

Education

University of California at Berkeley. AB (1979) and PhD (1983) in Biophysics
Lowell High School, San Francisco CA (1977)

Primary professional appointments

2001– Princeton University

Professor of Physics and member of the Lewis–Sigler Institute for Integrative Genomics
(2003–) John Archibald Wheeler/Battelle Professor in Physics

1990–2001 NEC Research Institute¹

(1999–2001) Fellow; (1990–99) Senior Research Scientist

1986–90 University of California at Berkeley

Assistant Professor of Physics and Biophysics

1984–86 University of California at Santa Barbara

Institute for Theoretical Physics,² Postdoctoral fellow

1983–84 Rijksuniversiteit Groningen, the Netherlands

Faculty of Physics, postdoctoral fellow

Visiting appointments

2024– The Graduate Center, City University of New York. Visiting Research Scholar.

2024– Simons Foundation. Senior Fellow, Simons Society of Fellows.

2024– Howard Hughes Medical Institute. Janelia Scholar.

2022–23 Rockefeller University. Visiting Professor, Center for Studies in Physics and Biology

2023, '18, '12, '10, and '08 Università Sapienza, Roma.

Visiting scholar, Department of Physics and CNR Institute for Complex Systems

2019 Google. Visiting Researcher

2018 École Normale Supérieure, Paris. Professeur Invité, Faculty of Physics

2009–20 The Graduate Center, City University of New York. Visiting Presidential Professor of Physics.

2007–09 Rockefeller University. Visiting Professor, Center for Studies in Physics and Biology

2005–07 Columbia University. Consultant, Center for Theoretical Neuroscience

2001–02 NEC Research Institute. Consultant

2000–01 Princeton University. Visiting Lecturer with Rank of Professor, Department of Physics

2000 Scuola Internazionale Superiore di Studi Avanzati, Trieste. Visiting scholar

1999 and '94 Hebrew University of Jerusalem. Visiting scholar, Racah Institute for Physics and
Interdisciplinary Center for Neural Computation

1998, '93, and '91 Princeton University. Visiting Lecturer, Department of Physics

1994–2004: University of California at San Francisco. Visiting Faculty, Center for Theoretical Neurobiology

1991–2015: Marine Biological Laboratory, Woods Hole MA. Lecturer and co-director (1998–2002),
Summer Course on Computational Neuroscience

¹Founded as an institute for basic scientific research, it has moved to more applied topics, and continues as NEC Laboratories.

²Now the Kavli Institute for Theoretical Physics (KITP).

1990 Institute for Advanced Study. Visiting scholar, School of Natural Sciences
1990 Lawrence Berkeley Laboratory. Faculty Scientist, Materials and Chemical Sciences Division
1988–90 Jet Propulsion Laboratory. Consultant, Biotechnology group
1988–89 Universidade de São Paulo. Visiting scholar, Instituto de Física e Química de São Carlos

Professional recognition

Honors and awards

2025 Member, American Academy of Arts and Sciences
2021 John Simon Guggenheim Memorial Foundation Fellowship
2021 Simons Fellow in Theoretical Physics
2018 Max Delbrück Prize in Biological Physics, American Physical Society
2013 Swartz Prize for Theoretical and Computational Neuroscience, Society for Neuroscience
2012 Member, National Academy of Sciences (USA)
2011 Phi Beta Kappa Award for Excellence in Undergraduate Teaching
2010 Thomas D Jones Professorship in Mathematical Physics, Princeton University
2007 Latke–Hamentasch Debate Champion, Princeton University (with B. Amster '07)
2006 President's Award for Distinguished Teaching, Princeton University
1996 Fellow of the American Physical Society
1987–91 Presidential Young Investigator, National Science Foundation
1986–87 Miller Research Fellow and Regents' Junior Faculty Fellow
1980–84 National Science Foundation Predoctoral Fellow and NATO Postdoctoral Fellow
1979–80 President's Undergraduate Fellow and ARCS Foundation Fellow
1979 Phi Beta Kappa and AB with highest honors and distinction in general scholarship

Named lectures³

2026 Shih-I Pai lecture, University of Maryland
 Colloquium Pierre et Marie Curie, Sorbonne Université
2025 Schrödinger colloquium, University of Zürich
2024 Ehrenfest colloquium, Leiden University
2023 Frontiers in Physics, University of Washington
2018 Hoxton Lectures in Physics, University of Virginia
2017 Buhl Lectures in Physics, Carnegie Mellon University
 Shui–Chin Physics Lectureship, Academia Sinica, Taiwan
 WE Crill lecture in Physiology and Biophysics, University of Washington
2016–17 Phi Beta Kappa Visiting Scholar
2016 Turing Lectures, International Centre for Theoretical Sciences, Bangalore, India
 RE Bell Lecture in Physics, McGill University
2015 Bethe Lectures in Physics, Cornell University
 Mind/Brain Lecture, Stony Brook University
 Tracy and Ruth Storer Lecture in the Life Sciences, University of California at Davis
 HL Welsh Lectures in Physics, University of Toronto
2014 Williams Lecture for the Advancement of Logic and Philosophy, University of Pennsylvania
 Boeing Lectures in Applied Mathematics, University of Washington.

³For a full description of recent invited lectures (2010–), including some of these named lectures, see below.

2013 Abdus Salam Lectures, International Centre for Theoretical Physics, Trieste, Italy
William T. Patten Lectures, Indiana University

2012 Della Pietra Lectures, Simons Center for Geometry and Physics, Stony Brook University
Hans–Lukas Teuber Lecture in Brain and Cognitive Sciences, Massachusetts Institute of Technology

2011 George Whitfield Lecture in Physics, Pennsylvania State University

2010 Giorgio Careri Memorial Lecture in Physics, Università Sapienza, Roma

2009 Colloquium Pierre et Marie Curie, Université de Paris VI

2008 JD Crawford Lectures in Physics, University of Pittsburgh

2007 Hendrik de Waard Lecture in Physics, Rijksuniversiteit Groningen
Benjamin and Anne Pinkel Lecture in Cognitive Science, University of Pennsylvania
WA Crump '44 Lecture in Physics, St. Andrew's School

2006 Niels Bohr Lecture, Copenhagen University

2001 Dexter Lectures in Physics, Rochester University

1998 Porter Lectures in Physics, Vanderbilt University

1997 David H. Harris '22 Lectures in Physics, Massachusetts Institute of Technology

Service

Selected external advisory, editorial, and community service

2022– Alfred P. Sloan Foundation. Advisory committee, Matter to Life Program.

2021– South American Institute for Fundamental Research. Scientific Council.

2021– Boulder School for Condensed Matter and Materials Physics. Advisory Board.

2016– International Centre for Theoretical Sciences, Bangalore. International Advisory Board.

2026 National Academy of Sciences. Class Membership Committee, Physical and Mathematical Sciences.

2022 Janelia Research Campus, Howard Hughes Medical Institute. Advisory committee.

2021–22 American Physical Society. Selection committee, Early Career Award for Biological Physics.

2021 Harvard University. Visiting committee, Department of Physics.

2021 Chan Zuckerberg Initiative. Reviewer for CZI Investigator proposals.

2020–22 Phi Beta Kappa. Selection committee, Science Book Award.

2020 Open Philanthropy. Reviewer.

2020 Simons Foundation. Reviewer, Simons Investigator Nominations.

2020 American Physical Society. Fellowship committee, Division of Biological Physics.

2019–22 National Academies of Sciences, Engineering, and Medicine (USA).
Decadal Assessment on Biological Physics and the Physics of Living Systems, Chair.

2019 National Academy of Sciences. Selection committee, John J. Carty Award.

2019 University of California at San Diego. Visiting committee, PhD Program in Physics.

2019–21 American Physical Society. Fundraising committee, Division of Biological Physics.

2019–20 European Research Council. Grant review.

2019, '14 Gordon and Betty Moore Foundation. Reviewer for Science Program proposals.

2018–24 National Academies of Sciences, Engineering, and Medicine (USA).
Board on Physics and Astronomy.

2018–20 American Physical Society. Selection committee, George E Valley Jr Prize.

2018 American Physical Society. Selection committee, Max Delbrück Prize for Biological Physics.

2018–19 Simons Foundation. Selection committee for Simons Investigators.

2017–20 American Physical Society. Council of Representatives.

