounded more interesting than others, but I usually accepted the offer to visit and evaluate the possibilities. I recall visiting University of Alabama–Birmingham, University of Pennsylvania, University of Wisconsin, University of Washington, Yale, University of Chicago, Tufts, Brown, MIT, Duke, University of North Carolina, and the Medical College of Georgia. There may have even been a few others that I don't remember. Some of these institutions were just looking at me for a professor position, while others were interested in me as department chair. It was flattering to even be considered by some of these institutions, and in all cases the visits were educational. I got to see both the positives and negatives of other places and usually came away with the conclusion that there was no perfect academic institution, and I was happy to stay where I was.

I don't remember the exact year, but at some point between 2000 and 2002, Jim Patrick became a dean at Baylor. I'm sure that this was a good move for Jim, but unfortunately, it was not good for the division because he also remained as the chair. During the next few years, the environment in the division changed considerably for the worse. It was difficult for Jim to

advocate for the division as a chair should do because he was also dean with an obvious conflict of interest. As a result, the support and status for the division went downhill considerably. It became clear that the faculty were not happy with this situation, and it was only a matter of time before people started leaving. I think Rob Gereau was the first to leave, but over about a five-year period, the division lost eight senior faculty members, Rob, David Sparks, me, David Sweatt, Nikos Logothetis, John Maunsell, Mike Crair, John Dani, and perhaps a few others whom I don't remember. In my opinion, this was a major downfall of the division. Because I left in 2004, I won't dwell on what happened at Baylor because most of what I know is second- or third-hand information. Suffice it to say that Jim's decision to remain chair after becoming dean was a huge mistake for the division.

Harold Zakon from the Section of Neurobiology at the University of Texas at Austin (UT) invited me to give a seminar in the fall of 2001. It is a beautiful campus, and I met some of the faculty and learned a bit about neurobiology at UT. About six months later, Harold contacted me and asked whether I might consider a leadership position at UT. I said sure, but didn't really think much would come of it. At the time, they were considering someone else for the position, and I figured he would take it. During the next two years, I took many trips to Austin and met with many people, including members of both the faculty and the administration. The more I learned about the possibilities at UT and the resources that the administration was willing to devote to building neuroscience, the more interested I became. The dean of natural sciences at the time, Mary Ann Rankin, was a joy to work with. She and the provost, Sheldon Eckland-Olson, seemed committed to increasing the number of neuroscience faculty members, expanding the infrastructure, and making UT competitive in neuroscience with other similar institutions. Our negotiations continued for almost two years, until I finally signed a contract in early 2004. I was to become director of the Institute for Neuroscience (INS) as well as the director of the new Center for Learning and Memory (CLM).

The INS was an interdepartmental graduate program that had been established some years earlier but was in need of strong leadership. There were three main departments, all in different colleges, that were the core of the INS. Each had different views about graduate education, and they didn't agree on much. I thought that my experience as head of an interdepartmental graduate program at Baylor for so many years would serve me well in this position. There was also no real department of neuroscience at UT but there was a Section of Neurobiology within the School of Biological Sciences. Harold was chair of that section, and, although it was offered to me, I didn't really want his job. One of the main tasks of the section was teaching neuroscience to the large number of undergraduate students at UT. I had little experience with undergraduate education, and I wanted to focus my efforts on enhancing neuroscience research at UT. I felt I could do this

by establishing the CLM. I thought that CLM could provide a research focus and identity that would help to attract and recruit new faculty members. As part of the agreement, CLM was given 10 new faculty lines at any level and space in a new building. Although there was a core group of excellent neuroscientists at UT, the group was small and UT did not have a national reputation for neuroscience. My idea was to first try to recruit a few senior faculty who could provide some name recognition for CLM. I also thought that it would be easier to recruit into the new center (CLM) rather than to the faculty at large. I began contacting people I knew right away, well before I actually moved to UT. I also wanted to recruit outstanding senior women who would then help me recruit junior women so we could have a gender-balanced center. Although I wanted a diverse center both in terms of gender, race, and area of research (from molecular to humans), my motto was always to “hire the best athlete.”

My first recruit was Rick Aldrich from Stanford. Rick of course was a great scientist, who later was elected into the National Academy of Sciences, but it was also an opportune time to recruit him. He had just lost his Howard Hughes Medical Institute funding, his brother lived in College Station, and he grew up in the southwest (New Mexico and Arizona). Mary Ann offered him a great package, which included being chair of Neurobiology and two faculty lines. My second recruit was Kristen Harris. I met her many years earlier at a meeting at the MBL and had followed her and her work for many years. She had been at Harvard and Boston University but recently had moved to the Medical College of Georgia. She actually tried to recruit me to Georgia but that fell through rather quickly. Kristen was also a great scientist, as well as a great role model for women in science, and her research was a perfect fit for CLM. After these two senior hires, we focused our efforts on recruiting junior faculty members. We formed a search committee, advertised in all the usual places, and contacted as many people as we could at other universities to let them know about our recruiting efforts. I applied successfully for a big state grant, which helped with Kristen’s recruitment (electron microscopes are expensive!), and an NIH stimulus grant, which helped me leverage an 11th faculty line for CLM from the college. Although there were a few people we tried to recruit who decided to go elsewhere, we were very successful in our recruiting efforts and assembled an amazing group of faculty for the CLM. In addition to Rick and Kristen, we hired Ali Preston, Michael Drew, Kim Raab-Graham, Helmut Koester, Ila Fiete, Hiroshi Nishiyama, Laura Colgin, and Boris Zemmelman. Michael Mauk from UT Houston had written me a letter asking to be considered for a position at UT Austin. He was not that happy where he was, and he thought that his research would be a good fit for CLM. Although Mary Ann was not that enthusiastic about another senior hire, especially one from another Texas institution, Mike also brought with him his wife, Susan Cushman. I had known Susan from the time she was

a doctoral student with Paul Pfaffinger at Baylor. I thought that she would be an ideal person to help with development efforts for CLM. As a team, they seemed attractive enough to convince Mary Ann to make offers. Mike came in as a full professor and Susan as a senior administrator in charge of development and community relations.

