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Computational training for the next generation of neuroscientists

Mark S Goldman[1] and Michale S Fee[2]

Neuroscience research has become increasingly reliant upon quantitative and computational data analysis and modeling techniques. However, the vast majority of neuroscientists are still trained within the traditional biology curriculum, in which computational and quantitative approaches beyond elementary statistics may be given little emphasis. Here we provide the results of an informal poll of computational and other neuroscientists that sought to identify critical needs, areas for improvement, and educational resources for computational neuroscience training. Motivated by this survey, we suggest steps to facilitate quantitative and computational training for future neuroscientists.

Addresses
[1] Center for Neuroscience, Department of Neurobiology, Physiology, and Behavior, and Department of Ophthalmology and Vision Science, University of California – Davis, Davis, CA 95618, USA
[2] McGovern Institute and Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139, USA

Corresponding author: Goldman, Mark S (msgoldman@ucdavis.edu)

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Introduction

In 1952, in the *Journal of Physiology*, Hodgkin and Huxley published their famous series of papers describing the biophysical basis of the action potential and laying out the mathematical framework underpinning much of modern cellular neurophysiology [1–5]. Today, sixty-five years later, the qualitative basis of the action potential is widely taught in nearly every introductory neuroscience class. However, because most biology students lack sufficient quantitative training, the mathematical modeling so seminal to their work may be daunting and is rarely taught.

Computational and theoretical approaches shape and inform nearly every level of analysis in neuroscience. These include biophysical and biochemical characterizations of receptor and signaling proteins [6], conductance-based models of single neuron voltage dynamics [7,8], neural network models of circuit dynamics [9,10] and plasticity [11], and statistical approaches to cognition, reasoning, and behavior [12–14]. Computational neuroscience also provides many of the core data analysis techniques used throughout neuroscience, including bioinformatic analyses underlying genome-wide screens [15–17]; statistical analyses of electrophysiological, optical, and non-invasive functional imaging data [18–20]; and signal-processing algorithms underlying brain-machine interfaces and neural prosthetics [21,22]. More generally, computational neuroscience provides the intellectual framework within which many of the brain's computations are now described. Hodgkin and Huxley's [1] and Rall's [23,24] frameworks for describing single-neuron computation are classics. Sensory coding studies have been guided by principles of efficient coding [25] and information theory [26] and, more recently, by insights from deep networks [27]. Attractor dynamics provide a conceptual framework for describing memory networks [28,29]. Signal detection theory provides a foundation for studies of decision-making [30–32]. Learning theory provides a framework for understanding how changes at the behavioral level [e.g., 33,34] emerge from plasticity rules at the single synapse and single neuron levels [35,36].

The need for quantitative and computational approaches is growing rapidly. Recording technology now allows for simultaneous measurements of the activity of hundreds or thousands of neurons in a single brain area, or even throughout the entire brain of behaving animals [37]. New approaches to automated electron microscopic imaging of brain tissue allow large scale neural circuit reconstruction at single-synapse resolution [38]. Combining such advances with those in molecular genetics, cell biology, and functional imaging now makes it possible to explore a single system or disease in depth at the molecular, cellular, network, and behavioral levels. These advances will require new methods for the analysis of massive data sets and new theories and models to connect such measurements to underlying computational principles.

Neuroscience training must impart future neuroscientists with the core quantitative and computational skills necessary to keep up with these experimental advances, as emphasized by a number of national reports focusing on the future of neuroscience [39•,40•,41] and general biology education [42••,43•,44,45••,46]. These skills include not only the ability to perform sophisticated statistical analyses, but also the ability to interpret and build quantitative models, design experiments to test new models and theories, and form collaborations with interdisciplinary teams. Imparting this knowledge presents a significant challenge to neuroscience departments and programs.