2017–20 American Physical Society. Selection committees: APS Medal for Exceptional Achievement in Research, Julius Edgar Lilienfeld Prize, and George E. Valley Prize.
2017–20 Stony Brook University. WM Keck Foundation Project Advisory Board, Biomedical Engineering.
2017–19 South American Institute for Fundamental Research, São Paulo. Faculty search committee.
2017–19 Society for Neuroscience. Selection committee, Swartz Prize for Theoretical Neuroscience.
2017–18 American Physical Society. Selection committee, Fellowship in the Division of Biological Physics.
2016–25 *Journal of Statistical Mechanics: Theory and Experiment*. Board of Directors.
2016–21 Janelia Research Campus, Howard Hughes Medical Institute. External mentor.
2015–18 International Centre for Theoretical Physics, Trieste. Faculty search committee.
2017 John Templeton Foundation. Reviewer, grant proposals in the Natural Sciences.
2016 Institut Philippe Meyer. Jury, Meyer Prize in Theoretical Physics.
2016 Chan Zuckerberg Initiative. Reviewer, CZI Investigator proposals.
2015–17 *Proceedings of the National Academy of Sciences (USA)*. Editorial Board.
2014–19 Swartz Foundation. Chief scientific adviser.
2014–15 Simons Foundation. Selection committee, Simons Investigators.
2014 Northwestern University. Visiting committee, Department of Physics and Astronomy.
2014 National Science Foundation. Visiting committee, Kavli Institute for Theoretical Physics.
2014 National Science Foundation. Physics of Living Systems Program grant review panel.
2013 Simons Foundation. Roundtable on Quantitative Biology.
2013 Aalto University, Finland. External advisory committee for selection of Chair in Biophysics.
2012–21 Abdus Salam International Centre for Theoretical Physics, Trieste. Scientific Council.
2011 University of Southern California. Visiting committee, Neuroscience Initiative.
2010 National Science Foundation. Physics of Living Systems Program grant review panel.
2010–15 Burroughs Wellcome Fund. Advisory committee, Career Awards at the Scientific Interface.
2009 Hunter College, CUNY. Visiting committee, Department of Physics and Astronomy.
2007 University of Colorado. Co-organizer, Boulder Summer School on Condensed Matter Physics.
2006–16 Salk Institute for Biological Studies. Fellow, Crick–Jacobs Center for Theoretical Biology.
2004–10 Max Planck Institute for Dynamics and Self-Organization. Scientific Advisory Board.
2004–08 Kavli Institute for Theoretical Physics. Advisory board. Chair, 2005–06.
2004 Kavli Institute for Theoretical Physics. Co-organizer, program on Understanding the Brain.
2006–07 National Research Council. Condensed Matter and Materials Physics Report (CMMP 2010).
2002–06 *Annals of Physics*. Editorial Board.
2002–06 Human Frontier Science Program. Grant review committee.
2001–11 Scuola Internazionale Superiore di Studi Avanzati, Trieste. International advisory committee.
2001 Brown University. Visiting committee, Interdisciplinary Brain Sciences Program.
1999–2002 National Research Council. Board on Physics and Astronomy.
1997–90 *Journal of Statistical Physics*. Editorial Board.
1994–97 American Physical Society. Executive Committee, Division of Biological Physics.
1993–2003 *Neural Computation*. Editorial Board.
1990 Aspen Center for Physics. Co-organizer, program on Neural Networks.
1989 Los Alamos National Laboratory. Director's Fund review committee.

Selected departmental and campus service, Princeton University

2017– Co-Founder and co-Director, Center for the Physics of Biological Function.
2001– Associated faculty, Program in Applied and Computational Mathematics.
2001– Associated faculty, Program in Neuroscience.

2025 Co-organizer, PCTS Workshop: The Physics of John Hopfield.
2022–24 Faculty search committee for theoretical physics (Chair, 2023–24).⁴
2019–21 Coordinator, Lewis–Sigler Scholars Program.
2017–21 Faculty search committee for theoretical physics.
2016–19 Conflict of Interest in Research Panel.
2015–21 Physics PhD program, admissions committee.
2015–18 Organizer, weekly biophysics seminar series.
2015–16 Faculty search committee for experimental biophysics (joint with Neuroscience Institute).
2013–16 Faculty search committee for theoretical physics (Chair, 2013–14).
2009–13 Princeton University Press. Editorial Board.
2009–13 Physics PhD program, admissions committee.
2009 50th Reunion Seminar speaker.
2009 Development office briefing on theory in the natural sciences.
2008–14 Organizer, weekly biophysics seminar series.
2008–11 Lewis–Sigler Institute for Integrative Genomics, Associate Director.
2008–11 Committee on Honorary Degrees, Board of Trustees.
2007–15 Program in Translation and Intercultural Communication. Executive committee.
2007–10 Program in Teacher Preparation. Executive committee.
2006–22 Director, undergraduate Certificate Program in Biophysics.
2005–06 Chair, faculty search committee for experimental biophysics (joint with Lewis–Sigler Institute).
2007 Development office neuroscience retreat and Alumni visits.
2006–08 Committee on Committees.
2005–10 Faculty fellow, Princeton Center for Theoretical Sciences (founding group).
2005–06 Chair, faculty search committee for experimental biophysics (joint with Lewis–Sigler Institute).
2005 Development office alumni retreat for capital campaign, panelist.
2003–07 Organizer, weekly biophysics seminar series.
2002–05 Rockefeller College. Freshman/sophomore adviser.
2002–16 Coordinator, annual search for postdoctoral fellows in theoretical biophysics.⁵

Selected campus service, The CUNY Graduate Center

2009–20 Founder and Scientific Director, Initiative for the Theoretical Sciences.
2017–19, ‘15–16 Initiative for the Theoretical Sciences, Faculty search committee.
2010–11 Search committee, Dean of the Sciences.
2009–10 Program in Computer Science, Faculty search committee.

Mentoring

A wise colleague once noted that the most meaningful honor bestowed upon scientists is when bright young people come to work with us. By this measure I have been honored many times over. This somewhat bland listing of the current positions held by my junior colleagues doesn't convey the pleasure of working with them, and the joy of watching them grow into mature scientists.

⁴Our department is large enough that we search for new faculty essentially every year. We often have one search committee for theorists across all fields of physics, recognizing that some of the most exciting developments transcend traditional boundaries.

⁵This annual search continues as part of our Center for the Physics of Biological Function.

Postdoctoral fellows. I began to interact with postdocs when I moved to NEC. At Princeton, my colleagues and I formed a biophysics theory group, functioning in a collective mode that has long characterized other areas of theoretical physics, so that postdocs are recruited and advised jointly. This now is formalized as part of our Center for the Physics of Biological Function. I've also enjoyed sharing in the mentoring of experimentalists, and visiting faculty positions at the University of California at San Francisco and at The Graduate Center of the City University of New York have created opportunities to interact with more young colleagues. This list includes all of the postdocs and fellows who have passed through our theory group since 2001, postdocs from the NEC years, and others with whom I have had close mentoring relationships.

- 2025 ← **'22: Ofer Kimchi** Assistant Professor of Mathematics, New York University.
- 2025 ← **'21: Trevor GrandPre** Assistant Professor of Physics, Washington University in St Louis.
- 2024 ← **'18: Kamesh Krishnamurthy** Assistant Professor of Physics Georgia Institute of Technology.
- 2023 ← **'20: Christopher W Lynn** Assistant Professor of Physics and q-Bio, Yale University.
- 2023 ← **'19: Vudtiwat Ngampruetikorn** Senior Lecturer, School of Physics, University of Sydney.⁶
- 2023 ← **'20: Julia Steinberg** Quantitative Researcher, Radix Trading LLC.
- 2022 ← **'17: Andreas Mayer** Associate Professor, Quantitative Immunology and Biological Physics, University College London.
- 2021 ← **'18: Ricard Alert Zenon** ICREA Research Professor in Physics, Universitat de Barcelona.
- 2021 ← **'18: Marianne Bauer** Assistant Professor of Bionanoscience, Technische Universiteit Delft.
- 2021 ← **'19: Katherine Quinn** Science Fellow, Walsh School of Foreign Service, Georgetown University.
- 2021 ← **'17: Tankut Can** Assistant Professor of Physics, Emory University.
- 2021 ← **'16: Pierre Ronceray** Principal Investigator, Centre Turing (CENTURI) Université Aix-Marseille.
- 2021 ← **'15: Yaojun Zhang** Assistant Professor of Physics and Biophysics, Johns Hopkins University
- 2020 ← **'19: Ivana Cvijović** Member of Technical Staff, Anthropic.
- 2019 ← **'16: Yuval Elhanati** Senior Research Scientist, Memorial Sloan Kettering Cancer Center
- 2019 ← **'16: Anna Frishman** Senior Lecturer in Physics, Technion Israel Institute of Technology.
- 2019 ← **'14: Zhiyuan Li** Assistant Professor of Physics and Quantitative Biology, Peking University
- 2018 ← **'13: Benjamin Machta** Associate Professor of Physics, Yale University.
- 2018 ← **'09: Kanaka Rajan** Associate Professor of Neurobiology, Harvard Medical School.
- 2018 ← **'15: Tiberiu Teșileanu** Research Engineer, Meta CTRL Labs.
- 2017 ← **'13: Serena Bradde** Knowledge expert, Meta. Formerly founding editor, *PRX Life*.
- 2017 ← **'12: Armita Nourmohammad** Associate Professor of Immunobiology, Biomedical Engineering, and Physics, Yale University.
- 2016 ← **'12: Thibaud Tallefumier** Associate Professor of Mathematics and Neuroscience, University of Texas at Austin.
- 2015 ← **'09: Gordon Berman** Associate Professor of Biology and of Physics, Emory University.
- 2015 ← **'12: Anne-Florence Bitbol** Associate Professor of Bioengineering, School of Life Sciences, École Polytechnique Fédérale de Lausanne.
- 2015 ← **'11: Chase Broedersz** University Research Chair Professor on the Theoretical Physics of Life, Vrije Universiteit Amsterdam.
- 2015 ← **'11: Michele Castellana** Chargé de Recherche, Physical Chemistry Unit, Institut Curie and CNRS.
- 2014 ← **'09: David Schwab** Associate Professor of Biology and of Physics, The CUNY Graduate Center.
- 2013 ← **'12: Lucy Colwell** University Associate Professor in Chemistry, Cambridge University, and Research Scientist, Google.
- 2012 ← **'08: Konstantin Doubrovinski** Assistant Professor of Systems Biology, University of Texas Southwestern Medical Center.

