Accomplishments and future plans in scholarly & creative work

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Introduction. My interest lies in the interdisciplinary field of Mathematical Biology. My general research objective is to understand the collective behavior of biological networks. I am particularly interested in employing and developing mathematical models, techniques in dynamical systems and control theory, and computational methods to model and analyze biological phenomena. I have been working on a variety of biological networks, such as (i) small neural circuits in invertebrate thoracic ganglia called central pattern generators (CPGs) that are responsible for generating locomotive activities, (ii) a population of bacteria (mostly, E.coli) that move toward food or flee from poison, and (iii) coupled scolopale cell and space of auditory systems. While the biological problems I study are quite diverse, they are unified by their common mathematical features. Indeed, their collective behavior (such as synchronization) can arise spontaneously from four main components in the network: (i) the dynamics of the isolated units, (ii) the properties of the interconnection among the units, (iii) the topological structure of the network, and (iv) exogenous control inputs. My recent research activity branches in 4 directions, as I summarize below.

Mentoring. Currently, I supervise three graduate students who are involved in the first three projects listed below. Most of my research projects require numerical investigations that undergraduate students can carry. I advised one undergraduate student last year. Two postdocs have been involved in two of the following projects; they were both our graduate students when I started the projects with them. I also mentored or co-mentored a graduate and an undergraduate student during my postdoc.

A. Contraction theory for nonlinear systems with applications to network synchronization

Introduction. Global stability is a central research topic in dynamical systems. Stability properties are typically defined in terms of attraction to an invariant set, for example, to an equilibrium or a periodic orbit, often coupled with a Lyapunov stability requirement that trajectories that start near the attractor must stay close to the attractor for all future times. A far stronger requirement than attraction to a pre-specified target set is to ask that any two trajectories should converge to each other exponentially and with no overshoot (i.e., the difference between the trajectories always decreases as time evolves) or, in more abstract mathematical terms, that the flow be a contraction map in the state space. Checking stability properties often involves constructing an appropriate Lyapunov function, which, in turn, requires a priori knowledge of the attractor location. In contrast, contraction-based methods do not require prior knowledge of attractors. Instead, one checks a property of the vector field defining the system, which guarantees exponential contractivity of the induced flow. A system with such property is called a contractive system. Contractivity is not a topological but a metric

property: it depends on the norm being used, in close analogy to the choice of an appropriate Lyapunov function. The proper tool for characterizing contractivity for nonlinear systems is provided by the matrix measures, also called logarithmic norms (see e.g. [1, 2]), of the Jacobian of the vector field, evaluated at all possible states. The idea of contraction theory is a classical one and can be traced back to the work of Banach in 1922 [3] and [4, 5, 6, 7, 8, 9, 10]. In control theory, the field attracted much attention after the work of Lohmiller and Slotine [11], and the important advances by others [12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23]. These papers reflect the power of contraction techniques for the study of not merely stability, but also observer problems, nonlinear regulation, and synchronization and consensus problems in complex networks.

This project initiated with my Ph.D. advisor, E. Sontag (2012–2015) and later developed with Y. Shafi & M. Arcak & E. Sontag (2014), E. Davison & B. Dey & N. Ehrich Leonard (2018), and V. Shrivastava (2021).

Main contributions on contraction theory.   Turing instability is a type of instability arising from diffusive coupling. That is, a stable system may lose its stability when diffusion is added or connected to another system. Inspired by Turing instability and using semi-inner products and logarithmic Lipschitz constants in Banach spaces, we studied the effect of three types of perturbations (either through coupling to the neighbors or exogenous input) on contractive nonlinear ODEs. In [24] we considered diffusively coupled networks and showed that coupling does not affect the contractivity of isolated ODEs. Then, we studied reaction-diffusion PDEs and showed that diffusion does not affect the contractivity of underlying ODE. Later in [25], I showed how a noisy exogenous input might foster contractivity in Itô stochastic differential equations. As mentioned above, choosing a norm is essential to check contractivity. Semi-inner products and logarithmic Lipschitz constants in Banach spaces allowed us to extend existing results based on L^2 norms to L^p norms for $1 \leq p \leq \infty$.

