Computational training for the next generation of neuroscientists

Highlights:

- Reports results of a survey on training needs in computational neuroscience
- More quantitative training is needed for students from life science backgrounds
- Experience with real biological data is needed for non-life science students
- A well-organized, centralized repository is needed to host training resources
- Cultural barriers are holding back widespread computational neuroscience training

Title: Computational Neuroscience Training for the Next Generation of Neuroscientists

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Abstract

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.

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, the mathematical modeling that was seminal to their work is rarely taught and, because of lack of quantitative training, may be daunting to most biology students, hindering their deeper understanding of the associated concepts.

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 theoretically, 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]. Hebbian and homeostatic learning rules provide a conceptual underpinning for synaptic plasticity studies [33], while reinforcement learning underlies descriptions of neuronal and behavioral data ranging from dopamine signaling [34] to motor control [35,36].

Despite these significant accomplishments, the need for quantitative and computational approaches is growing rapidly. Whereas past studies were considered cutting edge if they recorded from two neurons at a time, recent revolutions in recording technology now allow 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]. Recent advances in automated electron microscopic imaging of brain tissue will allow large scale neural circuit reconstruction at single-synapse resolution [38]. At the same time, advances in molecular genetics, cell biology, functional imaging, and bioengineering now make it possible to gather data sets that explore a single system, or a single 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 [39-41] and general biology education [42-46]. 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 students from life science backgrounds lacked 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, probability theory and linear algebra were most commonly cited as important subjects. Interestingly, the training needs identified by experimental neuroscientists and theoretical neuroscientists were highly consistent (Table 1). Several 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. 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]. 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 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.

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Table captions

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 or experimental. 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.

Table 2: Survey results on biggest barriers to training in computational neuroscience.

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.

References

1. Hodgkin AL, Huxley AF: **A quantitative description of membrane current and its application to conduction and excitation in nerve**. *J Physiol* 1952, **117**:500-544.
2. Hodgkin AL, Huxley AF: **The dual effect of membrane potential on sodium conductance in the giant axon of Loligo**. *J Physiol* 1952, **116**:497-506.
3. Hodgkin AL, Huxley AF: **The components of membrane conductance in the giant axon of Loligo**. *J Physiol* 1952, **116**:473-496.
4. Hodgkin AL, Huxley AF: **Currents carried by sodium and potassium ions through the membrane of the giant axon of Loligo**. *J Physiol* 1952, **116**:449-472.
5. Hodgkin AL, Huxley AF: **Movement of sodium and potassium ions during nervous activity**. *Cold Spring Harb Symp Quant Biol* 1952, **17**:43-52.
6. Hille B: *Ion channels of excitable membranes* edn 3rd. Sinauer; 2001.
7. Johnston D, Wu SM-S: *Foundations of cellular neurophysiology*. MIT Press; 1995.
8. Koch C: *Biophysics of computation : information processing in single neurons*. Oxford University Press; 1999.
9. Arbib MA: *The handbook of brain theory and neural networks* edn 2nd. MIT Press; 2003.
10. Hertz J, Krogh A, Palmer RG: *Introduction to the theory of neural computation*. Addison-Wesley Pub. Co.; 1991.
11. Gerstner W, Kistler WM: *Spiking neuron models : single neurons, populations, plasticity*. Cambridge University Press; 2002.
12. Gershman SJ, Horvitz EJ, Tenenbaum JB: **Computational rationality: A converging paradigm for intelligence in brains, minds, and machines**. *Science* 2015, **349**:273-278.
13. Pouget A, Beck JM, Ma WJ, Latham PE: **Probabilistic brains: knowns and unknowns**. *Nat Neurosci* 2013, **16**:1170-1178.
14. Tenenbaum JB, Kemp C, Griffiths TL, Goodman ND: **How to grow a mind: statistics, structure, and abstraction**. *Science* 2011, **331**:1279-1285.
15. Maze I, Shen L, Zhang B, Garcia BA, Shao N, Mitchell A, Sun H, Akbarian S, Allis CD, Nestler EJ: **Analytical tools and current challenges in the modern era of neuroepigenomics**. *Nat Neurosci* 2014, **17**:1476-1490.
16. Rosen GD, Chesler EJ, Manly KF, Williams RW: **An informatics approach to systems neurogenetics**. *Methods Mol Biol* 2007, **401**:287-303.