⁶Regarding titles: Senior lecturer (Australia, Israel) and Lecturer (UK) are roughly equivalent to Assistant Professor in the US system; W2 Professor (Germany) is roughly equivalent to Associate Professor; and Reader (UK) spans Associate/Full Professor. Chargé de Recherche (France) spans Assistant/Associate Professor, with continuing tenure, and Directeur/Directrice de Recherche spans Associate/Full Professor; while CNRS positions are for research, all those listed here are involved in teaching and advising.

2012 ← '08 **Olivier Marre** Directeur de Recherche, Institut de la Vision, Paris.

2012 ← '06: **Stephanie Palmer** Associate Professor of Organismal Biology and Anatomy, and of Physics, The University of Chicago.

2012 ← '07: **Eva-Maria Schötz Collins** Associate Professor of Biology and Physics, Swarthmore College.

2011 ← '06: **Matthias Kaschube** Professor of Computer Science and Mathematics, Goethe University, and Senior Fellow, Frankfurt Institute for Advanced Studies.

2011 ← '08: **Lisa Manning** William R. Kenan, Jr. Professor of Physics, Syracuse University.

2011 ← '06 **Greg Stephens** Associate Professor of Physics, Vrije Universiteit Amsterdam, and Okinawa Institute of Science and Technology.

2010 ← '08: **Jeremy England** Founder and Chief Technical Officer, Conquest Technologies.

2010 ← '06: **Pankaj Mehta** Professor of Physics, Boston University.

2010 ← '09: **Matthieu Wyart** WH Miller Professor of Physics, Johns Hopkins University.

2009 ← '06: **Michael Desai** Fisher Professor of Natural History, Harvard University.

2009 ← '06: **Thierry Mora** Directeur de Recherche, Laboratoire de Physique de l'École Normale Supérieure, and CNRS, Paris

2009 ← '00: **Leslie Osborne** Program Director, Systems and Computational Neuroscience, National Institutes of Health.

2009 ← '06: **Aleksandra Walczak** Directrice de Recherche, Laboratoire de Physique de l'École Normale Supérieure, and CNRS, Paris

2008 ← '04: **Kerwyn Huang** Associate Professor of Bioengineering, Stanford University.

2008 ← '03: **William Ryu** Professor of Physics, University of Toronto.

2007 ← '03: **Robert Endres** Professor in Systems Biology, Imperial College London.

2007 ← '01: **Tatyana Sharpee** Edwin K. Hunter Chair and Professor, Salk Institute for Biological Studies.

2006 ← '01: **Elad Schneidman** Joseph and Bessie Feinberg Professor of Brain Sciences, Weizmann Institute of Science.

2006 ← '02: **Noam Slonim** Distinguished Engineer, IBM Research, Haifa.

2005 ← '02: **Gurinder Atwal** Chief Data and AI Officer, Pioneering Intelligence, Flagship Pioneering Inc.

2004 ← '00: **Susanne Still** Professor of Physics, University of Hawai'i at Mānoa.

2003 ← '98: **Adrienne Fairhall** Professor of Neurobiology and Biophysics, University of Washington.

2003 ← '02: **Jonathan Miller** Professor, Okinawa Institute of Science and Technology.

2003 ← '02: **Sima Setayeshgar** Professor of Physics, Indiana University.

2002 ← '97: **Kamal Sen** Associate Professor of Biomedical Engineering, Boston University.

2000 ← '97: **Dmitry Rinberg** Professor of Neuroscience and Physiology, New York University.

1999 ← '96: **Naama Brenner** Julius and Bernice Naiman Chair in Engineering, Technion.

1996 ← '95: **Thomas Powers** Professor of Engineering and Physics, Brown University.

1996 ← '94: **Steven Strong** Quantitative Analyst, DE Shaw and Company, retired.

PhD students. I had the good fortune to be given great freedom as a PhD student, while still benefiting from the advice of a senior mentor—an “adviser” in a more literal sense. I have tried to do this for the next generation, adjusting to the needs of each student. It has been a particular pleasure to advise students jointly with colleagues, sometimes as part of a theory/experiment collaboration, in other cases in response to evolution of the student's interests. Prior to 1994, all students were from UC Berkeley; from 1994 onward all students are from Princeton unless otherwise noted.

2025: **Camilla Sarra** Postdoctoral fellow, Bioengineering, École Polytechnique Fédérale de Lausanne.

2024: **Jim Wu** (jointly with DJ Schwab). Senior Associate, Cerebrus Capital Management.

2023: **Caroline M Holmes** (jointly with SE Palmer). Postdoctoral fellow, Departments of Physics and Organismal and Evolutionary Biology, Harvard University.

2022: **Luisa F Ramirez Ochoa** (jointly with R Dickman and SE Palmer). Postdoctoral fellow, Faculty of Neurobiology, Johannes Gutenberg Universität, Mainz.⁷

⁷Student at Universidade Federal de Minas Gerais, Brasil.

2020: Xiaowen Chen Chargé de Recherche, Laboratoire de Physique de l'École Normale Supérieure and CNRS, Paris.

2018: Leenoy Meshulam (jointly with CD Brody and DW Tank). June and Howard Zimmerman Assistant Professor of Physics, Neuroscience, and Brain Science, Brown University.

2018: Daniel J Strouse (jointly with DJ Schwab). Member of Technical Staff, Open AI.

2018: Lauren McGough (jointly with H Verlinde). Postdoctoral fellow, Center for the Physics of Evolving Systems, The University of Chicago.

2017: Mark L Ioffe (jointly with MJ Berry II). Associate Research Scholar, Princeton Neuroscience Institute, Princeton University.

2017: Vasyl Alba (jointly with JM Maldacena). Postdoctoral fellow, Department of Applied Mathematics, Northwestern University.

2016: Ji Hyun Bak (jointly with JW Pillow). Senior Data Scientist, Delfi Diagnostics.

2014: Mikhail Tikhonov (jointly with T Gregor and NS Wingreen). Associate Professor of Physics, Washington University in St Louis.

2014: Dmitry Krotov (jointly with AM Polyakov) Research scientist, IBM Research, Cambridge MA.

2012: Julien Dubuis (jointly with T Gregor). Senior Vice-President, Nym, New York NY.

2011: Dario Amodei (jointly with MJ Berry II). Founder and CEO, Anthropic.

2011: Audrey Sederberg (jointly with M Kaschube). Assistant Professor of Physics, Georgia Institute of Technology.

2008: Fariel Shafee Writer and artist.

2008: Feraz Azhar (jointly with A Zee).⁸ Assistant Professor of Philosophy, University of Notre Dame.

2007: Gašper Tkačik (jointly with CG Callan) Professor, Institute of Science and Technology Austria.

2007: Yuan Sophie Liu (jointly with PJ Holmes). Deceased. Formerly Senior Data Scientist, Experian.

2005: Thomas Gregor (jointly with DW Tank and EF Wieschaus). Professor of Physics and the Lewis-Sigler Institute, Princeton University, and Director, Laboratory for the Physics of Biological Function, Institut Pasteur, Paris.

2000: Ilya Nemenman Samuel Candler Dobbs Professor of Physics and Biology, Emory University.

1998: Seth Bruder Chief Technology Officer and co-founder, Webalo, retired.

1995: Michael DeWeese Professor of Physics and Neuroscience, University of California at Berkeley.

1994: Marc Potters Chief Investment Officer, Capital Fund Management.

1993: Daniel Ruderman Distinguished Scientist, Roche Diagnostics.

1992: Nicholas Socci Head of Engineering and Bioinformatics, Marie-Josée & Henry R. Kravis Center for Molecular Oncology, Memorial Sloan Kettering Cancer Center.

1992: Julian Joseph Formerly Assistant Professor of Psychology, University of Nevada at Reno.⁹

1991: Frederick Rieke Professor of Neurobiology and Biophysics, University of Washington.

1991: Spiros Skourtis Professor of Physics, University of Cyprus.

1991: David Warland (jointly with JP Miller). Research Professor of Complexity Sciences, Emeritus, University of California at Davis. Previously Chief Technology Officer, IQ Engines (acquired by Yahoo).

1991: Michael Crair Ziegler Professor of Neuroscience and Vice Provost for Research, Yale University.

1990: Leonid Kruglyak Diller-von Furstenberg Chair in Human Genetics, University of California at Los Angeles; Investigator, Howard Hughes Medical Institute.

1989: William Bruno Staff Scientist, Emeritus, Theoretical Biology and Biophysics Group, Los Alamos National Laboratory.