Survey

To develop a more complete picture of the challenges and opportunities facing computational neuroscience education, we conducted an informal poll of a range of leaders in computational neuroscience training, from textbook authors to course directors, program officers, and faculty representing different subfields of computational neuroscience from cellular biophysics to cognitive neuroscience (Supplementary material 1). Our survey asked respondents to give their opinions on three topics: (1) Necessary curricular training for general neuroscience and computational neuroscience-focused students (Table 1), (2) Barriers to training in computational neuroscience (Table 2), and (3) Suggestions for improvements to computational neuroscience training (Table 3). In addition, we used the survey to gather a list of computational neuroscience training resources available to the general community (Supplementary material 2).

Below, we summarize the key themes that emerged from the survey responses. We note that the poll consisted of open-ended rather than multiple choice questions. This led to many rich and insightful comments. However, for the tabulation of requisite training topics (Table 1), this format led to some ambiguities in interpretation; namely, it was sometimes unclear, when a respondent failed to mention a particular subject area, whether it was viewed as already standard in most neuroscience program curricula, viewed as unnecessary, or simply overlooked. Many responses also did not clearly differentiate undergraduate and graduate training needs, so we merged these categories in our analysis. Despite these ambiguities, several recurring themes emerged across the set of responses, and we focus our discussion around these.

Theme 1: More quantitative training is needed for students from life science backgrounds. The most common refrain from both theorists and experimentalists was that many students from life-science backgrounds lacked sufficient training in quantitative approaches, programming, and algorithmic thinking (Table 2). For general neuroscience students, the most commonly emphasized needs were for further coursework and training in statistics and data analysis, mathematics, and computer programming or computer science. Also emphasized was the need for coursework in computational neuroscience or other biological modeling. Within the category of statistics and data analysis, many respondents explicitly distinguished 'data analysis' from statistics per se, emphasizing the need for students to perform hands-on work with real data sets. Within the mathematics curriculum, linear algebra and probability theory were most commonly cited as important subjects. Interestingly, the training needs identified by experimental neuroscientists and theoretical neuroscientists were highly consistent (Table 1). Several

Table 1

Survey results on essential training for all neuroscience students and for students in computational neuroscience. "Respondent" refers to whether the survey-taker's research is primarily theoretical (24 respondents) or experimental (20 respondents). Indented items indicate specific subtopics mentioned by respondents. Responses are merged across graduate and undergraduate students. Note that some respondents may have omitted topics that are already standard in the curriculum. For survey questions and methodology, see Supplementary material 1

Topic	Coursework for general neuroscience students			Additional coursework for computational neuroscience students		
	Respondent		Totals	Respondent		Totals
	Theorists	Experimentalists		Theorists	Experimentalists	
Core Neuro/Bio/Chem	10	16	26	6	5	11
Computational Neuro	6	7	13	9	10	19
Programming/CS	11	11	22	8	9	17
Math Foundations	15	11	26	15	16	31
Linear Algebra	8	5	13	5	7	12
Probability Theory	3	4	7	5	7	12
Differential Equations	3	1	4	2	6	8
Nonlinear Dynamics	2	2	4	6	6	12
Statistics/Data Analysis	14	12	26	7	8	15
Statistics	9	11	20	6	6	12
Data Analysis	9	4	13	2	4	6
Signal Processing	4	4	8	3	2	5
Machine Learning	0	0	0	7	6	13
Other Math/Eng/Phys	6	7	13	9	10	19

Table 2

Survey results on biggest barriers to training in computational neuroscience

Category	Barrier	# of responses
Students from life science backgrounds	Insufficient quantitative training	21
	Insufficient training in programming or algorithmic thinking	10
	Student fear of not being good at math/programming	3
	Lack of rigor of life science courses	1
	Poor quality of teaching in math/computational techniques	1
	The (wrong) idea that you need to come from a computational background to become a computational neuroscientist	1
Students from quantitative non-life science backgrounds	Insufficient biology training or experience with real biological data	8
	Insufficient training in asking scientific questions and experimental design	2
	Poor biological intuition or understanding of the big picture	2
Challenges of teaching in a highly interdisciplinary field	Breadth of different mathematical topics needed, or lack of consensus for which topics are most important to teach	8
	Hard to teach to heterogeneous student population of those coming from quantitative versus life science backgrounds	5
	Need for an introductory-level textbook	3
	Time required to learn math competes with time doing research and reading literature	2
	Not enough computational neuroscientists to provide the needed training	1
Value of computational neuroscience	Perception of computational neuroscience as a specialty rather than as part of core training needs	4
	Lack of understanding of the value of computational neuroscience or quantitative methods	3

respondents emphasized the need, at both the undergraduate and graduate levels, for quantitative classes tailored to students from life science backgrounds. Finally, many respondents who recommended quantitative coursework beyond calculus and introductory statistics emphasized the importance of beginning this training at the undergraduate level.