Laura Colgin and Boris Zimmelman were our last recruits, bringing the total number of faculty members in CLM to the 11 we were promised, with me making it an even dozen. We were also balanced in terms of research areas, which spanned levels of analysis from molecular to human, and in terms of gender (5 of the 11 hires were women). I also tried hard to recruit another outstanding scientist (a woman of color), but the university at that time was not as committed as they should have been in applying the resources necessary to attract minorities. Other than this and a few other failed searches, faculty recruitment turned out to be much easier than I had anticipated. Once we had an identity with Rick, Kristen, and me, it was more attractive for the outstanding junior scientists on the market to consider UT. Also, we could make a pretty attractive offer compared with many other places with nine month's salary for only teaching one course, new and generous lab space, and some other perks that stood out above other competing places. People also liked the idea of joining something new (CLM). Susan had many great ideas, such as establishing a yearly (later changed to biannual) community outreach program called Memory Matters; a yearly CLM retreat; and a biannual symposium, which we called the Austin Conference on Learning and Memory (ACL&M, which was a takeoff from the name of the famous Austin City Limits). CLM was on its way to becoming a nationally and internationally recognized center of excellence. I also resisted the notion of having CLM encompass everyone on campus whose research was remotely related to learning and memory. I thought that this would be a mistake; there were other, less successful, all-encompassing centers on campus that helped convince me of this. I wanted to keep CLM small and collegial, including only those interested and willing to contribute toward the goals of CLM. Nicholas Priebe, Jonathan Pierce (two recruits while Rick Aldrich was chair of Neurobiology), and Nace Golding later joined CLM and were great members and contributors. One of the things we did to help keep CLM collegial and collaborative was to have weekly faculty meetings over lunch, with different people giving informal 30-minute talks about their research each week. We also used this time for people working on their grants to get critiqued by the rest of CLM. This could only happen if it was a relatively small and friendly group. I think the grant critiques helped a great deal in everyone's success in grant funding. Overall, I think CLM was a winner, with many of the things we did perhaps serving as a model for other centers. I need to acknowledge that none of this would have been possible without the help and support of outstanding staff members: Kathleen Pantalion, Cindy Thompson, and Jason Goltz.

While developing CLM was relatively easy, being director of the INS was challenging, to say the least. There were serious structural problems that I was never able to fully overcome. The most difficult problem was the financing of the INS by the three main colleges that had a significant number of faculty as members of INS. The three colleges were Natural Sciences, Liberal Arts, and Pharmacy. As part of my contract, each college was supposed to contribute a yearly amount to the INS roughly based on the number of their faculty in the INS. For many reasons, this was a struggle to make happen every year. The second problem was in teaching. To develop a strong educational program for graduate students, we had to have faculty willing and able to teach graduate courses. The INS had no teaching budget to pay part of the salaries of the faculty teaching graduate courses. The teaching load in each of the three colleges was quite different, and faculty received teaching credit only for teaching undergraduate courses in their respective colleges. We had to get the approval from the different department chairs each year to allow faculty to get credit toward their required teaching load for teaching a graduate course. This made it difficult to establish a graduate curriculum in neuroscience. The third problem was in the standards for graduate students. Each college and department felt differently about graduate students. Before I came to UT, graduate students were directly admitted to a particular lab with the graduate stipend being paid by having the graduate student work as a teaching assistant (TA) in that department each semester. This meant that research progress by students was slow, and many students took seven or more years to finish their doctorates.

I did have some success with these and other core issues. With the help of Kristen Harris and some of the other new faculty members in CLM, we established a new set of bylaws for the INS. This included higher standards for admission of applicants, which was mediated by a general admission committee. There were no direct admits allowed into particular labs. We required research rotations during the first year with the stipends being paid by the INS and established new courses. There were some growing pains, however. For example, the INS was used to admitting some 20 students per year. I think in the first year of implementing the new admissions standards, we admitted only a handful of students. Also, while it was typical for students in the old system to take seven years to complete their degree, we implemented a number of financial incentives to shorten this to five years. This meant that there were fewer TAs to help with teaching the many undergraduate courses. After a few years, however, the quality of the graduate students increased significantly, and we had a large number of outstanding applicants every year. The curriculum was improved somewhat, although I had to endure a lawsuit brought against me by one of the faculty members who I had removed from teaching. The problems I was never able to solve, however, mostly related to the financial and teaching issues.

After about eight years at UT, I was asked to become chair of the Section of Neurobiology. Rick Aldrich had completed his five-year term as chair and was ready to devote more of his time to research. My goal for being chair was to help bring the section together and to convince the administration that we should become an independent department rather than a section in the School of Biological Sciences. Unfortunately, Mary Ann Rankin had stepped down as dean of the College of Natural Sciences and moved to the University of Maryland. Linda Hicke from Northwestern University was hired to replace her as dean. Dean Hicke was not supportive of neurobiology/neuroscience and terminated much of the money that had been going to the Section of Neurobiology and INS. Also, she changed the status of the CLM from an independent research unit to being a part of the Section of Neurobiology. Needless to say, we did not get along. I felt that she had violated many of the provisions of my contract, but there was little I could do about it other than bring a lawsuit, which I was not about to do. The one good thing she did, however, was to abolish the School of Biological Sciences and establish three independent departments: Integrative Biology, Molecular Biosciences, and Neuroscience. We finally had our own department, but my struggles with the dean were never ending. After four years as chair, I stepped down and Mike Mauk took over. I thought that the department was in good shape when it was handed over to Mike and that most of the faculty thought I had done a reasonable job (you can't please everyone). My guiding principles were to be honest and transparent with the faculty and to advocate for them (and not yourself) whenever possible. Around that time, I also stepped down as director of INS. I did remain as director of CLM, however. That was my baby!

## Research at University of Texas

Thus far, I have devoted most of this section to my administrative successes and failures at the University of Texas, but I would be remiss if I did not also discuss some of our advances in research during my years at UT. Because more of my time was now being spent on administrative duties than it was at Baylor, research in my lab was very much dependent on Rick Gray. I had secured a partially funded research professor position for him as part of my recruitment package, and he earned it! I also received a similar kind of position for Randy Chitwood, who also helped considerably to keep the lab functioning. Both Rick and Randy were instrumental in whatever successes we had at UT. Rick especially was a unique individual to whom I devote a section at the end of this biography.

Shortly after leaving my lab, Jeff Magee made a fundamental discovery about the gradient of HCN or h-channels in dendrites of CA1 hippocampal neurons. This turned out to be a similar, or even steeper, gradient than what we had shown previously for A-type potassium channels. Although I tried hard not to infringe on Jeff's findings, it seemed like everything we

did related to dendrites turned out to depend on h-channels. Fortunately, after several landmark papers, Jeff pursued other things and did not dwell on h-channels. I certainly did not want to compete with Jeff. Some of the unexpected findings we made that ended up being due at least in part to h-channels were the so-called E-S potentiation described many years earlier with long-term potentiation (LTP), intrinsic plasticity, dopamine regulation of excitability, mGluR-dependent changes in excitability, excitability gradients, epilepsy, depression, actions of ketamine, and oscillations.

I had some outstanding students and postdocs during my years at UT. One in particular was Rishi Narayanan. I met him one summer at the MBL. He was taking the Methods in Computational Neuroscience course in which students had to do a project supervised by a summer scientist. He came to me and asked if I could help him, which I was delighted to do. I don't remember what his summer project was, but we certainly hit it off, and he later asked to do a postdoc in my lab. Rishi had an engineering background, but very little experience doing wet lab experiments. I had previously accepted other computationally oriented people with no experimental training for postdocs who didn't turn out very well. Rishi, however, was so smart and engaging that I was glad to accept him into my lab. Rishi was amazing and had great success transitioning from purely computational work to hard-core electrophysiology. He took the lab in many new directions and published several seminal papers. Another postdoc was Darrin Brager. He joined my lab while I was still at Baylor and actually stayed at Baylor for a few years after I left because his wife was finishing up her pediatric residency at Baylor. Darrin commuted between Houston and Austin on a weekly basis for almost two years so he could do experiments in the lab. Darrin was very successful and produced many great papers. After his wife moved to Austin, she joined a medical practice in San Marcos. With his family now in Austin, Darrin decided to stay at UT with a promotion to an independent research faculty position. In retrospect, he probably should have transitioned to a faculty position at another institution, but he was happy where he was. Darrin's work was outstanding, he received his own federal funding, and had many excellent trainees, but UT was never willing to put him in a tenure track position. I always regretted this, but there was little I could do.