17. Mo A, Mukamel EA, Davis FP, Luo C, Henry GL, Picard S, Urich MA, Nery JR, Sejnowski TJ, Lister R, et al.: **Epigenomic Signatures of Neuronal Diversity in the Mammalian Brain**. *Neuron* 2015, **86**:1369-1384.
18. Kass RE, Eden UT, Brown EN: *Analysis of neural data*. Springer; 2014.
19. Kramer MA, Eden UT: *Case studies in neural data analysis : a guide for the practicing neuroscientist*. The MIT Press; 2016.
20. Mitra P, Bokil H: *Observed brain dynamics*. Oxford University Press; 2008.
21. Gilja V, Pandarinath C, Blabe CH, Nuyujukian P, Simeral JD, Sarma AA, Sorice BL, Perge JA, Jarosiewicz B, Hochberg LR, et al.: **Clinical translation of a high-performance neural prosthesis**. *Nat Med* 2015, **21**:1142-1145.
22. Shenoy KV, Carmena JM: **Combining decoder design and neural adaptation in brain-machine interfaces**. *Neuron* 2014, **84**:665-680.
23. Rall W: **Theory of physiological properties of dendrites**. *Ann N Y Acad Sci* 1962, **96**:1071-1092.
24. Segev I, Rall W: **Excitable dendrites and spines: earlier theoretical insights elucidate recent direct observations**. *Trends Neurosci* 1998, **21**:453-460.
25. Barlow HB: **Possible principles underlying the transformations of sensory messages**. In *Sensory Communication*. Edited by Rosenblith W: MIT Press; 1961:217-234.
26. Rieke F: *Spikes : exploring the neural code*. MIT Press; 1997.
27. Yamins DL, DiCarlo JJ: **Using goal-driven deep learning models to understand sensory cortex**. *Nat Neurosci* 2016, **19**:356-365.
28. Hopfield JJ: **Neural networks and physical systems with emergent collective computational abilities**. *Proc Natl Acad Sci U S A* 1982, **79**:2554-2558.
29. Wills TJ, Lever C, Cacucci F, Burgess N, O'Keefe J: **Attractor dynamics in the hippocampal representation of the local environment**. *Science* 2005, **308**:873-876.
30. Bogacz R, Brown E, Moehlis J, Holmes P, Cohen JD: **The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced-choice tasks**. *Psychol Rev* 2006, **113**:700-765.
31. Green DM, Swets JA: *Signal detection theory and psychophysics*. R. E. Krieger Pub. Co.; 1974.

32. Ratcliff R, McKoon G: **The diffusion decision model: theory and data for two-choice decision tasks**. *Neural Comput* 2008, **20**:873-922.
33. Abbott LF, Regehr WG: **Synaptic computation**. *Nature* 2004, **431**:796-803.
34. Schultz W, Dayan P, Montague PR: **A neural substrate of prediction and reward**. *Science* 1997, **275**:1593-1599.
35. Franklin DW, Wolpert DM: **Computational mechanisms of sensorimotor control**. *Neuron* 2011, **72**:425-442.
36. Kao MH, Doupe AJ, Brainard MS: **Contributions of an avian basal ganglia-forebrain circuit to real-time modulation of song**. *Nature* 2005, **433**:638-643.
37. Ahrens MB, Li JM, Orger MB, Robson DN, Schier AF, Engert F, Portugues R: **Brain-wide neuronal dynamics during motor adaptation in zebrafish**. *Nature* 2012, **485**:471-477.
38. Helmstaedter M, Briggman KL, Turaga SC, Jain V, Seung HS, Denk W: **Connectomic reconstruction of the inner plexiform layer in the mouse retina**. *Nature* 2013, **500**:168-174.
39. *Akil H, Balice-Gordon R, Cardozo DL, Koroshetz W, Posey Norris SM, Sherer T, Sherman SM, Thiels E: **Neuroscience Training for the 21st Century**. *Neuron* 2016, **90**:917-926.

    *Emphasizes the need for greater training in quantitative and computational skills, and suggests ways to impart these. Also emphasizes the need for integrating scientists and approaches from different disciplines.