Main contributions on applications of contraction theory to networks synchronization.
Since in contractive systems any two solutions exponentially converge to each other and diffusive types of coupling (any skew-symmetric coupling of the form $H(x_i, x_j) = h(x_i) - h(x_j)$) vanish on a synchronization manifold ($x_i = x, \forall x_i$), a network of diffusively coupled contractive systems automatically synchronizes. Therefore, to study synchronization, we do not assume contractivity of the individuals. Instead, based on contraction theory, we find a condition for global exponential stability of synchronization solutions that depends on the intrinsic dynamics of individuals, coupling functions, and the structure of the underlying graph. We studied exponential stability of (i) synchronization solutions in diffusively coupled homogeneous systems [26], (ii) cluster synchronization solutions in diffusively coupled heterogenous systems [27], and (iii) stochastic synchronization in stochastic networks [28]. Analogue to the discrete networks, we studied exponential stability of spatial uniform solutions of reaction-diffusion PDEs with Neumann boundary conditions [29, 30, 31].

On going & future projects. Despite an intense effort to understand synchronization behaviors in *diffusively* coupled systems, there are few analytical approaches to understanding them when they are coupled *non-diffusively*. Motivated by neural networks in which the neurons are connected through chemical synaptic coupling, our first goal is to find conditions that guarantee the global exponential stability of synchronization solutions in non-diffusively coupled networks. The neurons may connect through chemical synapse (non-diffusive), gap junction (diffusive), or ephaptic coupling (coupling through the environment). Our second goal is to understand the simultaneous interaction of these types of coupling in *multiple-layer* networks. *This project is part of the Ph.D. thesis of my student, Fatou Ndow.*

B. Small neural networks

B1. Coupled CPGs & gait patterns in insects' locomotion

Introduction. Central Pattern Generators (CPGs) are groups of neurons that produce rhythmic motor patterns, such as walking. Walking is the coordinated movement of several legs, where coordination is required between the legs (inter-leg coordination) and between the segments of a single leg (intra-leg coordination). Insects are capable of complex walking gaits in which various combinations of legs can be simultaneously in stance and swing. It has been observed that fast-running insects employ a tripod gait with three legs lifted off the ground simultaneously in a swing. In comparison, slow-walking insects use a tetrapod gait with two legs lifted off the ground simultaneously. Fruit flies use both gaits and exhibit a transition from tetrapod to tripod at intermediate speeds. Addressing these problems of what CPGs configurations produce gait patterns and what causes the gait transition benefits neuroscientists by providing insights into the underlying mechanism of CPGs and their coupling configurations. It also benefits engineers by suggesting new approaches for building legged robots.

Main contributions. In this project, *developed with P. Holmes and V. Srivastava,* by focusing on the inter-leg coordination, we identified, characterized, and simulated underlying neural mechanisms and networks of insect CPGs that produce insect locomotion coordination patterns. We investigated the dependence of the gait patterns on walking velocity.

In [32], we considered six *homogeneous* coupled CPGs described by ion-channel bursting neuron model (developed in [33, 34]). We assumed that a network of CPGs governs each leg, and the legs are weakly connected to their nearest neighbors (this assumption is supported by studies of freely running cockroaches [35]). A system of 24 equations (3-dim ion-channel bursting model and 1-dim inhibitory synaptic coupling dynamics for each leg) describe these 6-coupled CPG oscillators. Employing phase reduction and assuming contralateral symmetry (motivated by experimental data), we reduced the 24 equations to 2 phase-difference equations. We showed that bifurcations occur from *multiple* stable tetrapod gaits to a *unique* stable tripod gait as speed (the CPGs' oscillatory period) increases. However, these multiple stable tetrapod patterns generated from this model at low speed are not typically observed as insect gaits. In a follow-up paper [36], by adding a *heterogeneous* external input to each oscillator, we modified the bursting neuron model so that its corresponding phase oscillator system produces only one stable gait at each speed, specifically a unique stable tetrapod gait at low speed, a unique stable tripod gait at high speed, and a unique branch of stable transition gaits connecting them. This suggests that control signals originating in the brain and central nervous system can modify gait patterns. In both [32] and [36], we validated our models by a set of data taken from fruit flies walking and running.