## The Transition Period toward Retirement

Although I tried to be active in the lab again after so many years as directors of the two centers and chair of what was now a department, it was clear that I was unable to be as engaged in research as I once was. I still had NIH funding, with some 40 years of continuous NIH funding, including what might still be a record at National Institute of Mental Health (NIMH) of a grant with a perfect score of 100! However, there was one experience with the NIH that still grates on me. I put together what I thought was a very



interesting grant related to possible cellular mechanisms for the known comorbidity between epilepsy and depression. I contacted a program officer at the NIMH and asked if she would look at the aims of this grant and advise me on what study section would be best to send it to. She said she would be happy to do so. I sent them to her, and after several days, I called her again to see what advice she might have. She was someone with a doctorate, but she had little or no research experience beyond her graduate work. She told me that NIMH would not be interested in this grant and then proceeded to tell me what types of experiments I should be doing. I found it incredible that someone with her level of experience would have the chutzpah to tell a senior scientist with some 40 years of NIH funding what types of experiments I should be doing. She further told me that NIMH really didn't abide by priority scores anymore and that they just funded what they want to regardless of peer review. I related this experience to a number of other colleagues who had dealt with NIMH, and no one was surprised and many had similar experiences. NIMH seemed to be doing more top-down micro-managing of grant funding than they used to. Although I previously had funding from other institutes, such as National Institute of Neurological Disorders and Stroke (NINDS), and could have pursued funding there, this experience really soured me on the NIH and funding in general. I had always thought that peer review was the foundation and principle that led to the highest quality and most innovative research possible and was the essence of what made the NIH and research in the United States so special.

In addition to not being as focused on research as I used to be, the atmosphere in the department had changed considerably, which made me uncomfortable at best. Divisions clearly had formed between different groups in the department, with some getting favorable treatment by the chair at the expense of others. Many of the faculty would come to me to complain, but there was little I could do about it. The department was just not the happy place that it used to be. These and other things made me begin to think about my eventual retirement, but I didn't know when to pull the trigger. When Covid hit in 2020, the labs were closed, and I had to work from home. Fortunately, most of the trainees in my lab had left for other jobs before Covid, so ongoing research was not that affected by the lab closures. However, I was in the middle of teaching my yearly neuro-physiology course at the time, so all of the lectures from then on were done remotely. I definitely did not like remote teaching. I always enjoyed the close interaction and engagement with students, which was just not possible over Zoom. This teaching experience also made me think about retirement. A few years before Covid, my wife and I had purchased a house on North Padre Island just southeast of Corpus Christi. We loved the beach and fishing, so we basically moved there during Covid. We really loved it there, making me think more seriously about retirement. The final straw, so to speak, was the untimely and tragic death of my long-time friend and colleague

Rick Gray (see “Memorial to Rick Gray”). With Rick’s passing, I had little motivation to reinvigorate my lab and research, so I decided to finally retire in January 2022. Laura Colgin had already taken over as director of the CLM; Darrin Brager was moving to University of Nevada, Las Vegas; and the one research assistant I had in the lab, Brandy Routh, had been accepted into graduate school and began working in another lab. It seemed like the right time to retire, but other than fishing, I really had no plans for doing anything in retirement. I would have been happy to contribute in some way to the department, but the new chair who had taken over from Mike Mauk never really asked me to do anything, so we just sold our house in Austin and moved completely to North Padre Island.

## Conclusion

Although I may have had a few regrets along the way, I am satisfied that I did my best during my career to advance my area of neuroscience. I also tried to be a leader and help others achieve their own successes. From my time in college, the motto of working hard and separating work from play (including family life) has helped guide me through the years. I’ve had a wonderful career. If I could return briefly to my drifting ocean water analogy at the beginning, the “influencers” for my drift to science were many, and I am forever grateful. My wife and family may not have directly influenced my drift toward science, but they had an enormous impact on whatever success in science I may have had. Although my career has been immensely satisfying, nothing comes close to the joy of being with family and friends.

## Memorial to Rick Gray

Richard Gray was born on a family farm near Miles, Iowa. He did his undergraduate work at the University of Illinois, Urbana, and came to BCM as a research assistant with Mike Merickel. He later joined the graduate program, and my lab, where he completed his doctoral work. He did a brief postdoc with John Connor at the Roche Institute of Molecular Biology in New Jersey and then rejoined my lab as a research associate. He was later promoted to assistant professor at Baylor and as a research scientist at the University of Texas. Rick was an amazing individual both due to his technical skills and his personal interactions with everyone in my lab. He could fix anything, probably from his experience in growing up on a farm. Rick became highly skilled in electronics, computer programming, and all types of experimental electrophysiology. His real love was in channel biophysics, and that is where most of his experimental work was focused. He helped and mentored virtually everyone who came through my lab. Especially during my time in Austin, he was simply indispensable for whatever successes we had in research. Everyone who came in contact with Rick adored him. He

had a bad heart and always thought he would die of a heart attack, but in the end, it was cancer that took him at the early age of 68. He is sorely missed by everyone who knew him. I do not know what my scientific career would have been like if I had not had Rick Gray by my side.

## Acknowledgment

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## Trainees

In addition to Rick Gray, I had many simply outstanding students, postdocs and collaborators throughout my career. I would like to thank all of them for their important contributions to both my research and to my personal development as a scientist and academician.

## Graduate Students

John W. Whisler, MS UofMN; Warren Watson, MS, UofMN; Carl E. Stafstrom, MD/PhD, UofMN; William F. Hopkins, PhD, Baylor; Richard Gray, PhD, Baylor; Ronald Fisher, MD/PhD, Baylor; Nelson Spruston, PhD, Baylor; David Jaffe, PhD, Baylor; Erik Cook, PhD, Baylor; Craig Powell, MD/PhD, Baylor; Robert Avery, MD/PhD, Baylor; Lalan Schexnayder, MD/PhD, Baylor; Dax Hoffman, PhD, Baylor; Xixi Chen, PhD, Baylor; Yuan Fan, PhD, Baylor; Yul Young Park, PhD, UT; Chung Sub Kim, PhD, UT; Ann Clemens, PhD, UT; Sachin Vaidya, PhD, UT; Andrea Haessly, MS, UT; Elizabeth Arnold, PhD, UT; Brandy Zrubek Routh, student researcher, UT.