40. *Brain Research through Advancing Innovative Neurotechnologies (BRAIN) Working Group: *BRAIN 2025: A scientific vision* National Institutes of Health; 2014.

    *Describes the necessary and pervasive roles of computational neuroscience in the future of neuroscience research. Provides recommendations for imparting computational neuroscience training.

41. Posey Norris SM, Palmer, C., Stroud, C., Altevogt, B.M., Rapporteurs; Forum on Neuroscience and Nervous System Disorders, Board on Health Sciences Policy; Institute

of Medicine of the National Academies: *Developing a 21st century neuroscience workforce: workshop summary*. National Academies Press; 2015.

42. **American Association for the Advancement of Science, National Science Foundation Directorate for Education and Human Resources, Division of Undergraduate Education and Directorate for Biological Sciences: *Vision and change in undergraduate biology education: a call to action*. Edited by Brewer CA, Smith D; 2011.

    **Makes a strong case for educational reform in biology. Describes six core competencies for undergraduate biology education. These include the ability to use quantitative reasoning, the ability to use modeling and simulation, and the ability to tap into the interdisciplinary nature of science.

43. *AAMC-HHMI Committee: *Scientific foundations for future physicians*. Association of American Medical Colleges; 2009.

    *Emphasizes quantitative reasoning and facility with mathematics as core competencies for undergraduate and medical school training.

44. Committee on a New Biology for the 21st Century: Ensuring the United States Leads the Coming Biology Revolution, Board on Life Sciences, Division on Earth and Life Studies, National Research Council of the National Academies: *A new biology for the 21st century*; 2009.
45. **Committee on Undergraduate Biology Education to Prepare Research Scientists for the 21st Century, Board on Life Sciences, Division of Earth and Life Sciences, National Research Council of the National Academies: *BIO 2010: Transforming Undergraduate Education for Future Research Biologists*. National Academies Press; 2003.

    **Provides a thorough examination of needs in undergraduate biology education for future researchers. Includes heavy emphasis on quantitative and interdisciplinary skills, as well as guidance on how to implement necessary curricular and structural changes.

46. Bialek W, Botstein D: **Introductory science and mathematics education for 21st-Century biologists**. *Science* 2004, **303**:788-790.
47. Dayan P, Abbott LF: *Theoretical neuroscience : computational and mathematical modeling of neural systems*. Massachusetts Institute of Technology Press; 2001.

	Coursework for general neuroscience students			Additional coursework for computational neuroscience students		
	Respondent			*Respondent*		
Topic	**Theorists**	**Experimentalists**	***Totals***	**Theorists**	**Experimentalists**	***Totals***
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 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 or experimental. 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.

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 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

Table 2: Survey results on biggest barriers to training in computational neuroscience.

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

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.

Supplementary Material 1: Survey Methodology

The survey was emailed to 107 individuals. Responses were received from 24 individuals we classified as primarily theorists and 20 individuals we classified as primarily experimentalists. Free-form responses to the question about the required training were quite diverse and were initially coded into a set of broad categories that comprised subcategories. These were core neuroscience (including molecular, systems, cognitive, behavioral/psychophysics, methods/laboratory), computational neuroscience (including information theory, sensory codes, dimensionality reduction, neuronal biophysics, neural circuits), computer science/programming, math (including probability theory, linear algebra, differential equations, nonlinear dynamics), statistics and data analysis, engineering (including signal processing, control theory, machine learning), physics (basic physics, statistical mechanics), chemistry, biology, and others. These responses were condensed into the categories displayed in Table 1. For some overarching categories (e.g., Math foundations) the number of respondents was broken out for individual subcategories (e.g. linear algebra, differential equations). Within each overarching category, the total number of responses was computed from the union of the set of respondents indicating the overarching category or any of its subcategories. We note that, because of the free-form nature of the responses, there likely exist some biases in the responses that may inaccurately reflect respondents' attitudes. For example, the fact that only slightly more than half of the respondents indicated that students should be trained in core neuroscience, biology, or chemistry likely reflects that most respondents believe students in modern neuroscience programs already receive sufficient training in these topics, and therefore did not include them in their written responses. This bias could be corrected through a future questionnaire that explicitly lists subject areas and asks respondents to select those areas in which students should receive training. For Table 2 (barriers to training) and Table 3 (missing resources and ideas for improvement), we grouped similar responses into the shown categories and subcategories so as to better identify how the responses clustered around particular themes.

