Statements Concerning Research, Teaching and Service

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Research Statement

I use mathematical modeling to study communication and control in complex adaptive biological systems. I am interested in the impact of stochastic fluctuations in nonlinear dynamical systems arising in biology, and in the role of sensorimotor feedback in motor control systems. I use a variety of mathematical ideas in these investigations, including stochastic processes, dynamical systems theory, information theory, and elements of control theory. I have enjoyed productive collaborations with experimental biologists with interests ranging from the biochemistry of bacterial polymers (Miraldi et al., 2008) and chemotaxis in the social amoeba *Dictyostelium discoideum* (Rappel et al., 2002), to the control of feeding movements in the sea slug *Aplysia californica* (Shaw et al., 2015; Lyttle et al., 2017) and the regulation of mammalian breathing rhythms (Diekman et al., 2012, 2017). My research has enjoyed uninterrupted support from the National Science Foundation (DMS-0720142 (2007-2010), DMS-1010434 (2010-2013), EF-1038677 (2010-2013), DMS-1413770 (2014-2017), DEB-1654989 (2017-2020), see C.V. for details). I describe three broad areas of interest below.

Mathematical Neuroscience: Stochastic Neural Dynamics. Mainen and Sejnowski (1995) showed that nerve cells in the brain can generate highly reproducible patterns of spike trains when driven by realistically fluctuating "frozen noise" inputs, even though the same neurons fire imprecise, unreliable spike patterns in response to piecewise constant inputs. In Hunter et al. (1998) we proposed a resonance effect underlying this phenomenon. The interplay of nonlinear (deterministic) and stochastic effects in neural dynamics has fascinated me ever since. As a postdoc in Sejnowski's laboratory I collaborated with experimental neurophysiologists to test the resonance basis for the reliability effect (Thomas et al., 2003), and helped establish protocols for detecting spike time patterns with submillisecond precision using fuzzy clustering techniques and metric space methods (Fellous et al., 2004; Toups et al., 2011, 2012). With experimentalist Klaus Stiefel I quantified the persistence of "phase" information in subthreshold oscillations in cortical cells (Stiefel et al., 2010), and worked with neurophysiologist B. McNaughton on improvements in spike train analysis through smooth (rather than discretized) measures of spike train similarity (Kruskal et al., 2007).

Although my mathematical training is in deterministic dynamical systems, I realized that understanding information processing at the cellular and network levels would require methods from stochastic processes. In Thomas (2011a) I investigated a first passage time problem motivated by the noisy, leaky integrate-and-fire model. With Ermentrout and Anderson I compared exact stochastic simulation methods with the popular, but approximate, Gillespie algorithm (Anderson et al., 2015). Gillespie's algorithm is exact for Markov processes with piecewise constant transition propensities, but must be adapted for stochastic neural models with voltage-dependent ion channel transition rates. With postdoc Deena Schmidt (now tenure track at Univ. Nevada, Reno) we analyzed the "stochastic shielding" (SS) approximation for stochastic hybrid models. SS was first introduced by Roberto Galán (CWRU Neuroscience) as a fast, accurate simplification for stochastic ion channel gating models (Schmandt and Galán, 2012). In contrast to traditional methods, which lump together cliques or eliminate rarely visited nodes, SS preserves the graph structure of the process while projecting within the sample space, eliminating independent noise sources with small impact on model observables (Schmidt and Thomas, 2014). We are extending the method to systems with multiple timescales (Schmidt et al., 2017).