## Postdoctoral Fellows

Gerald E. Slater, MD, UofMN; Howard Wood, PhD, Baylor; Frank J. Lebeda, PhD, Baylor; Douglas A. Baxter, PhD, Baylor; Richard Gray, PhD, Baylor; William H. Griffith, PhD, Baylor; Paul A. Rutecki, MD, Baylor; Richard J. Hallworth, PhD, Baylor; Flavio Villani, MD, Baylor; Stephen Williams, PhD, Baylor; Paul E. Schulz, MD, Baylor; Lise Eliot, PhD, Baylor; Jeff Magee, PhD, Baylor; Costa Colbert, PhD, Baylor; Brian Christie, PhD, Baylor; Ajay Kapur, PhD, Baylor; Mark F. Yeckel, PhD, Baylor; Nicholas Poolos, MD/PhD, Baylor; Li-Lian Yuan, PhD, Baylor; Shigeo Watanabe, PhD, Baylor; Andreas Frick, PhD, Baylor; Yong Liang, PhD, Baylor; Randy Chitwood, PhD, Baylor; Desdemona Fricker, M.D./PhD, Baylor; Helmut Koester, PhD, Baylor; Mala Shah, PhD, Baylor; Andreas Jeromin, PhD, Baylor; Amiel Rosenkranz, PhD, Baylor; Darrin Brager, PhD, Baylor; Laurea Diaz, PhD, UT; Rishikesh Narayanan, PhD, UT; Clifton Rumsey, PhD, UT;

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### Visiting Scientists

John J. Hablitz, PhD; Claudio Frank, MD; Thomas H. Brown, PhD; Nicholas, T. Carnevale, MD/PhD; Massimo Avoli, MD; Henri Conde, PhD; Michele Migliore, PhD; Geri Christofi, PhD; Christophe Bernard, PhD; Darrin Brager, PhD; Richard Gray, PhD.

### Chronological Bibliography of Selected Peer-Reviewed Publications

- Johnston, D., and Ayala, G.F. Diphenylhydantoin: The action of a common anticonvulsant on bursting pacemaker cells in *Aplysia*. *Science* 189:1009–1011, 1975.
- Johnston, D., and Wachtel, H. The electrophysiological basis for the spatial dependence of the inhibitory coupling in the *Limulus retina*. *J. Gen. Physiol.* 67:1–25, 1976.
- Johnston, D. Voltage clamp reveals basis for calcium regulation of bursting pacemaker potentials in *Aplysia* neurons. *Brain Res.* 197:418–423, 1976.
- Ayala, G.F., Lin, S., and Johnston, D. The mechanism of action of diphenylhydantoin on invertebrate neurons. I. Effects on basic membrane properties. *Brain Res.* 121:245–258, 1977.
- Ayala, G.F., Johnston, D., Lin, S., and Dichter, H. Mechanisms of action of diphenylhydantoin on invertebrate neurons. II. Effects on excitatory and inhibitory synaptic mechanisms. *Brain Res.* 121:259–270, 1977.
- Ayala, G.F., and Johnston, D. The influences of phenytoin on the fundamental properties of simple neural systems. *Epilepsia* 18:299–307, 1977.
- Whisler, J.W., and Johnston, D. Epileptogenesis: A model for the involvement of slow membrane events and extracellular potassium. *J. Theor. Biol.* 75:271–288, 1978.
- Slater, G.E., and Johnston, D. Sodium valproate increases potassium conductance in *Aplysia* neurons. *Epilepsia* 19:379–384, 1978.
- Johnston, D. Phenobarbital: Concentration dependent biphasic effect on *Aplysia* burst firing neurons. *Neurosci. Lett.* 10:175–180, 1978.
- Johnston, D. Voltage, temperature and ionic dependence of the slow outward current in *Aplysia* burst firing neurons. *J. Physiol.* (London) 298:145–157, 1980.
- Johnston, D., Hablitz, J.J., and Wilson, W.A. Voltage clamp discloses slow inward current in hippocampal burst firing neurons. *Nature* (London) 286:391–393, 1980.
- Stafstrom, C.E., Johnston, D., Wehner, J.M., and Sheppard, J.R. Spontaneous neural activity in fetal brain reagregate cultures. *Neurosci.* 5:1681–1689, 1980.

- Johnston, D. Passive cable properties of hippocampal CA3 pyramidal neurons. *Cell. Mol. Neurobiol.* 1:41–55, 1981.
- Johnston, D., and Brown, T.H. The giant synaptic potential hypothesis for epileptiform activity. *Science* 211:294–297, 1981.
- Johnston, D., and Lam, D.M.-K. Regenerative and passive membrane properties of isolated horizontal cells from a teleost retina. *Nature (London)* 292:451–454, 1981.
- Hablitz, J.J., and Johnston, D. Endogenous nature of spontaneous bursts in hippocampal neurons. *Cell. Mol. Neurobiol.* 1:325–334, 1981.
- Carnevale, N.T., and Johnston, D. Electrophysiological characterization of remote chemical synapses. *J. Neurophysiol.* 47:606–621, 1982.
- Bryan, R.N., and Johnston, D. Epileptogenic effects of radiographic contrast agents: An experimental study. *J. Neuroradiol.* 3:117–120, 1982.
- Lebeda, F.J., Hablitz, J.J., and Johnston, D. Antagonism of GABA-mediated responses by d-tubocurarine in hippocampal neurons. *J. Neurophysiol.* 48:622–632, 1982.
- Baxter, D.A., Johnston, D., and Strittmatter, W.J. Protease inhibitors implicate metalloendoprotease in synaptic transmission at the mammalian neuromuscular junction. *Proc. Nat. Acad. Sci. (USA)* 80:4174–4178, 1983.
- Brown, T.H., and Johnston, D. Voltage-clamp analysis of the mossy fiber synaptic input to hippocampal pyramidal neurons. *J. Neurophysiol.* 50:487–507, 1983.
- Johnston, D., and Brown, T.H. Interpretation of voltage-clamp measurements in hippocampal neurons. *J. Neurophysiol.* 50:464–486, 1983.
- Johnston, D. Valproic acid: Update on its mechanisms of action. *Epilepsia* 25:1–4, 1984.
- Johnston, D., and Brown, T.H. The synaptic nature of the paroxysmal depolarizing shift in hippocampal neurons. *Ann. Neurol.* 16:S65–S72, 1984.
- Hopkins, W.F., and Johnston, D. Frequency-dependent noradrenergic modulation of long-term potentiation in the hippocampus. *Science* 226:350–352, 1984.
- Gray, R. A., and Johnston, D. Rectification of single GABA-gated chloride channels in adult hippocampal neurons. *J. Neurophysiol.* 54:134–142, 1985.
- Rutecki, P. A., Lebeda, F. J., and Johnston, D. Epileptiform activity induced by changes in extracellular potassium in hippocampus. *J. Neurophysiol.* 54:1363–1374, 1985.
- Barrionuevo, G., Kelso, S.R., Johnston, D., and Brown, T.H. Conductance mechanism responsible for long-term potentiation in monosynaptic and isolated excitatory synaptic inputs to hippocampus. *J. Neurophysiol.* 55:540–550, 1986.
- Griffith, W.H., Brown, T.H., and Johnston, D. Voltage-clamp analysis of synaptic inhibition during long-term potentiation in hippocampus. *J. Neurophysiol.* 55:767–775, 1986.
- Gray, R., and Johnston, D. Noradrenaline and beta-adrenoceptor agonists increase the activity of voltage-dependent calcium channels in hippocampal neurones. *Nature (London)* 327:620–622, 1987.
- Rutecki, P.A., Lebeda, F.J., and Johnston, D. 4-Aminopyridine produces epileptiform activity in hippocampus and enhances synaptic excitation and inhibition. *J. Neurophysiol.* 57:1911–1924, 1987.