Undergraduate students. At Princeton, all students do independent research, writing junior papers and senior theses. At Berkeley senior theses are done only by students hoping to graduate with honors. At both institutions, I have had the pleasure of working closely with roughly one undergraduate each year. In

⁸Student at University of California at Santa Barbara.

⁹Left academia for health reasons.

addition, my colleagues and I have hosted visiting students, including from the City University of New York system as part of the CPBF Summer School program. Listed here is a selection from all of these students, including those whose work led to published papers or e-prints.

- 2020: Gentian Muhaxheri** PhD student, Department of Physics, Syracuse University.
- 2019: Victoria Antonetti** PhD student, Department of Applied Mathematics, Brown University.
- 2019: Helena Casademunt** PhD student, Department of Physics, Harvard University.
- 2019: Rebecca Rousseau** PhD student, Department of Physics, California Institute of Technology.
- 2018: Gavin T Hall** Fellow in Rheumatology, Washington University in St Louis.
- 2012: Mariela D Petkova** Postdoctoral fellow, Biophysics and Neuroscience, Harvard University.
- 2012: Edward D Lee** Assistant Professor of Physics, Seoul National University (from F'26).
- 2010: Elizabeth Jerison** Assistant Professor of Physics, The University of Chicago.
- 2007: Tamara Broderick** Associate Professor of Electrical Engineering and Computer Science, Massachusetts Institute of Technology.
- 1999: Fei Fei Li** Sequoia Capital Professor of Computer Science, Stanford University.
- 1999: Greg Corrado** Distinguished Scientist and Senior Research Director, Google.
- 1998: Blaise Agüera y Arcas** Vice-President, Fellow, and CTO of Technology & Society, Google.
- 1990: Wulfram Gerstner** Professor of Computational Neuroscience, École Polytechnique Fédérale de Lausanne.
- 1990: KT Moortgat** Founder and Managing Partner, Dalena Capital
- 1989: Daniel Ruderman** Distinguished Scientist, Roche Diagnostics.

Invited lectures (2010–)

Named lectures

- Colloquium Pierre et Marie Curie, Sorbonne Université. *Pushing the physical limits: Optimization in living systems*. May 28, 2026.
- Schrödinger colloquium, University of Zurich. *Ambitions for theory in the physics of life*. May 15, 2025.
- Ehrenfest colloquium, Leiden University. *Physics for maggots*. May 29, 2024.
- Physics Frontiers Lecture Series, University of Washington. *More perfect than we imagined: A physicist's view of life* (for a general audience). Oct 17, 2023.
- Hoxton Lectures in Physics, University of Virginia. *Physics of life* (for a general audience); *Statistical mechanics for networks of real neurons* (physics colloquium). Mar 22–23, 2018.
- Max Delbrück Prize Lecture, American Physical Society. *Precision and emergence in the physics of biological function*. Los Angeles CA. Mar 7, 2018.
- Shui-Chin Lee Lectureship in Physics, Academia Sinica. *The physics of life: How much can we calculate?* (for a general audience). Taipei, Taiwan. Oct 31, 2017.
- Buhl Lecture in Physics, Carnegie Mellon University. *The physics of life: How much can we calculate?* (for a general audience). Apr 13, 2017.
- Phi Beta Kappa Visiting Scholar (2016–17). Lectures for general audiences.
More perfect than we imagined: A physicist's view of life. St Michael's College VT. Apr 4, 2017; Notre Dame University. Mar 29, 2017; Williams College. Feb 28, 2017; Eckerd College. Feb 21, 2017; University of South Dakota. Feb 7, 2017.
The Galilean imperative: A physicist's search for simplicity. Emory University. Jan 25, 2017; University of Pittsburgh. Jan 18, 2017; Loyola University at Chicago. Nov 1, 2016.
- WE Crill lecture in Physiology and Biophysics, University of Washington. *Thinking about a thousand neurons*. Jun 20, 2017.

Bell Lecture in Physics, McGill University. *The physics of life: How much can we calculate?* (for a general audience). Apr 8, 2016.

Turing Lectures, International Centre for Theoretical Sciences, Bangalore, India. *More perfect than we imagined: A physicist's view of life* (for a general audience); *Statistical mechanics for real biological networks* and *Optimization principles and information flow in biological networks* (for a discussion meeting on Information Processing in Biological Systems). Jan 4–6, 2016.

HL Welsh Lectures in Physics, University of Toronto, Canada. *More perfect than we imagined: A physicist's view of life* (for a general audience); *Are biological networks poised at criticality?* (physics colloquium). May 7–8, 2015.

Tracy and Ruth Storer Lecture in the Life Sciences, University of California at Davis. *Searching for simplicity: Theoretical physics meets experimental biology*. May 4, 2015.

Mind/Brain Lecture, Stony Brook University. *Searching for simplicity: A physicist's quest for theories of mind and brain* (for a general audience). Mar 30, 2015.

Bethe Lectures in Physics, Cornell University. *Predictive information and the problem of long time scales in the brain* (Laboratory for Atomic and Solid State Physics seminar); *Are biological networks poised at criticality?* (physics colloquium); *More perfect than we imagined: A physicist's view of life* (for a general audience). Mar 16–18, 2015.

Williams Lecture for the Advancement of Logic and Philosophy, University of Pennsylvania. *Why did we get that one wrong?*. Dec 5, 2014.

Boeing Lectures in Applied Mathematics, University of Washington. *Statistical mechanics for real biological networks*. Jun 5, 2014.

William T Patten Lectures, Indiana University. *The Galilean imperative: A physicist's search for understanding: (1) What have we learned, and how should we teach?; (2) Toward the physics of life itself.* (for general audiences). Oct 28–30, 2013.

Abdus Salam Lectures, International Centre for Theoretical Physics, Trieste, Italy. *The Physics of Life: Searching for a Theory: (1) Taming the phenomena; (2) Finding signals in the noise; (3) Living on bits; (4) More than the sum of its parts; (5) Predictions.* Jan 28–Feb 1, 2013.

Della Pietra Lectures, Simons Center for Geometry and Physics, Stony Brook University. *150 years of Entropy* (for a general audience); *Signals, noise, and the physical limits to biological function; Statistical mechanics for real biological networks; More perfect than we imagined: A physicist's view of life* (for a general audience). Apr 19–20, 2012.

Hans–Lukas Teuber Lecture in Brain and Cognitive Sciences, Massachusetts Institute of Technology. *Collective behaviors in networks of real neurons*. Mar 8, 2012.

Whitfield Lecture in Physics, Pennsylvania State University. *Statistical mechanics for real biological networks*. Oct 20, 2011.

Inaugural Giorgio Careri Memorial Lecture, Department of Physics, Università Sapienza, Roma. *Old dreams, revisited: A physicist's search for order in biological systems* May 27, 2010.

Summer schools, short courses, and guest teaching

Scaling, criticality, and the statistical physics of biological networks (five lectures). School on biological physics across scales, South American Institute for Fundamental Research, São Paulo, Brasil. Jan 19–23, 2026.

Optimization principles in neural coding and computation. Latin American School on Computational Neuroscience: LASCON X, São Paulo, Brasil. Jan 22, 2026.

Searching for scale invariance. Summer course on Methods in Computational Neuroscience, Marine Biological Laboratory, Woods Hole MA. Aug 13, 2025.

Ambitions for theory in the physics of life (four lectures). Theoretical Biophysics, Les Houches Summer School on Theoretical Physics. Jul 4–7, 2023.

The physics of life. A summer school for advanced undergraduates (co-organizer and lecturer), Center for the Physics of Biological Function, Princeton University. Jun 19–30, 2023.

Physics for maggots (two lectures). Biophysics course, Faculty of Physics, Università Sapienza, Roma. Jun 5–6, 2023.

Bits, brains, and Boltzmann: Physics of information in living systems. Short course on computational modeling and information theory. March Meeting of the American Physical Society, Las Vegas, NV. Mar 5, 2023.

The physics of life. A summer school for advanced undergraduates (co-organizer and lecturer), Center for the Physics of Biological Function, Princeton University. Jun 6–17, 2022.

Biophysics (three lectures). Serrapilheira Training Program in Quantitative Biology and Ecology, South American Institute for Fundamental Research, São Paulo, Brasil (online). Jul 13–15, 2021.

Adventures in the Theoretical Sciences. An informal, online summer school (organizer and lecturer), Initiative for the Theoretical Sciences, The Graduate Center, CUNY. Jun 4–Jul 10, 2020.

The physics of life. An online summer school for advanced undergraduates (co-organizer and lecturer), Center for the Physics of Biological Function, Princeton University. Jun 15–Aug 3, 2020.

Statistical physics of biological systems: From molecules to minds (four lectures). Summer school on Physics in Biology, South American Institute for Fundamental Research, São Paulo, Brasil. Jan 20–24, 2020.

Physics problems in early embryonic development (four lectures). Winter School on Quantitative Systems Biology, International Centre for Theoretical Sciences, Bangalore, India. Dec 17–20, 2019.

RG-inspired approaches to the analysis of real neural networks. Theoretical Biophysics, Boulder Summer School on Condensed Matter Physics. July 19, 2019.

Precision and emergence in the physics of biological systems. Journeys into Theoretical Physics, South American Institute for Fundamental Research, São Paulo, Brasil. July 6, 2019.