SURVEY QUESTIONS:

1. What type of training do you think is essential for:
   - all neuroscience graduate students?
   - computational neuroscience graduate students?
   - undergraduates interested in graduate school in neuroscience?
   - undergraduates interested in graduate school in computational neuroscience?

2. What do you see as the biggest barrier(s) to training in computational neuroscience

3. What training resources or educational materials do you think are missing or could be improved?

4. If you could do one thing today (assuming you had the time…) to improve computational neuroscience education, what would that be?

5. Are there particular educational resources you know of that would be worth pointing out to the audience of a computational neuroscience education article?

6. What computational neuroscience oriented courses do you teach and/or programs do you direct and who is the target audience?

Supplementary Material 2: Computational Neuroscience Training Resources

Here we list computational neuroscience resources identified by survey respondents in the categories of data sets, software, books, lectures and course materials, and training courses. Although potentially very useful, we do not attempt to provide a compendium of the many seminal review articles or edited book volumes on various subjects. The list below likely has many prominent omissions – our hope is that this list may form the starting point for a publicly supported, curated website, with user ratings and comments, that can serve as a centralized repository for these and other materials.

Data sets and model code repositories

- Collaborative Research in Computational Neuroscience (CRCNS) data sharing website: https://crcns.org/
- Neurodata Without Borders (NWB) project: http://www.nwb.org/ and https://crcns.org/NWB
- Allen Institute Brain Atlas (Data & Tools): http://www.brain-map.org/
- ModelDB (database of computational models): https://senselab.med.yale.edu/modeldb/
- Open Source Brain (open-source database of computational models): http://www.opensourcebrain.org/

Software

Simulators & model description languages:

- NEURON (multi-scale simulation environment, from subcellular to networks): https://www.neuron.yale.edu/neuron/
- GENESIS (multi-scale simulation environment, from subcellular to networks): http://www.genesis-sim.org/
- MOOSE (multi-scale simulation environment, from subcellular to networks): https://www.neuron.yale.edu/neuron/
- NEST (spiking neural network simulator): http://www.nest-simulator.org/
- Brian (spiking neural network simulator): http://briansimulator.org/
- Nengo (spiking neural network simulator): http://www.nengo.ca/
- Emergent (formerly PDP++) (neural network simulator): https://grey.colorado.edu/emergent/index.php/Main_Page
- XPP/XPP-Aut (differential equation solver, including phase plane analysis): http://www.math.pitt.edu/~bard/xpp/xpp.html
- NeuroML (model description language for computational neuroscience): https://www.neuroml.org/

For additional comparison of simulators, see
https://grey.colorado.edu/emergent/index.php/Comparison_of_Neural_Network_Simulators

Topic-specific software:

- Chronux (MATLAB library for neural data analysis, including multi-taper spectral analysis): http://chronux.org/
- TensorFlow (machine learning, neural network software library): https://www.tensorflow.org/

Books

General computational neuroscience:

- Dayan & Abbott, Theoretical Neuroscience
- Gerstner et al., Neuronal dynamics: from single neurons to networks and models of cognition: http://neuronaldynamics.epfl.ch/online/index.html
- Trappenberg, Fundamentals of Computational Neuroscience (2nd Ed.)

Mathematical neuroscience & neuronal dynamics:

- Börgers, An introduction to Modeling Neuronal Dynamics
- Ermentrout & Terman, Mathematical Foundations of Neuroscience
- Gabbiani & Cox, Mathematics for Neuroscientists: http://www.sciencedirect.com//science/book/9780123748829
- Izhikevich, Dynamical Systems in Neuroscience
- Wilson, Spikes, decisions, and actions: dynamical foundations of neuroscience

Networks-focused computational neuroscience:

- Anastasio, Tutorials on Neural Systems Modeling
- Hertz, Krogh, & Palmer, Introduction to the Theory of Neural Computation
- Sutton & Barto, Reinforcement Learning (2nd edition draft available at: https://webdocs.cs.ualberta.ca/~sutton/book/the-book.html)