- Hopkins, W.F., and Johnston, D. Noradrenergic enhancement of long-term potentiation at mossy fiber synapses in the hippocampus. *J. Neurophysiol.* 59:667–687, 1988.
- Terrian, D.M., Johnston, D., Claiborne, B.J., Ansah-Yiadom, R., Strittmatter, W.J., and Rea, M.A. Glutamate and dynorphin release from a subcellular fraction enriched in hippocampal mossy fiber synaptosomes. *Brain Res. Bull.* 21:343–351, 1988.
- Williams, S.H., and Johnston, D. Muscarinic depression of long-term potentiation in CA3 hippocampal neurons. *Science* 242:84–87, 1988.
- Williams, S., and Johnston, D. Long-term potentiation of hippocampal mossy fiber synapses is blocked by postsynaptic injection of calcium chelators. *Neuron* 3:583–588, 1989.
- Fisher, R., Gray, R., and Johnston, D. Properties and distribution of single voltage-gated calcium channels in adult hippocampal neurons. *J. Neurophysiol.* 64:91–104, 1990.
- Fisher, R., and Johnston, D. Differential modulation of single voltage-gated calcium channels by cholinergic and adrenergic agonists in adult hippocampal neurons. *J. Neurophysiol.* 64:1291–1302, 1990.
- Jaffe, D., and Johnston, D. The induction of long-term potentiation at hippocampal mossy fiber synapses follows a Hebbian rule. *J. Neurophysiol.* 64:948–960, 1990.
- Rutecki, P.A., Lebeda, F.J., and Johnston, D. Epileptiform activity in the hippocampus produced by tetraethylammonium. *J. Neurophysiol.* 64:1077–1088, 1990.
- Williams, S., and Johnston, D. Muscarinic depression of synaptic transmission at the hippocampal mossy fiber synapse. *J. Neurophysiol.* 64:1089–1097, 1990.
- Chetkovich, D.M., Gray, R., Johnston, D., and Sweatt, J.D. NMDA-receptor activation increases cAMP levels and voltage-gated Ca<sup>2+</sup>-channel activity in area CA1 of hippocampus. *Proc. Natl. Acad. Sci. USA* 88:6467–6471, 1991.
- Williams, S., and Johnston, D. Kinetic properties of two anatomically distinct excitatory synapses in hippocampal CA3 pyramidal neurons. *J. Neurophysiol.* 66:1010–1020, 1991.
- Jaffe, D.B., Johnston, D., Lasser-Ross, N., Lisman, J.E., Miyakawa, H., Ross, W.N. The spread of Na<sup>+</sup> spikes determines the pattern of dendritic Ca<sup>2+</sup> entry into hippocampal neurons. *Nature (London)* 357:244–246, 1992.
- Miyakawa, H., Ross, W.N., Jaffe, D., Callaway, J.C., Lasser-Ross, N., Lisman, J.E., and Johnston, D. Synaptically activated increases in Ca<sup>2+</sup> concentration of hippocampal CA1 pyramidal cells are primarily due to voltage-gated Ca<sup>2+</sup> channels. *Neuron* 9:1163–1173, 1992.
- Spruston, N., and Johnston, D. Perforated patch-clamp analysis of the passive membrane properties of three classes of hippocampal neurons. *J. Neurophysiol.* 67:508–529, 1992.
- Spruston, N., Jaffe, D.B., Williams, S.H., and Johnston, D. Voltage- and space-clamp errors associated with the measurement of electrotonically remote synaptic events. *J. Neurophysiol.* 70:781–802, 1993.
- Villani, F., and Johnston, D. Serotonin inhibits induction of long-term potentiation at commissural synapses in hippocampus. *Brain Res.* 606:304–308, 1993.

- Eliot, L.S., and Johnston, D. Multiple components of calcium current in acutely-dissociated dentate gyrus granule neurons. *J. Neurophysiol.* 72:762–777, 1994.
- Jaffe, D.B., Ross, W.N., Lisman, J.E., Lasser-Ross, N., Miyakawa, H., and Johnston, D. A model for dendritic Ca<sup>2+</sup> accumulation in hippocampal pyramidal neurons based on fluorescence imaging measurements. *J. Neurophysiol.* 71:1065–1077, 1994.
- Powell, C.M., Johnston, D., and Sweatt, J.D. Increase in autonomously active protein kinase C in the maintenance of NMDA-receptor-independent LTP. *J. Biol. Chem.* 269:27958–27963, 1994.
- Schulz, P.E., Cook, E., and Johnston, D. Changes in paired-pulse facilitation suggest presynaptic involvement in long-term potentiation. *J. Neurosci.* 14:5325–5337, 1994.
- Christie, B.R., Eliot, L.S., Ito, K.-I., Miyakawa, H., and Johnston, D. Different Ca<sup>2+</sup> channels in soma and dendrites of hippocampal pyramidal neurons mediate spike-induced Ca<sup>2+</sup> influx. *J. Neurophysiol.* 73:2553–2557, 1995.
- Magee, J.C., Christofi, G., Miyakawa, H., Christie, B., Lasser-Ross, N., and Johnston, D. Subthreshold synaptic activation of voltage-gated Ca<sup>2+</sup> channels mediates a localized Ca<sup>2+</sup> influx into the dendrites of hippocampal pyramidal neurons. *J. Neurophysiol.* 74:1335–1342, 1995.
- Magee, J.C., and Johnston, D. Characterization of single voltage-gated Na<sup>+</sup> and Ca<sup>2+</sup> channels in dendrites of rat CA1 hippocampal neurons. *J. Physiol.* (London) 487.1:67–90, 1995.
- Magee, J.C., and Johnston, D. Synaptic activation of voltage-gated channels in dendrites of hippocampal pyramidal neurons. *Science* 268:301–304, 1995.
- Migliore, M., Cook, E.P., Jaffe, D.B., and Johnston, D. Computer simulations of morphologically reconstructed CA3 hippocampal neurons. *J. Neurophysiol.* 73:1157–1168, 1995.
- Schulz, P.E., Cook, E., and Johnston, D. Using paired-pulse facilitation to probe the mechanism of LTP. *J. Physiol.* (Paris) 89:3–9, 1995.
- Avery, R.B., and Johnston, D. Multiple channel types contribute to the low-voltage activated calcium current in hippocampal CA3 pyramidal neurons. *J. Neurosci.* 16:5567–5582, 1996.
- Christie, B.R., Magee, J.C., and Johnston, D. Dendritic calcium channels and hippocampal long-term depression. *Hippocampus* 6:17–23, 1996.
- Christie, B.R., Magee, J.C., and Johnston, D. The role of dendritic action potentials and Ca<sup>2+</sup> influx in the induction of homosynaptic long-term depression in hippocampal CA1 pyramidal neurons. *Learn. & Mem.* 3:160–169, 1996.
- Colbert, C.M., and Johnston, D. Axonal action-potential initiation and Na<sup>+</sup> channel densities in the soma and axon initial segment of subicular pyramidal neurons. *J. Neurosci.* 16:6676–6686, 1996.
- Magee, J.C., Avery, R.B., Christie, B.R., and Johnston, D. Dihydropyridine-sensitive, voltage-gated Ca<sup>2+</sup> channels contribute to the resting intracellular Ca<sup>2+</sup> concentration of hippocampal CA1 pyramidal neurons. *J. Neurophysiol.* 76:3460–3470, 1996.