Motivated by stochastic conductance based models, B. Lindner and I developed a new definition of the "phase" of an oscillator appropriate to the stochastic setting. For a deterministic oscillator $\dot{x} = F(x)$ with a stable T-periodic limit cycle solution $x_{\mathrm{LC}}(t) = x_{\mathrm{LC}}(t+T)$, the asymptotic phase function θ maps the stable manifold of the limit cycle to the circle in such a way that $d\theta/dt = \text{const}$ along trajectories. The phase function identifies initial data that converge to the limit cycle along the same asymptotic trajectory; such points lie on an "isochron". For a system with stochastic oscillatory dynamics, the classical definition of the phase function breaks down. Noise prevents convergence to a unique periodic trajectory. Instead, we consider the density $\rho(y, t \mid x, s) = \frac{1}{|dy|}\Pr[X(t) \in [y, y+dy) \mid X(s) = x]$ (for $s < t$). The partial derivatives $\partial\rho/\partial t$ and $-\partial\rho/\partial s$ give rise to the forward and backward (adjoint) operators $\mathcal{L}$ and $\mathcal{L}^\dagger$. In (Thomas and Lindner, 2014) we introduce a notion of "robustly oscillatory" stochastic oscillators in terms of the spectral decomposition of $\mathcal{L}$ and $\mathcal{L}^\dagger$ in a biorthogonal basis of eigenfunctions. We show that the complex angle ψ of the eigenfunction $Q^* = ue^{i\psi}$ of the adjoint operator with slowest decaying nontrivial complex eigenvalue provides a natural generalization of θ to the stochastic case. Our "stochastic asymptotic phase" does not require the underlying mean field oscillator to have a well defined limit cycle. In Giner-Baldó et al. (2017) we use a semianalytic approach to obtain the power spectrum of such a nonlinear stochastic oscillator, for which the underlying deterministic system is a stable heteroclinic cycle lacking a finitely periodic solution.

Mathematical Neuroscience: Mechanisms of Motor Control. From 2006 to the present I have collaborated with Hillel Chiel (CWRU Biology) to understand principles of motor control underlying rhythmic feeding behaviors of the marine mollusk *Aplysia californica.* Central pattern generator networks believed to produce rhythmic behaviors (swimming, walking, breathing, swallowing), are typically modeled as dynamical systems with an orbitally stable limit cycle (a closed, isolated periodic orbit forming the ω-limit set for an open set of initial conditions). Standard limit cycle attractors are robust against small perturbations of the dynamics, but can be insensitive to changing environmental conditions, such as swallowing food with different viscosities or walking on terrain with different degrees of roughness. We have proposed an alternative framework for robust motor control in which the underlying dynamical architecture has an attracting stable heteroclinic cycle structure. In Shaw et al. (2012) we studied the sensitivity of a family of limit cycles undergoing a heteroclinic bifurcation. A significant mathematical contribution of this paper was to exhibit a broad class of piecewise linear (hence, nonlinear) dynamical systems with limit cycle dynamics for which the infinitesimal phase response curve may be computed analytically. An extension of this approach to arbitrary piecewise linear dynamical systems is under review as of this writing (Park et al., 2017). Building on this idea, in Shaw et al. (2015) we constructed a model for the *Aplysia* feeding system using heteroclinic cycling (aka. "winnerless competition", Rabinovich et al. (2001)). We showed that the passage of trajectories near a sequence of unstable fixed points indeed gave the system greater robustness against applied loads, and analyzed the mechanisms underlying robustness further in Lyttle et al. (2017). In a similar spirit, I worked with postdoc Casey Diekman (now tenure track at NJIT) and neurophysiologist C. Wilson (CWRU Pediatrics) to show in (Diekman et al., 2012, 2017) the significance of considering the full closed-loop brain-body system in models for the generation of the breathing rhythm by circuits in the brain stem.

Information Theoretic Analysis of Biochemical Signal Transduction. As a postdoc at the Salk Institute I became interested in biochemical signal transduction, and the potential for information theory to shed light on mechanisms of communication and control in cell biology. In Rappel et al. (2002) we proposed a novel mechanisms for detection of chemical gradients by the social amoeba *Dictyostelium discoideum.* I subsequently developed an information theoretic framework for analysis of concentration and gradient signal detection in chemotaxis (Thomas et al., 2004; Kimmel et al., 2007). Since 2011 I have collaborated with information theorist A. Eckford (York University) on information theoretic analysis of signal transduction pathways. We have introduced a novel communications channel model based on biochemical signal transduction, and rigorously obtained its capacity (Eckford and Thomas, 2013, 2015; Thomas and Eckford, 2016a). We recently extended these results to the case of multiple independent receptors (Thomas and Eckford, 2016b) and more complicated channel models including channel rhodopsin and the nicotinic acetylcholine receptor (Eckford et al., 2016; Eckford and Thomas, 2017). Although information theory provides a powerful perspective for investigating fundamental constraints on biological communications systems, its application to specific biological systems should be approached with care. As a cautionary example, in (Agarwala et al., 2012) we constructed an exactly solvable Markovian perception-action loop model of an organism searching for food, and proved rigorously that the efficacy of information-optimal search strategies (versus utility-optimal and hybrid strategies) was parameter dependent. In other words, information optimization alone is not a sufficient explanatory principle for biological systems, despite the popularity of this assumption.