Statistical physics for real biological networks. Preparatory School for StatPhys 2019, South American Institute for Fundamental Research, São Paulo, Brasil. July 5, 2019.

Physical limits to biological function. Preparatory School for StatPhys 2019, South American Institute for Fundamental Research, São Paulo, Brasil. July 4, 2019.

Statistical mechanics for networks of real neurons. Summer Course on Cellular, Computational and Cognitive Neuroscience, Princeton University. Jul 1, 2019.

The physics of life. A summer school for advanced undergraduates (co-organizer and lecturer), Center for the Physics of Biological Function, Princeton University. Jun 10–21, 2019.

Why do input/output relations look the way they do? Multiscale integration in biological systems, Institut Curie, Paris. Nov 8, 2018.

Tutorial on quantitative approaches to behavior. Q-bio summer school, Kavli Institute for Theoretical Physics. Aug 22, 2018.

Statistical mechanics for networks of real neurons. Summer Course on Cellular, Computational and Cognitive Neuroscience, Princeton University. Jul 2, 2018.

The physics of life. A summer school for advanced undergraduates (co-organizer and lecturer), Center for the Physics of Biological Function, Princeton University. Jun 11–22, 2018.

Precision and emergence in the physics of biological systems. A short course (15 hours), Faculty of Physics, École Normale Supérieure, Paris, France. May–Jun 2018.

Searching for simplicity: Analyzing large populations of neurons using ideas from the renormalization group. VII Latin American School on Computational Neuroscience, São Paulo, Brasil. Jan 26, 2018.

Precision and emergence in the physics of biological systems. A short course (13.5 hours), Summer school on Physics in Biology, South American Institute for Fundamental Research, São Paulo, Brasil. Jan 22–26, 2018.

Statistical mechanics for networks of real neurons. Summer Course on Neurotechnologies for Analysis of Neural Dynamics, Princeton University. Jul 1, 2017.

Physics problems in early embryonic development. Physiology course guest lecture, Eckerd College. Feb 21, 2017.

Precision and emergence in the physics of biological systems. A short course (14 hours), Faculty of Physics, École Polytechnique Fédérale de Lausanne, Switzerland. Sep 5–9, 2016.

Statistical mechanics for networks of real neurons. Summer Course on Neurotechnologies for Analysis of Neural Dynamics, Princeton University. Jul 4, 2016.

Precision and emergence in the physics of biological systems. A short course (6 hours), Summer school on Physics in Biology, South American Institute for Fundamental Research, São Paulo, Brasil. Jan 18–22, 2016.

Statistical mechanics for real biological networks. A short course (9 hours), Summer school on Statistical Physics, Beg Rohu, France. Aug 31–Sep 4, 2015.

Statistical mechanics for networks of real neurons. Summer Course on Neurotechnologies for Analysis of Neural Dynamics, Princeton University. Jun 23, 2015.

Searching for simplicity. Summer course on Methods in Computational Neuroscience, Marine Biological Laboratory, Woods Hole MA. Aug 8, 2014.

Lessons from the problem of photon counting in vision; Information flow in biological networks; and Searching for collective behavior. Winter School on Quantitative Systems Biology, International Centre for Theoretical Physics, Trieste, Italy. Nov 26–28, 2012.

More questions than answers. Summer course on Methods in Computational Neuroscience, Marine Biological Laboratory, Woods Hole MA. Aug 23, 2012.

Searching for simplicity. Summer school on Computational Neuroscience, Okinawa Institute of Science and Technology, Japan. Jun 21, 2012.

Information, noise, and optimization; and Tutorial on information theory. Summer course on Methods in Computational Neuroscience, Marine Biological Laboratory, Woods Hole MA. Aug 1–2, 2011.

Some current theoretical issues in biophysics. A short course (8 hours), Faculty of Physics, Universitat de Barcelona and Centre for Genomic Regulation, Spain Jan 2011.

Noise and information. Summer course on Methods in Computational Neuroscience, Marine Biological Laboratory, Woods Hole MA. Aug 9, 2010.

Some current theoretical issues in biophysics A short course (12 hours), Faculty of Physics, Università Sapienza, Roma. May 2010.

Seminars, colloquia, and other invited lectures

Pushing the physical limits: Optimization in living systems. Laboratoire de Physique Théorique et Modèles Statistiques, Université Paris Saclay. May 27, 2026.

Ensembles of near-optimal organisms. 130th Statistical Mechanics Meeting, Rutgers University, May 12, 2026.

Optimization principles in the physics of life. ITS seminar, The CUNY Graduate Center. Feb 13, 2026.

Optimization principles in the physics of life. IFT colloquium, State University of São Paulo. Jan 21, 2026.

Optimization principles, revisited. Mind Center for Outreach, Research and Education, University of Pennsylvania. Dec 5, 2025.

Optimization principles, revisited. Center for Theoretical and Computational Neuroscience, Washington University in St Louis. Sep 25, 2025.

Scale invariance in the physics of life. Inaugural lecture, Physics of life: South American Network (online). Jun 12, 2025.

Thinking about thousands of neurons. Biophysics day, Vrije Universiteit Amsterdam. May 23, 2025.

Thinking about thousands of neurons. Distinguished lecture, Padova Neuroscience Center. May 8, 2025.

Extended mean-field theories for networks of neurons. Informal seminar, CNR Institute for Complex Systems, Rome. May 13, 2025.

Physics for maggots. Physics seminar, Università Sapienza, Roma. May 7, 2025.

Physics for maggots. Joint physics/chemistry colloquium, Vanderbilt University. Apr 10, 2025.

Moving the boundaries of physics: Perspectives on the 2024 Nobel Prize. Joint lecture with DJ Schwab. Initiative for the Theoretical Sciences, The CUNY Graduate Center. Mar 28, 2025.

Physics for maggots. Physics colloquium, Indiana University. Nov 14, 2024.

Physics of life. Physics colloquium, University of British Columbia. Jul 11, 2024.

Physics of life. Physics colloquium, Simon Fraser University. Jul 10, 2024.

Optimization and variability. Q-bio seminar, École Normale Supérieure, Paris. May 23, 2024.

Toward a theory of genetic networks. Neurobiology and Computation & Neural Systems seminar, California Institute of Technology. Jan 16, 2024.

Physics for maggots. Physics colloquium, Massachusetts Institute of Technology. Nov 2, 2023.

Scaling, zero modes, and correlations in a developing embryo. Department of Physics, University of Washington. Oct 18, 2023.

Searching for scale invariance in animal behavior. Computational Neuroscience Center, University of Washington. Oct 16, 2023.

Ambitions for theory in the physics of life. Physics colloquium, Ohio State University. Aug 29, 2023.

Finding evidence for scale invariance in animal behavior. Biological Physics/Physical Biology seminar (online series). Jul 14, 2023.

Recent progress in statistical mechanics for networks of real neurons. Physics colloquium, Università Sapienza, Roma. May 31, 2023.

Recent progress in statistical mechanics for networks of real neurons. Colloquium, Department of Computing Sciences, Bocconi University. May 19, 2023.

Theoretical physics meets the complexity of real genetic networks. Computation in the Sciences seminar, The University of Chicago. May 10, 2023.

Searching for scale invariance in neurons and behavior. Neuroscience seminar, The University of Chicago. May 9, 2023.

Descriptive and prescriptive theorizing. Janelia Research Campus, Howard Hughes Medical Institute. Nov 18, 2022.

Ambitions for theory in the physics of life. Physics colloquium, Johns Hopkins University. Nov 17, 2022.

Searching for scaling in neurons and behavior. Special colloquium, Department of Physics, University of Pittsburgh. Nov 4, 2022.

Information flow in neural and genetic networks. Student invited speaker, Program in Molecular Biophysics and Structural Biology, University of Pittsburgh. Nov 3, 2022.

Information flow in neural and genetic networks. Special seminar, Rockefeller University. Oct 19, 2022.

Searching for scaling in neurons and behavior. Center for Studies in Physics and Biology, Rockefeller University. Oct 11, 2022.

Physics of Life: A survey from the US National Academy of Sciences. Colloquium, International Centre for Theoretical Sciences, Bangalore. Jul 29, 2022.

Optimizing information flow in a genetic network. Student invited speaker, Program in Molecular Biophysics, Johns Hopkins University. Mar 30, 2022.

More than a quantitative biology: Toward theory, in the sense of physics.. Burroughs Wellcome Fund Board of Directors (online). May 19, 2021.

The physics of life: Taking theory seriously. Physics colloquium, University of Georgia (online). Oct 15, 2020.

Apparent action-at-a-distance in gene regulation. Mathematical physics seminar, Rutgers University (online). Aug 20, 2020.

Statistical mechanics for networks of real neurons. Queensland Brain Institute and Department of Physics, Queensland University, Australia (online). May 20, 2020.

The physics of life: How much can we calculate? (for a general audience). South American Institute for Fundamental Research, São Paulo, Brasil. Jan 23, 2020.

150 years of entropy. Kaapi with Kuriosity (a public lecture series), Bangalore, India. Dec 21, 2019.

Searching for simplicity: The lessons of period doubling. Symposium dedicated to Mitchell Feigenbaum, Rockefeller University. Oct 25, 2019.