- Williams, S., and Johnston, D. Actions of endogenous opioids on NMDA receptor-independent long-term potentiation in area CA3 of the hippocampus. *J. Neurosci.* 16:3652–3660, 1996.
- Avery, R.B., and Johnston, D. Ca<sup>2+</sup> channel antagonist U-92032 inhibits both T-type Ca<sup>2+</sup> channels and Na<sup>+</sup> channels in hippocampal CA1 pyramidal neurons. *J. Neurophysiol.* 77:1023–1029, 1997.
- Christie, B.R., Schexnayder, L.K., and Johnston, D. Contribution of voltage-gated Ca<sup>2+</sup> channels to homosynaptic long-term depression (LTD) in the CA1 region in vitro. *J. Neurophysiol.* 77:1651–1655, 1997.
- Colbert, C.M., Magee, J.C., Hoffman, D., and Johnston, D. Slow recovery from inactivation of Na<sup>+</sup> channels underlies the activity-dependent attenuation of dendritic action potentials in hippocampal CA1 pyramidal neurons. *J. Neurosci.* 17:6512–6521, 1997.
- Cook, E.P., and Johnston, D. Active dendrites reduce location-dependent variability of synaptic input trains. *J. Neurophysiol.* 78:2116–2128, 1997.
- Hoffman, D., Magee, J.C., Colbert, C.M., and Johnston, D. Potassium channel regulation of signal propagation in dendrites of hippocampal pyramidal neurons. *Nature* 387:869–875, 1997.
- Magee, J.C., and Johnston, D. A synaptically-controlled, associative signal for Hebbian plasticity in hippocampal neurons. *Science* 275:209–213, 1997.
- Colbert, C.M., and Johnston, D. Protein kinase C activation decreases activity-dependent attenuation of dendritic Na<sup>+</sup> current in hippocampal CA1 pyramidal neurons. *J. Neurophysiol.* 79:491–495, 1998.
- Hoffman, D.A., and Johnston, D. Down-regulation of transient K<sup>+</sup> channels in dendrites of hippocampal CA1 pyramidal neurons by activation of PKA and PKC. *J. Neurosci.* 18:3521–3528, 1998.
- Kapur, A., Yeckel, M.F., Gray, R., and Johnston, D. L-type calcium channels are required for one form of hippocampal mossy fiber LTP. *J. Neurophysiol.* 79:2181–2190, 1998.
- Cook, E.P., and Johnston, D. Voltage-dependent properties of dendrites that eliminate location-dependent variability of synaptic input. *J. Neurophysiol.* 81:535–543, 1999.
- Hoffman, D.A., and Johnston, D. Neuromodulation of dendritic action potentials. *J. Neurophysiol.* 81:408–411, 1999.
- Migliore, M., Hoffman, D.A., Magee, J.C., and Johnston, D. Role of an A-type K<sup>+</sup> conductance in the back-propagation of action potentials in the dendrites of hippocampal pyramidal neurons. *J. Computational Neurosci.* 7:2–15, 1999.
- Poolos, N.P., and Johnston, D. Calcium-activated potassium conductances contribute to action potential repolarization in the soma but not the dendrites of hippocampal CA1 pyramidal neurons. *J. Neurosci.* 19:5205–5212, 1999.
- Yeckel, M.F., Kapur, A., and Johnston, D. Multiple forms of LTP in hippocampal CA3 neurons use a common postsynaptic mechanism. *Nature Neurosci.* 2:625–633, 1999.
- Johnston, D., Hoffman, D.A., Magee, J.C., Poolos, N.P., Watanabe, S., Colbert, C.M., and Migliore, M. Dendritic potassium channels in hippocampal pyramidal neurons. *J. Physiol.* 525:75–81, 2000.



- Kapur, A., Yeckel, M.F., and Johnston, D. Hippocampal mossy fiber activity evokes Ca<sup>2+</sup> release in CA3 pyramidal neurons via a metabotropic glutamate receptor pathway. *Neuroscience* 107:59–69, 2001.
- Liang, Y., Yuan, L.-L., Johnston, D., and Gray, R. Calcium signaling at single mossy fiber presynaptic terminals in the rat hippocampus. *J. Neurophysiol.* 87: 1132–1137, 2002.
- Nakazawa, K., Quirk, M.C., Yeckel, M.F., Watanabe, M., Chitwood, R.A., Sun, L.D., Kato, A., Carr, C.A., Johnston, D., Wilson, M.A., and Tonegawa, S. Evidence for a crucial role of hippocampal CA3 NMDA receptors in associative memory recall. *Science* 297:211–218, 2002.
- Poolos, N.P., Migliore, M., and Johnston, D. Pharmacological upregulation of h-channels reduces the excitability of pyramidal neuron dendrites. *Nature Neurosci.* 5:767–774, 2002.
- Watanabe, S., Hoffman, D.A., Migliore, M., and Johnston, D. Dendritic K<sup>+</sup> channels contribute to spike-timing induced long-term potentiation in hippocampal pyramidal neurons. *Proc. Natl. Acad. Sci. USA* 99: 8366–8371, 2002.
- Yuan, L.-L., Adams, J.P., Swank, M., Sweatt, J.D., and Johnston, D. Protein kinase modulation of dendritic K<sup>+</sup> channels in hippocampus involves a MAPK pathway. *J. Neurosci.* 22:4860–4868, 2002.
- Bernard, C., and Johnston, D. Back-propagation in dendrites is controlled by a distance-dependent modifiable threshold. *J. Neurophysiol.* 90:1807–1816, 2003.
- Frick, A., Magee, J.C., Koester, H., and Johnston, D. Normalization of Ca<sup>2+</sup> signals by small oblique dendrites of CA1 pyramidal neurons. *J. Neurosci.* 23:3243–3250, 2003.
- Jeromin, A., Yuan, L.-L., Frick, A., Pfaffinger, P., and Johnston, D. A modified Sindbis vector for prolonged gene expression in neurons. *J. Neurophysiol.* 90:2741–2745, 2003.
- Bernard, C., Anderson, A.E., Poolos, N.P., and Johnston, D. Acquired dendritic channelopathy in temporal lobe epilepsy. *Science* 305:532–535, 2004.
- Chen, X., and Johnston, D. Properties of single voltage-dependent K<sup>+</sup> channels in dendrites of CA1 pyramidal neurons of rat hippocampus. *J. Physiol.* 559:187–203, 2004.
- Frick, A., Magee, J.C., and Johnston, D. LTP is accompanied by an enhanced local excitability of pyramidal neuron dendrites. *Nature Neurosci.* 7:126–135, 2004.
- Shah, M.M., Anderson, A.E., Leung, V., and Johnston, D. Seizure-induced plasticity of h-channels in entorhinal cortical layer III neurons. *Neuron* 44:495–508, 2004.
- Varga, A.W., Yuan, L.-L., Anderson, A.E., Schrader, A., Wu, G.-Y., Gatchel, J.R., Johnston, D., and Sweatt, J.D. CaMKII modulated Kv4.2 channel expression and upregulates dendritic A-type K<sup>+</sup> currents. *J. Neurosci.* 24:3643–3654, 2004.
- Wang, J., Yeckel, M.F., Johnston, D., and Zucker, R.S. Photolysis of postsynaptic caged Ca<sup>2+</sup> can potentiate and depress mossy fiber synaptic responses in rat hippocampal CA3 pyramidal neurons. *J. Neurophysiol.* 91:1596–1607, 2004.
- Chen, X., and Johnston, D. Constitutively active GIRK channels in dendrites of hippocampal CA1 pyramidal neurons. *J. Neurosci.* 25:3787–3792, 2005.