For students planning to work in computational neuroscience, respondents suggested additional training in mathematics, physics and engineering, computer science, statistics, and notably, machine learning. Also emphasized was the need for this material at both the graduate and undergraduate levels. In addition, several respondents thought that students interested in computational neuroscience would be best served by majoring in a subject such as physics, math, or computer science rather than in biology.

Respondents commented on the challenge of teaching computational approaches in the context of neuroscience programs in which students have remarkably heterogeneous quantitative backgrounds (Table 2). Courses often comprised a bimodal population of students coming from the life sciences versus the mathematical and physical sciences, creating challenges in presenting both the math and the biology in a way that is interesting and accessible to all students. Another commonly noted challenge was that the wide array of different mathematical tools used in neuroscience makes it difficult to teach all of these different topics in a single course. Further complicating matters is the lack of consensus on which topics and methods are most critical.

Theme 2: More biology training is needed for students from non-life science backgrounds. The greatest challenge noted for students from non-life science backgrounds was insufficient training in biology or experience with real biological data (Table 2). Several respondents noted that this lack of experience can lead to poor biological intuition, lack of understanding of big picture concepts, and difficulty in formulating good scientific questions or experimental designs. To convey this background, it was suggested that there should be broad, cross-topic biology courses for such students that parallel the need for broad mathematical modeling courses for students from life science backgrounds. Other suggestions included rotations through experimental laboratories and experience with real biological data sets.

Theme 3: More training resources are needed for computational neuroscience. The most commonly cited need was for a general computational neuroscience textbook at a more introductory level than the oft-used Dayan and Abbott [47] (Table 3). Also noted was the need for more training resources as well as a centralized repository in which to host these resources. Suggested training resources for students included online courses, tutorials, and topic-specific modules and specialized books. Desired resources for instructors included course notes, pedagogical exercises, and data sets for statistical analysis and modeling. Computational neuroscience software

Table 3

Survey results on ideas to improve computational neuroscience education and on identification of computational neuroscience training resources that are missing or need improvement

Topic	Idea for improving computational neuroscience training	# of responses
Training resources in computational neuroscience	General computational neuroscience textbook, written at a more introductory level than current books	10
	Additional online courses, tutorials, and topical modules; more special-topics training schools	8
	Advanced general computational neuroscience book, or textbooks covering various specialty fields	6
	Canon of pedagogical exercises in computational neuroscience	2
	Training materials to teach students to think in high dimensions	1
	Ethics training in scientific rigor and reproducibility	1
Quantitative/computational training for students from life-science backgrounds	Offer or require biological modeling, computer science, or physics-concepts courses targeted to life science students	7
	More courses and teaching materials in data analysis, including the incorporation of real-world data sets	6
	More computational neuroscience in regular neuroscience textbooks	1
Biological training for students from non-biology backgrounds	Require computational neuroscience students to do lab rotations	2
	Offer broad survey biology courses for non-life science students	1
Repositories for training resources	Centralized repository for computational neuroscience training materials and exercises	3
	Require papers to publish data sets and computer code	1
	Create a practical guide to what computational neuroscience coursework is necessary for different applications	1
Development of computational neuroscience software	Open source software infrastructure and standardized data formats	2
	Improvements to NEURON to make it easier to use and learn	1
	Software engineering summer course	1
Outreach and diversity	Expose high school students to the field	1
	Create pipelines for recruiting under-represented minorities	1

platforms for data analysis and modeling were identified as a need for the field, as well as mandatory posting of code and data sets to public repositories. Available resources suggested by respondents are provided in Supplementary material 2; ideally, such materials could be brought together in a single, well-organized, public repository that includes user ratings and intuitive search criteria.

