

## An interview with Professor G. Bard Ermentrout

Neil C. MacLachlan

### Biographical sketch

Bard Ermentrout is a mathematician and theoretical biologist known for his influential work in computational neuroscience and networks of coupled oscillators. Born in 1954, he earned his bachelor's and master's in mathematics from Johns Hopkins University in 1975, and obtained his PhD in Biophysics and Theoretical Biology from the University of Chicago in 1979 advised by Jack Cowan. He has been recognized with a SIAM fellowship, a Sloan fellowship, the Math Neuroscience Prize, and most recently the Moser Prize.

Neil C. MacLachlan: *Could you describe your early interest in math and how it developed over time?*

G. Bard Ermentrout: Well, I was the best kid in mathletes in high school. I was always pretty good at math. When college came around, I thought I would be a chemist. I was also good at chemistry. I still kept my hand in math. I was taking an advanced calc course at Johns Hopkins. There were only three kids in the class, so it was really cool. I also took a course in advanced inorganic chemistry—there was all this stuff about molecular orbitals and group theory. That's when I decided to switch to pure math, because I really liked all that group theory. I still sort of had the idea that I might go to med school. I did pretty well. I took a lot of graduate courses as an undergrad, enough that I managed to get a master's degree at the same time as my bachelor's in three years.

I did research in number theory. I was trying to do some stuff on Euler's phi function. I think I wrote something in some small undergraduate journal. Me and two of my best buddies in college were also the editors of the undergraduate science bulletin. There wasn't any math in that, but it was all people that did chemistry and biochemistry and things like that. Some of those people actually went on to become esteemed scientists.

When it came time to graduate from college, I was still thinking of being a pre-med because I didn't think that getting a job in academia and math was tenable. So I took the MCAT, but I also took the GREs. I started looking into why math

would be useful if you were in medicine. There really wasn't too much. There was some really awful slop on theoretical biology. There was a series of volumes called "Towards a Theoretical Biology" that came out in 1968. There was this article in it by Rene Thom about applying catastrophe theory to problems in biology. I thought, this is really awesome.

When it was time to apply for grad school and med school, this conference in Chicago actually had a program in theoretical biology at the University of Chicago so I decided on a lark to apply to that. I also applied to Yale to work with some guy in number theory, because I was still really interested in it. In fact, I had done most of the exercises in Borevich and Shafarevich, which is a famous number theory book. In any case, I got into both programs. I ended up going to University of Chicago and started working with Jack Cowan and right around that time was when Heinrich Klüver's book was reprinted on mescaline and hallucinations. At the same time David Sattinger did a sabbatical at Chicago in the math department and I sat in on a series of lectures he had using group theory and symmetry to study bifurcation theory. Bifurcation theory was super hot then with pattern formation and everything, so that led to my thesis work. That's sort of how I got into theoretical biology.

NCM: *You have self-described as a fake mathematician. What do you mean by this?*

GBE: Well, my PhD is in biophysics and theoretical biology. So I'm sort of not really technically a trained mathematician. Pitt's been really good about that because, you know, they hired People like David Swigon, who doesn't have a PhD in math and Brent Doiron, who did not have a PhD in math. Carson Chow, who is a PhD in physics. So they've been pretty good about accepting people so it's worked out.

NCM: *Could you explain the significance of your most notable research contributions?*

GBE: Certainly my most cited work is my book on XPP, but I guess there's a couple of things I've done that I think are notable. One is the hallucinations work, of course. That started when I was a grad student with Jack. I would say probably my most notable work is the stuff I've done on oscillations. That was a collaboration that I started with Nancy Kopell. Everybody always thinks she was my postdoc advisor, but she wasn't. There was a conference in 1978 at the University of Utah. Art Winfree gave a series of lectures on what he called 24 hard problems on 24-hour rhythms. They weren't really on 24-hour rhythms, but they were on rhythms, oscillations and stuff like that. That really got me excited about oscillations. In my postdoc I solved three of those problems that Art had posed. One of the best known collaborations is the one with Nancy Kopell. I think we wrote 22 papers together. That happened when I was working on this problem of something called frequency plateaus. In the intestine, which is a chain of coupled oscillators, if the frequency gradient gets too great the