On going & future projects. Knowing that the data taken from insect locomotion are quite noisy, a natural next step is to incorporate stochasticity in the model. To this end, we first need to understand the dynamics of coupled noisy oscillators and their phase reduction. In [37], using techniques from Itô Calculus and the notion of second-order PRCs, we developed a stochastic phase reduced model and studied the effect of noise on a single noisy oscillator. As an extension, we will consider two (or more) coupled oscillators with additive white noise, derive the coupled phase model, and study the influence of the second-order PRCs on their synchronization and phase locking. This approach would help to understand the gait transition in the presence of noise.

On going & future projects. In our previous work, the focus was only on the coordination between the legs. We assumed that each leg in insects is governed by a network of CPGs and explored the

generation of various gait patterns and their transitions. A complex six-leg model for stick insect locomotion has been developed by S. Daun and her collaborators (see [38] and references therein). Although this model successfully produces various gait patterns and the transition between them, an in-depth analysis of how these gaits are generated is missed. The main objective is to employ techniques from dynamical systems and bifurcation theory to analyze the existing network model and understand how the coordination between the segments of a single leg and the coupled legs are produced and controlled by any of the key sub-networks. *In this project, I collaborate with J. Rubin and S. Daun, and supervise a Ph.D. student, Parker Evans.*

B2. Unidirectional Coupled FitzHugh Nagumo

Introduction. Efforts to gain insight into the complex dynamics of neural networks benefit from a detailed understanding of each neuron and its interactive dynamics. To this end, we analyze the complex dynamics that emerge in networks of coupled neuronal oscillators described by the FitzHugh-Nagumo (FHN) model. The FHN model is a simple two-dimensional model which captures key properties of the activation and deactivation dynamics of the neuronal action potential. Using bifurcation theory and geometric singular perturbation theory and leveraging multiple time scales in the dynamics of neurons, we identify the possible behavioral regimes of the oscillators in the network. This work furthers the understanding of the dynamics of coupled oscillatory neurons.

Main contribution. In [39], we analyzed the dynamics of two coupled FHN model neurons in a setting where the first FHN model has a constant external input I, the second FHN model has no input, and there is a unidirectional coupling with strength γ from the first FHN model to the second. We rigorously characterized all of the different regions of dynamic behavior for the two-FHN system in I-γ space. We proved new necessary conditions in terms of both I and γ for the existence of canards and MMOs. We leveraged this result to find a similarly new sufficient condition for phase locking and extend to systems of FHN models in directed tree networks. *In this project, I collaborated with E. Davison, B. Dey, and N. Ehrich Leonard. I co-mentored Davison, who was a graduate student at Princeton University.*

On going & future projects. Motivated by the FHN model with periodic input, we study the bursting behavior of a class of $4-$dimensional slow-fast system with three time scales. First, we numerically derive a bifurcation diagram of the FHN model by varying the frequency and amplitude of the input and observe that as the frequency decreases and the amplitude increases, the number of spikes in the burst increases. Using geometric singular perturbation theory and computing critical and super-critical manifolds, we analyze the corresponding spike-adding mechanism for three ranges of values for the frequency. *This is joint work with R. Curtu and P. Melland. Melland was a graduate student at U. Iowa when we started this project. Hw is a postdoc at Southern Methodist University.*

C. Ion Transport Mechanisms in Coupled Sensory Epithelia

Introduction. There is significant diversity in auditory mechanoreceptor structure across phyla; however, in most animals, a precondition for their operation is a high extracellular potassium concentration, $[K^+]$. An inability to generate a sufficiently high $[K^+]$ in the endolymph, the cochlear fluid that bathes the stereocilia of hair cells in mammals, leads to deafness. Johnston's organ (the inner ear of Drosophila melanogaster) is comprised of mechanosensory cells termed scolopidia and can serve as an excellent model for the mammalian cochlea. The goal is to develop a mathematical model based on experimental data that accounts for the ion distributions in scolopidia. Models that incorporate

the flux of ions and how they affect ion transport and the development of a membrane potential have been around for a long time. However, for the most part, they do not incorporate ion accumulation. There is a further level of complexity that is not often included and that is water fluxes. This may not seem much of an addition however when it is included one has to start thinking about cellular stability, because water fluxes bring about changes in volume.