Editorial contributions include invited perspectives and editorial introductions to special issues on dynamical systems and neural engineering (Chiel and Thomas, 2011), stochastic neuronal networks (Bressloff et al., 2016), information theory in biology (Thomas, 2011b; Dimitrov et al., 2016a,b), and comparison of statistical and dynamical systems perspectives on computational neuroscience (Kass et al., 2017).

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Teaching Statement

My goal as a teacher and mentor is to create the conditions under which my students can reach their fullest potential as scholars, and to communicate my enthusiasm for mathematics, regardless of whether the students are mathematics majors, undergraduates from the sciences and engineering, or mathematics graduate students. My teaching career began in 1990 as a charter corps member in the first years of the Teach for America program. From 1990-92 I taught physics and chemistry to approximately 300 students at the Fine and Performing Arts Magnet High School in Baton Rouge, Louisiana. In total, I bring to the classroom 25 years of teaching experience, ranging from high school to the post-doctoral level. At CWRU I teach a range of courses spanning the discipline of mathematics, from classical elementary analysis (Math 321-322) to applied mathematics courses cross-listed in the departments of biology, neuroscience, and physiology (Math 319/419, Math 378/478). I enjoy teaching at the graduate level (Math 419, 435, 441, and 478) at the service level (Math 223-224), and core courses in the major (Math 321-322, Math 380). From 2006-2017 I have taught 32 semester courses, with a total of 709 students enrolled in that time. The C.V. provides a detailed breakdown of courses and enrollments.

Before coming to Case, I was on the faculty of Oberlin College, a highly rated four-year liberal arts college, where excellence in teaching is the faculty's first priority. While at Oberlin I learned that successful teaching requires thorough preparation, frequent assessment of student learning, and sensitivity to the backgrounds and abilities present in a given class. As a faculty member at Case I have kept these lessons in mind, while making the most of the high level of technical sophistication which is a hallmark of Case's student body.

In teaching service level courses (Math 223: Calculus for Science and Engineering III; Math 224: Ordinary Differential Equations) I find that students benefit when I regularly engage them in hands-on problem solving in addition to traditional lecture. As a CWRU Active Learning Fellow (spring semester 2016) I gained additional skills in designing lessons around a mixture of traditional lecture and group problem-solving approaches. For example, when studying the theorems guaranteeing existence and uniqueness of solutions in the basic ODE course, I have students work in groups to understand how the uniqueness theorem ensures that solutions of the SIR epidemic model remain confined to a certain subset of the (S, I) plane. While teaching the introductory probability course (Math 380) I had students work in small groups using `Matlab` to generate samples from different probability distributions, explore their properties (for example under addition of random variables), conjecture relations (e.g. the density of the sum of two continuous random variables is the convolution of the densities of the summands) that we later established during more traditional lecture-based classes.

As another tool for actively engaging students, I used frequent short quizzes while teaching Analysis (Math 321-322), a course notorious among mathematics majors for its difficulty. When I surveyed student attitudes towards the course during the fifth week of the fall term, a large majority urged me to continue the quizzes; students said the quizzes positively impacted their comprehension. Although the short quiz takes some time away from lecture, I typically was able to use one as a springboard for the other. For example, when discussing differentiation, the quiz question was: *Give an example of a function* $f : \mathbb{R} \to \mathbb{R}$ *that is continuous everywhere, and which is differentiable everywhere except at the* n *points* $x_1 < x_2 < \cdots < x_n$. Immediately following the quiz, we reviewed the students' answers. During the ensuing discussion, exploring the (mistaken) reasoning leading to the *incorrect* answers was particularly valuable to the class. This approach helps expose and resolve common confusions quickly, which I found to be a helpful supplement to the traditional lecture. Students responded positively: in 2010-11 students from Math 321-322 nominated me for the Carl F. Wittke Award for Excellence in Undergraduate Teaching, for which I was one of twelve finalists.