oscillators split up. I was trying to understand that so I had worked out some sort of heuristics and stuff, but I couldn't prove it. I had known Nancy's work from stuff she had done on these Lambda-Omega systems with Lou Howard, which is a set of chemical oscillators. It happened that she was going to be down in Washington, D.C. for an NSF panel. So I met her. I think we met at the hotel bar and I explained the problem to her and she says, oh, that sounds like it should be pretty easy. Then a couple of days later, she called me up and she says she didn't think it was true and I said, no, no, it's definitely true and she says, if it's true, it's going to be a lot harder. I had a lot of know-how and she is really good at geometry and geometric thinking, while I'm really a whiz at linear algebra. So we managed to figure out the eigenspectrum and then she figured out where all the invariant manifolds were. That was our first big paper on frequency plateaus in oscillations. That was meant to be a model of the small intestine intestine. That led to work with a group of people on lamprey, which can also be modeled as a chain of oscillators. We wrote a whole series of papers on what happens in large  $n$  limits of nearest neighbor coupled oscillators. That was a really tough mathematical paper. Then we wrote a whole bunch of articles involving this group of experimentalists who worked on lamprey. Then Nancy and I went on to write a couple of little papers on cortical rhythms, which turned out to be highly cited.

NCM: *Are there any personal anecdotes or stories from your career that you'd like to share?*

GBE: Let me think of some. Oh, so right before I started at Pitt there was a conference in July of 1981. Jim Keener organized this conference in the desert in Utah, and we had to hike about 10 miles with 40 pound frame packs into the desert. I gave my lecture on a large sheet of paper with some markers in a cave. So that was an interesting conference. There was a second one, but I decided I didn't want to go. The thing was that when we were going back to to meet the van to pick us up. Hans Othmer lost the keys to the van so we had to hike another five miles to find another pickup location. I never forgave Hans for that.

NCM: *What advice would you give to high school students, undergrads and graduate students?*

GBE: Honestly students these days seem so career focused that I don't know, it feels like they suck out all the joy of doing math, but I guess it's just the way things are now. I mean, I don't think that the job situation is great. So I guess my big advice to any graduate student or undergraduate student is to get to know some ML. I'm not going to learn it, but I think that you're going to have to learn it. Otherwise, it's

going to take your job. I worry about what's happening now with respect to AI and all that stuff.

I would just say find somebody that's willing to work with you, start research early, especially if you're an undergrad. Because students always ask me to write letters for them for grad school and the only knowledge I have of them is from classes. You got an A in my class, but so did four other people. I can't really say anything that differentiates you from anybody else. That's why I think it's really important to find a mentor to do research with. For graduate school get your prelims done early and find an advisor who you're compatible with. Don't switch gears late in the business because it's going to be really hard to catch up. It's good to know sort of what you want to do. For me, I went into grad school knowing I was going to work with one person and that was it. I don't think that's the common thing in math, but that's a really common thing in biology and neuroscience. In math, there's a lot more classes. I guess my advice for grad students is try and get some papers out, find an advisor you're compatible with, and go to conferences.