Physics of information flow in genetic networks. Department of Genetics, Washington University in St Louis. April 25, 2019.

The physics of life: How much can we calculate? In celebration of the Schwinger Centennial (for a general audience), University of California at Los Angeles. Sep 27, 2018.

Precision and emergence in the physics of life. Seminar, DE Shaw, New York. Aug 6, 2018.

Towards a renormalization group for networks of neurons. Colloquium, Faculty of Physics, École Normale Supérieure, Paris, France. May 29, 2018.

City of science: The physics of life. Joint lecture with M Murthy, DJ Schwab, and EF Wieschaus (for a general audience), The CUNY Graduate Center. Mar 27, 2018.

Making the most of limited signals. Bioengineering seminar, California Institute of Technology. Mar 2, 2018.

Making the most of limited signals. Theoretical physics of biological systems seminar series, University of California at San Diego. Feb 9, 2018.

Searching for simplicity in large biological networks. Colloquium, Salk Institute for Biological Studies. Feb 8, 2018.

The physics of life: How much can we calculate? Physics colloquium, Yale University. Sep 11, 2017.

Genetic networks and the flow of positional information in embryonic development. Physics colloquium, Università Sapienza, Roma. Jun 6, 2017.

Birds, brains, and Boltzmann. Kavli Brain Forum lecture, Emory University. Jan 26, 2017.

A century (or more) of entropy. Physics colloquium, University of Pittsburgh. Jan 19, 2017.

Flocks of birds, families of proteins, and networks of neurons. Neuroscience and Biology seminar for undergraduates, University of Pittsburgh. Jan 18, 2017.

Statistical mechanics of real biological networks. Biophysics seminar, Koninklijke Nederlandse Akademie van Wetenschappen, Amsterdam, the Netherlands. Mar 29, 2016.

Physics problems in early embryonic development. Biophysics seminar, Vrije Universiteit, Amsterdam, the Netherlands. Mar 29, 2016.

Back to behavior(ism)? Kavli Institute for Brain and Mind, University of California at San Diego. Feb 17, 2016.

Searching for simplicity: A physicist's quest for theories of mind and brain. Kavli Institute for Brain and Mind (for a general audience), University of California at San Diego. Feb 16, 2016.

Learning from life: Biological strategies for (near-)optimal information processing. Seminar, Capital Fund Management, Paris, France. May 13, 2015.

Statistical mechanics for real biological networks. Institute for Genomics and Multiscale Biology, Mount Sinai School of Medicine. Feb 6, 2015.

Collective behavior in networks of neurons and flocks of birds. Neuroscience seminar, The University of Chicago. Jan 27, 2015.

Pattern formation and the flow of positional information. Integrative Genomics and Systems Biology seminar, The University of Chicago. Jan 26, 2015.

Information flow in a genetic network. Center for Life Sciences seminar, Peking University, China. Oct 23, 2014.

Statistical mechanics for real biological networks. Center for Quantitative Biology seminar, Peking University, China. Oct 22, 2014.

More perfect than we think. Lecture for undergraduates, New York University Shanghai, China. Oct 20, 2014.

Some adventures in teaching at the interface of physics and biology. New York University Shanghai, China. Oct 10, 2014.

Statistical mechanics for real biological networks. Applied Mathematics seminar, Brown University. Oct 1, 2014.

More than the sum of their parts: Collective behavior in flocks of birds and networks of neurons. Spring seminar, Capital Fund Management, New York. Jun 9, 2014.

More than the sum of their parts: Collective behavior in flocks of birds and networks of neurons. Seminar, Collège de France, Paris, France. May 16, 2014.

Physics of visual motion estimation, revisited. Colloquium, Faculty of Physics, École Normale Supérieure, Paris, France. May 15, 2014.

More perfect than we think. College of Science Spring Lectures (for a general audience). University of Arizona. Mar 10, 2014.

More than the sum of their parts: Collective behavior in flocks of birds and networks of neurons. Seminar, Champalimaud Institute, Lisbon, Portugal. Feb 20, 2014.

More than the sum of their parts: Collective behavior in flocks of birds and networks of neurons. Neuroscience seminar, University of Texas at Austin. Jan 29, 2014.

Statistical mechanics for real biological networks. Center for Theoretical Biological Physics seminar, Rice University. Jan 28, 2014.

Theoretical physics and the phenomena of life: How much can we calculate? Colloquium, National Institute of Standards and Technology. Jan 15, 2014.

Statistical mechanics for real biological networks. Physics colloquium, Georgetown University. Jan 14, 2014.

Theoretical physics and the phenomena of life: How much can we calculate? Colloquium, Mathematical and Physical Sciences Directorate, National Science Foundation. Jan 13, 2014.

The search for understanding. Princeton University Press Association Dinner. Dec 5, 2013.

More than the sum of their parts: Collective behavior in flocks of birds and networks of neurons. Monday evening seminar, Marine Biological Laboratory, Woods Hole MA. Aug 19, 2013.

More than the sum of its parts: Searching for collective behavior in a real neural network. Deans' seminar series on Theoretical and computational neurobiology, Duke University. May 3, 2013.

More than the sum of its parts: Searching for collective behavior in a real neural network. Institute for Research in Cognitive Sciences, University of Pennsylvania. Apr 12, 2013.

Information flow in embryonic development. Donnelly seminar series, University of Toronto, Canada. Apr 4, 2013.

Are biological systems poised at criticality? Physics colloquium, Boston University. Mar 5, 2013.

What can we say about the phase diagram of real neural networks? Center for Mind, Brain, and Computation, Stanford University. Feb 27, 2013.

Birds, brains, and B cells: Searching for collective behavior in real biological networks. Neuroscience seminar, University of California at San Diego. Dec 18, 2012.

Statistical mechanics for real biological networks. Frontiers in quantitative biology seminar, Stanford University. Jan 12, 2012.

Signals, noise and information flow in the regulation of gene expression. Cold Spring Harbor Laboratory, Dec 21, 2011.

Maximum entropy models for neural population activity. Center for Theoretical Neuroscience, Columbia University. Dec 9, 2011.

Statistical mechanics for real biological networks. Colloquium, Santa Fe Institute. Oct 27, 2011.

Some adventures in teaching at the interface of physics and biology. Mathematics for America Teachers' Program, New York. Sep 17, 2011.

More perfect than we imagined: A physicist's view of life (for a general audience). Kavli Institute for Theoretical Physics. Aug 31, 2011.

Chalk talk. Committee on Neurobiology, The University of Chicago, May 10, 2011.

Pushing the physical limits: Optimization principles in biological systems. Center for Network Biology, Technion, Israel. May 5, 2011.

Are biological systems poised at criticality? Physics colloquium, University of California at Berkeley. Apr 4, 2011.

Searching for collective states of neural networks. Psychology colloquium, Brooklyn College, City University of New York. Mar 16, 2011.

Are biological systems poised at criticality? Physics colloquium, Johns Hopkins University. Feb 17, 2011.

Information flow in genetic networks. Computational biology seminar, Memorial Sloan Kettering Cancer Center. Feb 3, 2011.

Information flow and the statistical mechanics of real neural networks. Neuroscience seminar, University of Southern California. Jan 7, 2011.

More perfect than we imagined: A physicist's view of life. Public lecture at The Graduate Center, City University of New York. Nov 3, 2010.

Some adventures in teaching at the interface of physics and biology. Physics department seminar, Yale University. Nov 2, 2010.

Critical phenomena and biological networks. Physics colloquium, Yale University. Nov 1, 2010.

Critical phenomena and biological networks. Physics colloquium, Queens College, City University of New York. Sep 20, 2010.

Invited conference and workshop presentations

Statistical mechanics for networks of real neurons. Global Physics Summit, American Physical Society. Mar 18, 2026.

Life and matter: An introduction. PCTS Workshop on the Physics of John Hopfield. Nov 14, 2025.

Theoretical concepts in biological physics. Logic of Life, in honor of Albert Libchaber; jointly with C Tang. ETH Zürich, Oct 19, 2025.

Search for scaling in the physics of life. Symposium in honor of Curtis Callan. École Normale Supérieure. Jun 25, 2025.

Physics for maggots. Condensed Matter Physics: New Frontiers in Long-Standing Problems, in honor of Steven Kivelson's 70th birthday. Stanford University. Mar 24, 2025.

Inference and the physics of life: From flies to flocks. Jaynes Centennial Symposium, Washington University in St. Louis. Oct 15, 2024.

Ambitions for theory in the physics of life. Frontiers in Biophysics. Vancouver. Jul 12, 2024.

Physical principles for the “design” of genetic networks. The International Symposium of Institut Curie. Paris. May 16, 2024.

Physics and biology in the early fly embryo. Joint lecture with EF Wieschaus. Frontier Science at the Interface of Physics and Biology. University of Strasbourg. May 13, 2024.

Ambitions for theory in the physics of life. ICTP-SAIFR Anniversary Symposium, South American Institute for Fundamental Research, São Paulo, Brasil. Feb 19, 2024.

Recent progress on statistical physics for networks of real neurons. 125th Statistical Mechanics Meeting, Rutgers University. Dec 17, 2023.