Neural Coding

- Rieke et al., Spikes: Exploring the Neural Code

Biophysics

- Koch, Biophysics of Computation

Cognitive Neuroscience focused computational neuroscience books

- O'Reilly et al., Computational cognitive neuroscience: https://grey.colorado.edu/CompCogNeuro/index.php/CCNBook/Main

Statistics for computational neuroscience:

- Kass, Eden, & Brown, Analysis of Neural Data
- Kramer & Eden, Case studies in neural data analysis: a guide for the practicing neuroscientist
- Mitra & Bokil, Observed Brain Dynamics (particularly multi-taper spectral/frequency-domain analysis)

Data visualization & presentation

- Tufte, The visual display of quantitative information

Lectures and Course Materials

(See also the websites of the various neuroscience summer schools and training courses below)

Online courses:

- Rao & Fairhall, "Computational neuroscience": https://www.coursera.org/learn/computational-neuroscience
- Gerstner, "Neuronal dynamics – Computational neuroscience of single neurons": http://lcn.epfl.ch/~gerstner/NeuronalDynamics-MOOC1.html
- Ng, "Machine Learning": https://www.coursera.org/learn/machine-learning

Lecture materials:

- Pillow, "Mathematical tools for neuroscience": http://pillowlab.princeton.edu/teaching/mathtools16/
- Simoncelli, "Mathematical tools for neural and cognitive science": http://www.cns.nyu.edu/~eero/math-tools/
- Stanford "Math tools for neuroscience": http://web.stanford.edu/class/nbio228-01/
- Wiskott, [videos, notes, & exercises on a range of topics, especially in Machine Learning]: https://www.ini.rub.de/PEOPLE/wiskott/Teaching/Material/

Tutorials & pedagogically oriented simulations:

- Goldman, MATLAB-based tutorials: http://goldmanlab.faculty.ucdavis.edu/tutorials/
- HHSim (MATLAB-based Hodgkin-Huxley model simulator): http://www.cs.cmu.edu/~dst/HHsim/
- MIT "Tutorial series in computational topics": https://stellar.mit.edu/S/project/bcs-comp-tut/index.html
- Murray, Python-based interactive modules: http://johndmurray.org/teaching/
- Neurons in action (NEURON-based simulation exercises): http://neuronsinaction.com/home/main
- Shlens, ICA: https://arxiv.org/abs/1404.2986
- Shlens, PCA and SVD: https://arxiv.org/abs/1404.1100
- Song et al., Recurrent neural network training code: https://github.com/frsong/pycog

Summer schools and training courses

Summer courses:

- Allen Institute/University of Washington, Workshop on the dynamic brain: http://courses.washington.edu/braindyn/
- Bernstein Center for Computational Neuroscience (Gottingen), Mathematical approaches to neural circuit dynamics: http://www.bccn-goettingen.de/events/cns-course
- Champalimaud Centre for the Unknown (Portugal), CAJAL Course in Computational Neuroscience: http://www.fens.org/Training/CAJAL-programme/CAJAL-Courses-2017/CCCN2017/

- Marine Biological Laboratory (Woods Hole), Methods in computational neuroscience (MCN): http://www.mbl.edu/mcn/
- Marine Biological Laboratory (Woods Hole), Brains, minds, and machines: http://www.mbl.edu/education/courses/brains-minds-and-machines/
- NYU-Shanghai University, Computational and cognitive neuroscience: http://www.ccnss.org/
- Princeton University, Neurotechnologies for analysis of neural dynamics (NAND): http://nand.princeton.edu/
- Okinawa Institute of Science & Techology, Computational neuroscience: https://groups.oist.jp/ocnc
- UC Berkeley, Mining and modeling of neuroscience data: http://crcns.org/course
- University of Waterloo, Nengo summer school on large-scale brain modeling: http://www.nengo.ca/summerschool

Winter (southern hemisphere summer) courses:

- Universidad Técnica Federico Santa Maria and Instituo de Sistemas Complejos de Valparaíso, Latin-American summer school in computational neuroscience (LACONEU): http://www.laconeu.cl/index.html
- University of Cape Town, IBRO-Simons computational neuroscience imbizo: http://isicni.gatsby.ucl.ac.uk/

Other training courses:

- NEURON training courses: see https://www.neuron.yale.edu/neuron/courses