The pump-leak model (PLM) [40] is central to comprehending the flux of water in cells. The PLM elegantly explains the asymmetry in sodium and potassium across the membranes of cells of all kinds [41, 42, 43]. In short, the action of the NKA, which pumps 3 sodium out of the cell and 2 potassium into at the expense of one ATP molecule, is to stabilize the volume of the cell. In doing so it establishes a high intracellular potassium concentration, low intracellular sodium and develops a negative membrane potential. The action of the NKA, acts against a Donnan effect induced by impermeant molecules that if left unopposed would lead to swelling and bursting. Central to its role in driving water transport the NKA stabilizes volume by ensuring that the intracellular osmolarity matches that of the extracellular osmolarity, even if there are fluctuations in ion concentrations and osmolarity. The operation of the NKA hence plays a key role in controlling water fluxes.

The CCC are members of the Solute Carrier transporter superfamily, which transport sodium and/or potassium, and chloride across the cell membrane in an electroneutral fashion. There are three types of CCCs: $KCC(1K^+ : 1Cl^-), NCC(1Na^+ : 1Cl^-)$ and $NKCC(1Na^+ : 1K^+ : 2Cl^-)$. The CCCs are secondary transporters that depend on the non-equilibrium ion gradients established by the NKA to drive chloride out of equilibrium, and perturb the equilibria of sodium and potassium. Hence, in the absence of an active NKA, the CCCs cannot drive ion concentrations out of equilibrium.

On going & future projects. In our first manuscript [44], we provided an in-depth analysis of the process of cell volume stabilization and ion homeostasis in a 5-dim algebraic-differential equations PLM where we incorporated the three CCCs explained above and considered intra- and extra-cellular impermeant molecules. Employing techniques from global sensitivity analysis (Sobol index), we examine the effect of main model parameters (e.g., transporters parameters) in cell volume stabilization and ions distribution across a cell membrane. To model $[K^+]$ accumulation in the scolopale space, we represent the scolopidium as two spaces coupled in series: the scolopale cell and the scolopale space, and generalize the PLM to two coupled spaces (containing ten algebraic differential equations). *This is joint work with A. Kay from the department of Biology at U. Iowa. This project is part of the Ph.D. thesis of my student, Kerry Tarrant. An undergraduate student (Ashley Kim) worked on this project for a few semesters.*

D. Bacterial Chemotaxis in Response to Multiple Stimuli

Introduction. The movement of bacteria involves a directed movement (run) and a random turning (tumble). Each individual carries an internal state which may be modeled as evolving according to a system of ordinary differential equations in the presence of time- and space-dependent external signals. In the presence of signals in the environment, the individual changes its direction at random, with a tumbling rate that depends on the internal state, biasing moves toward more favorable environments or away from noxious substances. This random reorientation introduces a stochastic character to the evolution equations, and jump-Markov state-dependent systems model the population behavior of such hybrid systems. The transport equation that describes a jump-markov system is complicated to study mathematically and cannot be validated by typical experimental techniques such as optical density measurements of bacteria in microfluidics chambers. Thus it is of great interest to derive a more straightforward macroscopic equation for the density of a population of bacteria based on their

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dynamics and the way they communicate (their coupling).

Main contributions. In [45, 46], we derived a one-dimensional advection-diffusion equation from the transport equations that describe the collective behavior of a population of bacteria in response to a single stimulus. We examined our theory with both Monte Carlo agent-based simulations and experiments. In [47], we modeled and analyzed the collective behavior of a population of *E. coli* bacteria in response to two stimuli, mainly Serine and Aspartate, in a one- and a two-dimensional environment. It is known experimentally [48] that if the ratio between Tar and Tsr receptors is small, the bacteria move to the gradient of Serine. If the ratio is large enough, they move toward Aspartate. We proved that if the ratio between Tar and Tsr receptors is less than one, the bacteria move to the gradient of Serine; if the ratio is greater than one, they move toward Aspartate. Finally, we examined our theory with Monte Carlo agent-based simulations. *The first part of the project collaborated with E. Sontag & F. Menolascina et al. during my Ph.D.; the second part of the project was a recent collaboration with J. Park, a graduate student at U. Iowa when we started the project. She was a postdoc at the University of Cincinnati when we finalized the paper.*

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