Recent progress in the statistical physics of real neural networks. March Meeting of the American Physical Society, Las Vegas, NV. Mar 7, 2023.

Efficient representation, far from the source. Vision and Mind: A Symposium in Honour of Horace Barlow. Cambridge University. Dec 16, 2022.

Searching for scaling in neurons and behavior. 20th Anniversary Conference, Center for Quantitative Biology, Peking University (hybrid). Dec 4, 2022.

Predictions. Biophysics: Searching for Principles. The CUNY Graduate Center. Sep 16, 2022.

Ambitions for theory. Keynote lecture, Future of the Physics of Life, Amsterdam. Jun 16, 2022.

Compressibility and the success of simple models for complex systems. More is Different, Collège de France. Jun 2, 2022.

Ambitions for theory. Inaugural workshop, Center for Computational Neuroscience, Flatiron Institute, New York. Mar 8, 2022.

Correlations, scaling, and dimensionality. Annual conference on Computational Neuroscience, Leipzig (online). Jul 4, 2021.

Ambitions for theory in biological physics. Quantum connections, in honor of Frank Wilczek’s 70th birthday, Högberga Gård, Lidingö, Sweden (hybrid). Jun 24, 2021.

Squeezing more bits out of fewer molecules. 3rd Annual Conference of Quantitative Approaches in Biology, NSF–Simons Center for Quantitative Biology, Northwestern University (online). Nov 21, 2020.

Statistical physics for networks of real neurons: Progress and problems. Physics of Brains, University of York (online). Nov 18, 2020.

An introduction to systems thinking. Applying Systems Thinking to Regenerative Medicine: A Workshop. National Academies of Sciences, Engineering, and Medicine (online). Oct 22, 2020.

Taking theory seriously. UK Physics of Life Network Launch, University of York (online). Oct 14, 2020.

Searching for simplicity. Bernstein Conference, Berlin (online). Oct 1, 2020.

Criticality in biological systems, from molecules to brains. ICAM Global Summit 2020 (online). Jul 24, 2020.

Statistical mechanics for networks of real neurons. Brain and Mind workshop, Shenasa Scientific Community, Sharif University of Technology, Tehran, Iran (online). May 22, 2020.

What do we mean by the dimensionality of behavior?. Physics of Behavior Virtual Workshop, Emory University (online). Apr 30, 2020.

Can we derive the structure of genetic networks from optimization principles?. Beyond the Cell Atlas: Theory, Models, and Computation, Berkeley. Oct 28, 2019.

Laudatio for Curtis Callan. 121st Statistical Mechanics Meeting, Rutgers University. May 13, 2019.

RG-inspired approaches to networks of real neurons. 121st Statistical Mechanics Meeting, Rutgers University. May 12, 2019.

Thinking about a thousand neurons. Workshop on Neurophysics, Center for Biological Physics, University of California at Los Angeles. Sep 28, 2018.

Conference summary. Quantitative approaches to naturalistic behaviors. Banbury Conference Center, Cold Spring Harbor Laboratory. Sep 26, 2018.

Outlook: Information theoretic principles for biological networks. Conference on Bits and Biology, The CUNY Graduate Center. Sep 14, 2018.

Coarse-graining and hints of scaling in a population of 1000+ neurons. Program on Recording, analyzing, manipulating, interpreting, and modeling whole brain activity, Kavli Institute for Theoretical Physics. Aug 29, 2018.

Life is like a river: Moving beyond metaphors in physics and biology. Triennial meeting, Phi Beta Kappa Society, Boston MA. Aug 2, 2018.

Optimization and criticality in biological systems. Physics Next workshop, *The Physical Review*, Riverhead NY. Apr 25, 2018.

Thinking about 1000 neurons. Workshop on Principles in complex biophysical systems and beyond, Academia Sinica, Taipei, Taiwan. Oct 30, 2017.

Intercellular interactions and patterns. Solvay Congress on The physics of living matter, Brussels, Belgium. Oct 19, 2017.

Interdisciplinary education. Panel discussion at Statistical Physics Cornucopia, in honor of Marc Mézard's 60th birthday, Paris, France. Sep 7, 2017.

Thinking about 1000 neurons. Human Frontiers Science Program Awardees Meeting, Lisbon, Portugal. Jul 11, 2017.

Physics meets biology in the fly embryo: An adventure story. Joint lecture with EF Wieschaus. The physics of living matter for tomorrow, sponsored by the Human Science Frontiers Program, Lisbon, Portugal. Jul 9, 2017.

Genetic networks and the flow of positional information in embryonic development. March Meeting of the American Physical Society, Baltimore MD. Mar 17, 2016.

How much can we calculate? Toward a theory of biological networks. Max Planck Symposium on Biological Networks, Berlin, Germany. Feb 24, 2016.

The physics of life: How much can we calculate? Walter Kohn Memorial Symposium, Kavli Institute for Theoretical Physics. Dec 8, 2016.

Provocations. Simons Foundation Workshop on Animal behavior, New York. Nov 29, 2016.

Statistical mechanics of real biological networks. Plenary lecture at StatPhys 26, Lyon, France. Jul 19, 2016.

Progress on the statistical mechanics of real neural networks. Workshop on Statistical physics methods in biology and computer science, École Normale Supérieure, Paris, France. Jul 11, 2016.

More than the sum of its parts: Collective phenomena in living systems, from single molecules to flocks of birds. American Society for Mass Spectrometry, San Antonio, TX. Jun 9, 2016.

Genetic networks and the flow of positional information in embryonic development. March Meeting of the American Physical Society, Baltimore MD. Mar 17, 2016.

Birds, brains, and Boltzmann. Frontiers in physics, pattern formation, and complex materials far from equilibrium, in honor of James Langer's 80th birthday. National Academy of Sciences, Washington DC. Oct 26, 2015.

Searching for universality in the state space of neural networks. Simons Collaboration on the Global Brain, annual meeting, New York. Sep 11, 2015.

Can we measure the dimensionality of perceptual space? Program on Deconstructing the sense of smell, Kavli Institute for Theoretical Physics. Jul 20, 2015.

Searching for simplicity. DARPA Biocomplexity workshop, Washington DC. Jun 9, 2015.

From correlations to collective activity: Lessons from the retina, and explorations beyond. Banbury workshop on Neuronal response variability and correlation, Cold Spring Harbor Laboratory. Apr 21, 2015.

Predictive information in the neural code. Information Theory and Applications, San Diego CA. Feb 2, 2015.

Some shared adventures. Allison Doupe Memorial Symposium, University of California at San Francisco. Jan 23, 2015.

Statistical mechanics for real biological networks. Cold Spring Harbor Asia Conference on Quantitative biology: From genes to cells to networks, Suzhou, China. Oct 15, 2014.

Are we asking the right questions? Closing lecture, q-bio conference, Santa Fe NM. Aug 16, 2014.

Bits and biology: Making models and testing principles. Challenges and opportunities for the science of information. National Academy of Sciences, Irvine CA. Aug 4, 2014.

Phenomenology and more. Overarching issues in the theory of highly correlated electron fluids, in honor of Steven Kivelson's 60th birthday. Stanford University. Jun 20, 2014.

Laudatio for John Hopfield. 111th Statistical Mechanics Meeting, Rutgers University. May 12, 2014.

Thermodynamics for networks of real neurons. 111th Statistical Mechanics Meeting, Rutgers University. May 12, 2014.

Perspectives on theory at the interface of physics and biology. First Simons Foundation Conference on Theory in Biology, New York. Apr 11, 2014.

Entropy, information, and the brain. International workshop on Information, Representation and Learning, in honor of Naftali Tishby's 60th birthday, Hebrew University of Jerusalem, Israel. May 30, 2013.

(re-)Opening remarks. National Science Foundation workshop on the BRAIN Initiative, Washington DC. May 6, 2013.

Are we asking the right questions? Tenth anniversary lecture, Conference on Computational and Systems Neuroscience, Salt Lake City UT. Feb 28, 2013.

Theories, models, and related matters. American Society for Cell Biology, San Francisco CA. Dec 17, 2012.

Paths to a predictive theory of biological systems: How much can we calculate, rather than fit? Center for the Science of Information, Purdue University. Dec 3, 2012.

Birds, brains, and B cells: Statistical mechanics for real biological networks. 10th Anniversary Conference, Mathematical Biosciences Institute, Ohio State University. Sep 12, 2012.

Birds, brains, and B cells: Statistical mechanics for real biological networks. Sensory coding and the natural environment, IST Austria. Sep 10, 2012.

Birds, brains, and B cells: Statistical mechanics for real biological networks. American Association of Physics Teachers Summer Meeting, Philadelphia PA. Jul 30, 2012.

Information flow and collective behavior in real biological networks. Statistical Mechanics in Systems Biology, Capri, Italy. May 30, 2012.

The mesoscale interface between physics and biology. March Meeting of the American Physical Society, Chicago IL. Feb 29, 2012.

The flow of positional information, in bits. Program on the Dynamics of development, Kavli Institute for Theoretical Physics. Aug 23, 2011.