NCM: *Could you describe the development of mathematical neuroscience as a field and note any key advances and influential people?*

GBE: Well, I mean you can say it started in some sense with Hodgkin and Huxley. They developed a mathematical model for the action potential in the 1950s. But subsequently there wasn't much really, you know, it wasn't a field at all. It was just these guys that did this stuff. That started to change a bit in the late 60s. Some people like Steve Grossberg and then Jack Cowan and Hugh Wilson wrote their seminal papers in '72 and '73 on the Wilson-Cowan equations. Then Shun'ichi Amari wrote this amazing paper in '77. Grossberg wrote a whole bunch of papers, I'd say he hasn't gotten as much recognition as he should. I guess the result was there was these different branches of theoretical neuroscience. There was the more physiology type stuff like what John Rinzel was working on. He wrote a really cool paper in 1980 with Rita Guttman, where they used simulations of the Hodgkin-Huxley equations to make some predictions about multi-stability between a fixed point and a limit cycle, and then they experimentally tested it. Jack, Hugh, and Amari were doing networks in the meantime. In the 80s, I think Hopfield published his first paper on recurrent networks. That was a whole different group of people. There was this sort of neural networks side that developed. First came the perceptron, and then Kunihiro Fukushima created the neocognitron. I remember these things because I went to a conference in Tokyo in 1982. Fukushima was there and Amari. At that point, people were starting to use these things to try and do computations. There was the famous exclusive or logic gate problem, you couldn't make a perceptron which would answer

that. That's when the idea of hidden layers came in.

Then there is the whole Jay McLelland and David Rumelhart stuff, which is the branch that led to Geoffrey Hinton and all the AI stuff. I was more interested in mechanisms and behavior.

I'd say computational neuroscience really started to take off in the 80s. In fact, Jim Bower and Christof Koch started this. They decided that this field was developed enough that there should be a course on it. That was in 1988, the first Woods Hole course on Methods in Computational Neuroscience. John Rinzel was invited to lecture there and that's how we wrote our chapter. I wrote some code to simulate the Morris Lecar equations so he could use that in his lectures and that sort of led to XPP. Ultimately that course started to train a new generation of computational and theoretical neuroscientists.

The first generation were people like Jack Cowan and Michael Arbib. Arbib was doing a lot of stuff on the cerebellum. Then there was Amari and Fukushima. That was that generation along with John Rinzel. Then I think I was the second generation. John Rinzel had been in it since the 70s. Since then it's sort of developed into its own thing.

There's a lot of conferences now. There is the CNS meeting, that was one of the first conferences. I think, again, Jim Bower started that. Jim really pushed this field to the rest of the world. He wrote a software program called Genesis, which competed with another software program called Neuron. Neuron was developed by Mike Hines, who was a postdoc at Chicago when I was a grad student. There's a lot of connections with all that old school stuff.

NCM: *You wrote an influential textbook in the field. Why did you decide to do it and what were you thinking about as you wrote it? In retrospect, if you could change anything about it, what would you change?*

GBE: Oh, let's see. Well, I've been asked multiple times to do a revised version. I would put more applications in, maybe some more stuff about pathology and disease, you know, Parkinson's, epilepsy and things like that. I wrote it mostly because I had lecture notes from teaching a comp neuro course over the years. I wrote a review in a journal called "Progress in Theoretical Physics" and that was sort of the shell of the book. I think it was like 60 or 70 pages long. It basically started with single cells, networks and reduced modeling. I was chatting with Dave Terman and he said he's going to be on sabbatical. So I said, let's write a book. It came about from lecture notes and earlier work I had done. I wanted one place to put it in.

I think I'm going to try and start another book in the fall because I'm on sabbatical again. It's going to be like a modern treatment of oscillations in biology, sort of like

Winfree's book, but using stuff from Koopman theory and more mathematical. I still haven't quite figured that out yet.

NCM: *What do you see as current active areas within computational neuroscience?*

GBE: Well, a lot of it's data-driven modeling. The technology for experiments has gotten so good that they can do whole brain imaging and all kinds of spatiotemporal stuff. I think that's super exciting. People are learning that brain activity is really organized not in synchrony, but in the spatiotemporal dynamics like waves. A challenge is going to be to figure out what the use of that is. There are the same issues with rhythms. People have been studying rhythms for, I don't know, 40 years, but does anybody have a good theory about what they're good for? I think the same thing can be said for these spatiotemporal patterns. I have some ideas, but, you know, are they just artifacts or are they actually real?