In addition to standard service and core mathematics courses, I have had the opportunity to introduce or re-design two courses integrating teaching and research through a combination of traditional lectures, hands-on computational modeling exercises, and team research projects. Math 378/478 (Computational Neuroscience) introduces students to mathematical modeling of dynamical systems in neuroscience at both a theoretical level and through computational tools such as the NEURON programming environment, Ermentrout's XPP phase plane analysis package, and Matlab. Students in Math 478 met for additional sessions during which we worked through parts of Ermentrout and Terman's graduate textbook, *Mathematical Foundations of Neuroscience*. Math 319/419 (Applied Probability and Stochastic Processes for Biology) introduces students to practical aspects of stochastic modeling in discrete and continuous time and space. The course draws from Pinsky and Karlin's text *An Introduction to Stochastic Modeling* as well as Wilkinson's book *Stochastic Modelling for Systems Biology* and Howard Berg's *Random Walks in Biology.* In 2011 I was honored to receive a T. Keith Glennan Fellowship, a CWRU program recognizing tenure-track faculty for leadership in teaching and scholarship; the fellowship allowed me to expand the hands-on computational component of Math 319/419. The computer exercises introduce students to computational aspects of biological random walks using both Matlab and the MCell simulation platform. Both Math 319/419 and Math 378/478 integrate teaching and research by incorporating current research topics into lectures and exercises as well as through students' course projects.

The teaching mission of the University is not limited to traditional classroom instruction, but includes mentoring of research students at the undergraduate, graduate and postdoctoral levels. During 2006-2017, I have directly supervised research projects for fifteen undergraduate students, ranging from one summer to multiple years. Several students who began working with me ultimately became coauthors on refereed journal articles (including Drew Kouri, David Kent, Edward Agarwala, and Youngmin Park). In the same interval, I have directed Masters theses in Applied Mathematics for seven students, some of whom began working with me as undergraduates and continued to complete a BS/MS program. The titles and dates of the MS theses are as follows:

1. Alexander Cao, "Dimension Reduction for Stochastic Oscillators: Investigating Competing Generalizations of Phase and Isochrons", Master's thesis, April 2017.
2. Casey A. Bennett, "Channel Noise And Firing Irregularity In Hybrid Markov Models Of The Morris-Lecar Neuron", Master's thesis, August 2015.
3. Youngmin Park, "Infinitesimal Phase Response Curves for Piecewise Smooth Dynamical Systems", Master's thesis, August 2013.
4. Suparat Chuechote, "Amplification and Accuracy in a Stochastic 2D Gradient Sensing Pathway Model", Masters's thesis, May 2010.
5. Edward Agarwala, "Food for Thought: When Information Maximization Fails to Optimize Utility", Master's thesis, May 2009.
6. Matthew Garvey, "Diffusion Mediated Signaling: Information Capacity and Coarse Grained Representations", Master's thesis, December 2008.
7. Drew P. Kouri, "A Nonlinear Response Model for Single Nucleotide Polymorphism Detection Assays", Master's thesis, June 2008.

I was honored to be nominated in 2017 by my graduate students for the Diekhoff mentoring award.

In addition to graduate students[1] I have supervised four postdoctoral scholars. Casey Diekman was a postdoctoral fellow at the Mathematical Biosciences Institute (MBI) at Ohio State University, and now holds a tenure-track position at New Jersey Institute of Technology. I worked with Dr. Diekman through MBI's external postdoctoral mentoring program. Deena Schmidt was supported by NSF grant EF-1038677 and now holds a tenure-track position at the University of Nevada, Reno. David Lyttle was supported by an NSF postdoctoral fellowship, and now holds a postdoc at University of Wisconsin, Milwaukee. I co-mentored Dr. Lyttle with my collaborator Hillel Chiel (CWRU Biology). Yangyang Wang is currently a postdoctoral fellow at MBI (Ohio State). I am co-mentoring Dr. Wang with Prof. Chiel. In addition, I am currently supervising three undergraduate summer students, one master's student, and one doctoral student.

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[1] I would point out that supervision of PhD students is not considered a requirement for faculty at any level. Indeed, several of the faculty currently holding the rank of Professor in my department have not supervised doctoral students.

Service Statement

Please see section 5, **Professional Service**, and section 6, **Service on Institutional Committees**, of the curriculum vitae.