Theme 4: Cultural barriers are holding back the widespread adoption of computational neuroscience approaches and training. Respondents noted multiple cultural barriers to the widespread teaching and adoption of computational neuroscience techniques. These included the intimidation many students experience from math and programming topics, and a cultural misperception that only students who start out in quantitative fields can become computational neuroscientists. More fundamentally, several respondents noted that computational neuroscience is too often undervalued or viewed as a specialty field rather than a core training need, impairing its adoption into standard neuroscience curricula. On a related note, several respondents forcefully noted that computational neuroscience should not exist as a distinct field, but rather should be fully integrated as a set of tools applied across the spectrum of neuroscience research.

Conclusions and recommendations

Computational neuroscience provides powerful data analysis tools, theoretical frameworks, and computational models that are applicable from the molecular to the behavioral scales. These applications will only increase as new experimental technologies enable the acquisition of ever more massive data sets and the performance of increasingly sophisticated experiments. Training in computational neuroscience will allow researchers to take full advantage of these data sets, revealing hidden structure through new data analysis methods and identifying new principles of brain function through mechanistic models and theories.

Our survey identified critical challenges and provided a number of suggestions to facilitate the widespread adoption of computational neuroscience training (Table 3).

First, life science students need better quantitative and biological modeling skills. Undergraduates should, at a minimum, take calculus; computer programming; statistics (with probability); and a mathematical modeling course that teaches core concepts from linear algebra, differential equations, and probability in the context of modeling neurobiological systems. The statistics and modeling courses should be fully integrated with a high-level programming language such as R or MATLAB that enable hands-on analysis of real data sets and simulation of mechanistic models. Students who enter neuroscience graduate programs without such background should be required to take remedial coursework in these areas.

Second, students from the mathematical and physical sciences need greater exposure to the details and diversity of real-world biological systems. Neuroscience programs should encourage physical and mathematical science students to take their courses by offering more flexible prerequisites and advertising their courses more broadly. Physical, mathematical, and engineering science departments should allow their students to take suitable neuroscience coursework as one of their electives and to perform for-credit research in a neuroscience laboratory.

Third, more training resources are needed, and these should be organized into an easily navigable repository that provides a centralized site for instructors and students alike. A particular need is for course materials, pedagogical exercises, and a textbook that address the vast majority of students in neurobiology who come from life science backgrounds and have little quantitative background.

Meeting these needs can be challenging in practice. Most fundamentally, it requires that life science departments re-think what skills are important for students who will be mid-career in 2050. This entails deciding what courses should be offered, which of these should be required, and what these courses' prerequisites should be. We recommend that such considerations start from the point of view of what core thinking skills will be most valuable to students' future endeavors. This viewpoint should take precedence over other factors such as a possible lack of popularity of quantitative courses among students, or departmental financial considerations that may be tied to enrollment numbers. As emphasized by a host of reports on undergraduate biology training from the AAAS [42••], National Academies [41,44,45••], and American Association of Medical Colleges [43•], modeling and simulation have been repeatedly identified as core competencies in modern biological and biomedical training. As such, we recommend that quantitative and computational coursework be required by neurobiology programs. Indeed, it is difficult to imagine that students without such skills will be able to fully engage in many of the most exciting future developments in neuroscience. The importance of quantitative approaches was cogently summarized by the Obama BRAIN initiative working group [40•]:

"Brains—even small ones—are dauntingly complex . . . In complex systems of this nature, our intuitions about how the activity of individual components (e.g. atoms, genes, neurons) relate to the behavior of a larger assembly (e.g. macromolecules, cells, brains) often fail, sometimes miserably. Inevitably, we must turn to theory, simulation, and sophisticated quantitative analysis in our search to understand the underlying mechanisms that bridge spatial and temporal scales, linking components and their interactions to the dynamic behavior of the intact system."

By training students to fully embrace quantitative approaches, the field of neuroscience will move closer to developing the tools and intuitions necessary to unravel the inner workings of the mind and brain.

Conflict of interest statement

Nothing declared.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.conb.2017.06.007.

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