NCM: *Where do you see mathematical neuroscience going in the future?*

GBE: I think it's going to go much more to machine learning. That will be more computational neuroscience. Mathematical neuroscience is more of a separate branch. I think there's going to be more tools developed for studying spatiotemporal stuff because that's needed. I can already see there's lots of places where neuroscientists have pushed mathematics. A whole a lot of the work on canards has been motivated by the separations of time scales. I wrote a paper with Bryce McLeod in the '90s on the existence of traveling waves in a non-local equation, and that spawned a little mini industry of people using that same approach to do lots of different kinds of traveling wave problems with non-local coupling. Non-local coupling is difficult since if you're looking for traveling waves, it doesn't reduce to a set of ODEs where you can use geometric methods like shooting and intersections of stable and unstable manifolds because they're infinite dimensional problems— so it required a different toolkit. From the point of view of working with experimentalists I think large-scale data sets and ways to analyze them with machine learning is valuable. For example, there's a whole lot of software out there that allows you to track behaviors in very fine detail based on video images.

NCM: *Are there any open problems that you'd like to bring to the attention of the math community?*

GBE: There's this problem that's really been bugging me, but it's very, very specific. It has to do with limits of coupling lengths in certain systems of non-locally coupled oscillators. There is this paper that I wrote with a postdoc Andrea Welsh. I was able to do something with it because I could convert this integral equation to an ODE, but it's for a very specific type of coupling and a very specific interaction function.

It seems to me that there should be something more general that can be done for this. There's something called inner and outer expansions in perturbation theory. The outer equations are really straightforward and very generalizable, but to try and to resolve the boundary value problems is something that I just don't know how to do. I think any of these non-local existence of patterns and things in these non-local problems is a very interesting problem. Another open problem which Jon Rubin has been doing some work on is transient behavior.

NCM: *How have you been able to balance theoretical, experimental, and computational approaches in your research?*

GBE: Well, for me, it was easier than some because my training was a pure math undergrad and masters and then a PhD in biophysics. I tell my students that if you want to work with experimentalists you have to learn their language, because they're not going to learn your language.

NCM: *You have a number of really interesting hobbies. Could you talk about a few of them?*

GBE: I love to cook and cooking led to gardening because you want certain kinds of vegetables and things like that that you can't get. In particular, peppers and good tomatoes. I also collect fountain pens. They're really cool. Some of my fountain pens were made in 1901, so 120 years old or so. They still work, they're just beautiful examples of instruments that are also practical. I still do all my lecture notes in fountain pen.

NCM: *You've given a spooky math talk every Halloween for many years at Pitt. Could you talk about this bit? What are some important open questions in Halloween math?*

GBE: It came about because this guy, Robert Smith, had started talking about zombies as a disease model. He was in Canada and he was putting together this book on the mathematics of zombie attacks. I think this is right around the time the book *World War Z* came out. So I decided, okay, I'll get in on this. My son was really into zombies and things like that. He was a philosophy major at Pitt. So I started chatting with him and he gave me some ideas for modeling. That's how I put together my first zombie model. That led to a series of different zombie models that I decided I could present at a Halloween talk. Then there was another undergrad who was a joint math and forensic science major. There was this dude in Slavic studies that teaches this course on vampires, and this student she took that course as part of her gen-eds. So she wanted to do a model for vampires. That led to a chapter that was going to come out in another book that this guy had called *monster math*, but I don't think it ever came out. Then one of the cool things was I put the zombie model

together with the vampire model with the assumption that there was no interaction between the zombies and vampires, it was all only through the humans. I just put the two models together and bam, I got chaotic behavior, which is really cool. We get the zombies coming and then the humans dying and then the vampires coming up. So open problems, well, where do werewolves fit in on this? I said a little bit in the last Halloween talk. I introduced some werewolves. Because werewolves have temporal periodicity in them, they only come out once a month so they can create some interesting dynamics.

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