- Fan, Y, Fricker, D., Brager, D., Chen, X, Lu, H.C, Chitwood, R, and Johnston, D. Activity-dependent decrease of excitability in hippocampal neurons through increases in *I<sub>h</sub>*. *Nature Neurosci.* 8:1542–1551, 2005.
- Koester, H.J., and Johnston, D. Target-cell dependent normalization of transmitter release at neocortical synapses. *Science* 308:863–866, 2005.
- Chen, X., and Johnston, D. Voltage-gated ion channels in dendrites of hippocampal neurons. *Pflugers Arch.* 453:397–401, 2006.
- Chen, X., Yuan, L.-L., Zhao, C., Birnbaum, S.G., Frick, A., Jung, W.E., Schwarz, T.L., Sweatt, J.D., and Johnston, D. Deletion of *Kv4.2* gene eliminates dendritic A-type  $K^+$  current and enhances induction of long-term potentiation in hippocampal CA1 pyramidal neurons. *J. Neurosci.* 26:12143–12151, 2006.
- Rosenkranz, J.A., and Johnston, D. Voltage-dependent dopaminergic regulation of neuronal excitability through modulation of *I<sub>h</sub>* in layer V entorhinal cortex. *J. Neurosci.* 26:3229–3244, 2006.
- Yuan, L.-L., Chen, X., Kunjilwar, K., Pfaffinger, P., and Johnston, D. Acceleration of  $K^+$  channel inactivation by the MEK inhibitor U0126. *Amer. J. Physiol.* 290:C165–C171, 2006.
- Brager, D.H., and Johnston, D. Plasticity of intrinsic excitability during long-term depression is mediated through mGluR-dependent changes in *I<sub>h</sub>* in hippocampal CA1 pyramidal neurons. *J. Neurosci.* 27:13926–13937, 2007.
- Gasparini, S., Losonczy, A., Chen, X., Johnston, D., and Magee, J.C. Associative pairing enhances action potential back-propagation in radial oblique branches of CA1 pyramidal neurons. *J. Physiol.* 580 (Pt.3):787–800, 2007.
- Narayanan, R., and Johnston, D. Long-term potentiation in rat hippocampal neurons is accompanied by spatially widespread changes in intrinsic oscillatory dynamics and excitability. *Neuron* 56:1061–1075, 2007.
- Rosenkranz, J.A., and Johnston, D. State-dependent modulation of amygdala inputs by dopamine-induced enhancement of sodium currents in Layer V entorhinal cortex. *J. Neurosci.* 27:7054–7069, 2007.
- Andrsfalvy, B.K., Makara, J.K., Johnston, D., Magee, J.C. Altered synaptic and non-synaptic properties of CA1 pyramidal neurons in *Kv4.2* KO mice. *J. Physiol.* 586(16):3881–3892, 2008.
- Narayanan, R., and Johnston, D. The *h* channel mediates location-dependence and plasticity of intrinsic phase response in rat hippocampal pyramidal neurons. *J. Neurosci.* 28:5846–5860, 2008.
- Shin, M., Brager, D.H., Jaramillo, T.C., Johnston, D., and Chetkovich, D.M. Mislocalization of *h* channel subunits underlies *h* channelopathy in temporal lobe epilepsy. *Neurobiol. Dis.* 32:26–36, 2008.
- Rosenkranz, J.A., Frick, A., and Johnston, D. Kinase-dependent modification of dendritic excitability after LTP. *J. Physiol.* 587:115–125, 2009.
- Routh, B. Johnston, D., Harris, K.M., and Chitwood, R. Anatomical and electrophysiological comparison of CA1 pyramidal neurons of the rat and mouse. *J. Neurophysiol.* 102:2288–2302, 2009.
- Dembrow, N.C., Chitwood, R.A., and Johnston, D. Projection-specific neuromodulation of medial prefrontal cortex neurons. *J. Neurosci.* 30:16922–16937, 2010.

- Narayanan, R., Dougherty, K., and Johnston, D. Calcium store depletion induces persistent perisomatic increases in the functional density of h channels in hippocampal pyramidal neurons. *Neuron* 68:921–935, 2010.
- Narayanan, R., and Johnston, D. The h current is a candidate mechanism for regulating the sliding modification threshold in a BCM-like synaptic learning rule. *J. Neurophysiol.* 104:1020–1033, 2010.
- Lewis, A.S., Vaidya, S., Blaiss, C.A., Liu, Z., Stroub, T., Brager, D.H., Chen, X., Bender, R.A., Estep, C.M., Popov, A.B., Kang, C., Van Veldhoven, P.P., Bayliss, D.A., Nicholson, D.A., Powell, C.M., Johnston, D., and Chetkovich, D.M. Deletion of the HCN channel auxiliary subunit TRIP8b impairs hippocampal Ih localization and function and promotes antidepressant behavior in mice. *J. Neurosci.* 31:7424–7440, 2011.
- Brager, D.H., Akhavan, A.R., and Johnston, D. Impaired dendritic expression and plasticity of h-channels in the *fmr1*–*y* mouse model of fragile X syndrome. *Cell Reports* 1:225–233, 2012.
- Dougherty, K.A., Islam, T., and Johnston, D. Intrinsic excitability of CA1 pyramidal neurons from the rat dorsal and ventral hippocampus. *J. Physiol.* 509:5707–5722, 2012.
- Kim, C.S., Chang, P.Y., and Johnston, D. Knockdown of HCN1 channels in dorsal hippocampus enhances network activity and leads to anxiolytic- and antidepressant-like effects. *Neuron* 75:503–516, 2012.
- Brager, D.H., Lewis, A.S., Chetkovich, D.M., and Johnston, D. Short-term potentiation and heterosynaptic plasticity in CA1 neurons from mice lacking the h-channel auxiliary subunit TRIP8b. *J. Neurophysiol.* 110:2350–2357, 2013.
- Dougherty, K.A., Nicholson, D.A., Diaz, L., Buss, E.W., Neuman, K.M., Chetkovich, D.M., and Johnston, D. Differential expression of HCN1 and HCN2 subunits alters voltage-dependent gating of h-channels in CA1 pyramidal neurons from the dorsal and ventral hippocampus. *J. Neurophysiol.* 109:1940–1953, 2013.
- Kalmbach, B.E., Chitwood, R., Dembrow, N., and Johnston, D. Dendritic generation of mGluR mediated slow afterdepolarization in layer 5 neurons of prefrontal cortex. *J. Neurosci.* 33:13518–13532, 2013.
- Park, Y.Y., Johnston, D., and Gray, R. Persistent Na<sup>+</sup> current mediates neuronal excitability in hippocampal CA1 pyramidal neurons. *J. Neurophysiol.* 109:1378–1390, 2013.
- Routh, B., Johnston, D., and Brager, D.H. Loss of functional A-type potassium channels in the dendrites of CA1 pyramidal neurons from a mouse model of fragile X syndrome. *J. Neurosci.* 33:19442–19450, 2013.
- Vaidya, S.P., and Johnston, D. Temporal synchrony and gamma to theta power conversion in the dendrites of CA1 pyramidal neurons. *Nature Neurosci.* 16:1812–1820, 2013.
- Clemens, A.M., and Johnston, D. Age- and location-dependent differences in store depletion induced h-channel plasticity in hippocampal pyramidal neurons. *J. Neurophysiol.* 111:1368–1382, 2014.
- Edwards, J., Daniel, E., Kinney, J., Bartol, T., Sejnowski, T., Johnston, D., Harris, K.M., and Bajaj, C. VolumeRover: Enhancing surface and volumetric reconstruction

- for realistic dynamical simulation of cellular and subcellular function. *Neuroinformatics* 12:277289, 2014.
- Moya, M.V., Siegel, J.J., McCord, E.D., Kalmbach, B.E., Dembrow, N., Johnston, and Chitwood, R.A.. Species-specific differences in medial prefrontal projections to the pons between rat and rabbit. *J. Comp. Neurol.* 13:3052–3074, 2014.
- Ashhad, S., Johnston, D., and Narayanan, R. Activation of inositol trisphosphate receptors is sufficient for inducing graded intrinsic plasticity in rat hippocampal pyramidal neurons. *J. Neurophysiol.* 113:2002–2013, 2015.
- Dembrow, N.C., Zemelman, B.V., and Johnston, D. Temporal dynamics of L5 dendrites in medial prefrontal cortex regulate integration versus coincidence detection of afferent inputs. *J. Neurosci.* 35: 4501–4514, 2015.
- Desai, N.S., Siegel, J.J., Taylor, W., Chitwood, R.A., and Johnston, D. Matlab-based automated patch clamp system for awake behaving mice. *J. Neurophysiol.* 114:1331–1345, 2015.
- Kalmbach, B., Johnston, D., and Brager, D.H. Cell-type specific channelopathies in the prefrontal cortex of the *fmr1-/-y* mouse model of fragile X syndrome. *eNeuro* 2(6):1–21, 2015.
- Kim, C.S., and Johnston, D. A1 adenosine receptor-mediated GIRK channels contributes to the resting conductance of CA1 neurons in the dorsal hippocampus. *J. Neurophysiol.* 113:2511–2523, 2015.
- Siegel, J.J., Taylor, W., Gray, R., Kalmbach, B., Zemelman, B.V., Desai, N.S., Johnston, D., and Chitwood, R.A. Trace eyeblink conditioning in mice is dependent upon the cerebellum, amygdala, and dorsal medial prefrontal cortex: Behavioral characterization and functional circuitry. *eNeuro* 2(4):1–29, 2015.
- Malik, R., Dougherty K.A., Parikh, K., Byrne, C., and Johnston, D. Mapping the electrophysiological and morphological properties of CA1 pyramidal neurons along the longitudinal hippocampal axis. *Hippocampus* 26:341–361, 2016.
- Desai, N.S., Gray, R., and Johnston, D. A dynamic clamp on every rig. *eNeuro* 4:1–17, 2017. <https://doi.org/10.1523/ENEURO.0250-17.2017>
- Kalmbach, B.E., Gray, R., Johnston, D., and Cook, E.P. A systems-based analysis of dendritic nonlinearities reveals temporal feature extraction in mouse L5 cortical neurons. *J. Neurophysiol.* 117:2188–2208, 2017.
- Malik, R., and Johnston, D. Dendritic GIRK channels gate the integration window, plateau potentials and induction of synaptic plasticity in dorsal but not ventral CA1 neurons. *J. Neurosci.* 37:3940–3955, 2017.
- Routh, B.M., Rathour, R.K., Baumgardner, M.E., Kalmbach, B.E., Johnston, D., Brager, D.H. Increased transient sodium conductance and action potential output in layer 2/3 prefrontal cortex neurons of the *fmr1-/-y* mouse. *J. Physiol.* 595:4431–4448, 2017.
- Siegel, J.J., Chitwood, R.A., Ding, J.M., Payne, C., Taylor, W., Gray, R., Zemelman, B.V., and Johnston, D. Prefrontal cortex dysfunction in Fragile X mice depends on the continued absence of Fragile X Mental Retardation Protein in the adult brain. *J. Neurosci.* 37:7305–7317, 2017.
- Kim, C.S., Brager, D.H., and Johnston, D. Perisomatic h-channels regulate depressive behaviors following chronic unpredictable stress. *Molec. Psych.* 23:892–903, 2018.

- Arnold, E.C., McMurray, C., Gray, R., and Johnston, D. Epilepsy-induced reduction in HCN channel expression contributes to an increased excitability in dorsal, but not ventral, hippocampal CA1 neurons. *eNeuro* 6:1–22, 2019.
- Baowang, L., Routh, B.N., Johnston, D., Seidemann, E., and Priebe, N.J. Voltage-gated intrinsic conductances shape the input-output relationship of cortical neurons in behaving primate V1. *Neuron* 107:185–196, 2020.
- Brandalise, F., Kalmbach, B.E., Mehta, P., Thornton, O., Johnston, D., Zemelman, B.V., and Brager, D.H. Fragile X mental retardation protein bidirectionally controls dendritic  $I_h$  in a cell-type specific manner between mouse hippocampus and prefrontal cortex. *J. Neurosci.* 40:5327–5340, 2020.
- Kim, C.S., and Johnston, D. Antidepressant effects of (S)-ketamine through a reduction of hyperpolarization-activated current  $I_h$ . *iScience*, 2020. <https://doi.org/10.1016/j.isci.2020.101239>
- Gray, R., and Johnston, D. Sodium sensitivity of  $K_{Na}$  channels in mouse CA1 neurons. *J. Neurophysiol.* 125:1690–1697, 2021. <https://jneurophysiol.podbean.com/e/sodium-sensitivity-of-kna-channels-in-mouse-ca1-neurons>
- Routh, B., Brager, D.H., and Johnston, D. Ionic and morphological contributions to the variable gain of membrane responses in layer 2/3 pyramidal neurons of mouse primary visual cortex. *J. Neurophysiol.* 128:1040–1050, 2022.