Statistical mechanics for a network of real neurons. Sloan-Swartz Meeting on Theoretical and Computational Neuroscience. Janelia Farm Research Campus, HHMI, Ashburn VA. Jul 12, 2011.

Fundamental physical limits in biological systems. Signal processing in biological systems. Brooklyn NY. Dec 11, 2011.

Physical principles in neural coding and computation. International Conference on Biological Physics, University of California at San Diego. Jun 22, 2011.

How much can we calculate? Opportunities at the Interface of Physics and Biology, sponsored by the Burroughs Wellcome Fund and the WM Keck Foundation, Chicago. Jul 29, 2010.

Some adventures in teaching at the interface of physics and biology. March Meeting of the American Physical Society, Portland OR. Mar 16, 2010.

The other half of western civilization: An experiment in multidisciplinary education. American Association of Physics Teachers, Washington DC. Feb 15, 2010.

Teaching

Regular courses. Working at the interface of two disciplines with very different pedagogical traditions, I have always been fascinated by the challenge of combining breadth and depth, achieving interdisciplinarity without loss of discipline. My goals have been to present the traditional canon of theoretical physics as inspiring rather than constraining, to present the striking phenomena of biology as beautiful rather than complicated, and to create a path for the advancing frontier of our understanding to feed back more efficiently into our teaching at all levels. In addition, I have long been concerned about the huge gap between a conventional undergraduate education and the working language of modern theoretical physics, and have tried to close this gap wherever possible. Descriptions here are aimed at a relatively broad audience.

Biophysics Princeton: 12+ times, most recently Spring 2025. The CUNY Graduate Center: Spring 2012.

We begin with one biological phenomenon that has a special appeal to physicists, the ability of the visual system to count single photons. Exploring this remarkable phenomenology, we meet physics problems at many different levels of organization, from single molecules to learning in the organism as a whole. We then shift to examine general physical principles—the balance between robustness and fine tuning or selection, the fact that life functions on scales where noise is not negligible, and the idea that biological systems can construct efficient representations of the information relevant for their function—and see how these principles play out in a wide variety of different biological systems, from bacteria to primate brains. The course formed the basis for *Biophysics: Searching for Principles* (Princeton University Press, 2012), which is the first graduate level textbook to present the physics of biological systems as a branch of physics, rather than as an application of physics methods to biology.

Thermal physics Princeton: Fall 2015–17, '21, and '23–24. Berkeley.¹⁰

A core course for physics majors, combining thermodynamics and statistical mechanics. These are among the most general and useful things one can learn as a physicist, and our understanding of the subject has been revolutionized, but the course typically remains as it was in 1950. I turned the traditional course upside down, starting with how systems come to equilibrium and the relations between fluctuations and dissipation, proceeding to the Boltzmann distribution and more traditional topics, concluding with an introduction to modern renormalization group ideas. Teaching the course again at Princeton, I developed my approach more fully, using simulation both as a method for solving problems and as motivation in exploring the behavior of realistic, interacting systems.

Topics in biophysics and quantitative biology Princeton: Fall 2015–17 and '20.
Rockefeller University: Fall 2008.

Exploring major themes at the interface of physics and biology, with a combination of lectures and student presentations of recent papers. Two examples are statistical physics approaches to biological networks (2015, '17, and '20) and signals, noise, and information flow (2008 and '16). In each case I tried to present unifying theoretical ideas in multiple biological contexts, spanning scales from single molecules to animal groups. Although cross-listed as a physics course, I also wanted these courses to be accessible to students in our quantitative biology program, and so a number of lectures were devoted to background material, with exercises.

An integrated, quantitative introduction to the natural sciences. Princeton: Fall 2004–13, and '19.

A full year, double course offered jointly by the departments of chemistry, computer science, molecular biology, and physics. Provides a mathematically and computationally sophisticated introduction to chemistry and physics, with connections to biology wherever possible, and is the first step in an educational experiment which we hope will enable students to combine the mathematical depth of physics with the phenomenological richness of modern

¹⁰During my four years on the Berkeley faculty (1986–90), I taught one course every year (below), and four courses once each, but I have lost track of which course was offered in which year.

biology. I was the chief architect of the curriculum; the key idea is that we achieve integration of the disciplines by organizing around the kinds of mathematical models that we use in describing the world. As hoped, students have distributed themselves among many majors, about half in biology and half in the physical sciences and engineering.

Mechanics II Princeton: Fall 2011–13.

Undergraduate physics majors take an advanced mechanics course. The Princeton version came to be known (affectionately?) as “death mechanics,” and it was realized that we needed a kinder, gentler version. My view was that the course should be gentler in what it demanded that the students produce, but not less ambitious in what the students could learn if they put in the effort. I chose Landau and Lifshitz as the main text, with supplements, the centerpiece of the course was the Caldeira–Leggett model for the origins of apparent dissipation in a Hamiltonian system, and we ended with a discussion of chaos. Evaluations suggest that ambition is not at all a bad thing.

Mechanics I Princeton: Fall 2001–02.

In my first experience of teaching freshmen, I feel that I learned as much as the students. In particular, I learned that “honors” courses don’t need gate keepers: by being honest about what we expect, and talking to the students about their own interests, students could self-select with high reliability. Indeed, the fraction of students who need to be discouraged because they overestimate their preparation is small; many more students, especially women, need to be encouraged because they perceive themselves not to be “the physics type” even when they perform very well on all functional measures. I also learned that elementary courses offer opportunities to discuss deep issues that touch the most sophisticated ideas of our field. Although many forces contributed, students who passed through our version of this course became physics majors with higher probability than in previous years.

Special topics in physics: Biophysics Berkeley.

Rather than seeing biophysics as being about molecules, or about quantitative approaches to physiology, or about some other isolated meeting point between the physical and biological sciences, I tried to give a feeling for the great sweep of questions that physicists ask about the phenomena of life: from the interplay between quantum and classical dynamics in single molecules to the function of biochemical networks to the long term dynamics of adaptation, learning, and memory in the brain. These ideas evolved into the biophysics course discussed above.

Special topics in physics: The surprising success of simple models Berkeley.

Sitting through the standard curriculum, students could be forgiven for thinking that physics “works” only on problems so simple as to be irrelevant to most of the natural world. But one of the striking themes in modern physics is the success of simple mathematical models in describing the essence of much more complex systems. The goal of this course was to expose students to these ideas in a systematic way. Some of this is classical, but our understanding was revolutionized by a very general theoretical framework, the renormalization group, which took its final form in the 1970s. In retrospect this course was a first effort at extrapolating from the profound successes of modern physics to more general lessons about the construction of models and their interaction with data.

Honors undergraduate seminar: Path integrals. Berkeley.

The path integral formulation of quantum mechanics plays an essential role in the contemporary theoretical physicist’s view of the world, yet it was (then) entirely absent from most undergraduate curricula. I experimented with a seminar course for advanced undergraduates. Topics included the emergence of classical mechanics as an approximation to quantum mechanics, parallel ideas of dominant paths for stochastic processes such as chemical reactions, and then new ideas about dissipation in quantum mechanics. In the second half of the course the students presented talks on papers from the literature, and I was astonished by their successful tackling of extremely technical material. This experience convinced me that we tend to underestimate what students can do, and that we shouldn’t shy away from teaching undergraduates in the same language that we think as practicing scientists.

Introduction to the biophysics of macromolecules Berkeley: Fall 1987–90.

When I inherited this course, it was about methods: X-ray diffraction, fluorescence, etc.. As an alternative, I started with how we reduce questions about biological function to questions about single molecules; methods were introduced as ways of answering these questions rather than as ends in themselves. I think that this was the start of my rebellion against the definition of biophysics as merely the methods of physics applied to biological problems. The course included mathematically rigorous treatments of helical diffraction theory and DNA structure, the statistical mechanics of allostery, kinetic proofreading, DNA topology, and more; problem sets routinely asked the students to make order of magnitude estimates and draw quantitative inferences from raw data.

Physics of the sensory systems Berkeley: Spring quarter 1982.

While still a PhD student at Berkeley I taught, together with Professor WG Owen, a course on vision and hearing; we developed the syllabus together and each gave half the lectures. This was a time when quantitative measurements on the electrical responses of single receptor cells still were fairly new, and we wanted to place these exciting results in the context of physical questions about sensitivity, reliability, and noise. In retrospect this was a rather forward looking experiment in multi-disciplinary education, and was very well received by the students.

Summer schools. There is a long tradition of summer schools in theoretical physics, and in several areas of experimental biology. These short, intense courses provide a bridge between the canon of classroom teaching and professional discussion in research seminars, nurturing the next generation of intellectual community. I have found this to be a very exciting teaching environment. These are courses that I helped to organize and guide, sometimes over an extended period; a full listing of recent activity is given under Invited lectures, above.

Physics of Life Princeton University, Summers 2018–20 (online in 2020), '22–23

Few undergraduates are exposed to the intellectual opportunities at the interface of physics and biology, and many of the core physics topics that provide the most useful foundation for such explorations are given short shrift in the traditional US curriculum. To address these issues we have mounted an intense two-week summer school aimed at rising seniors, supported by our Center for the Physics of Biological Function; Joshua Shaevitz and I are co-organizers. The course includes foundational lectures on both physics and biology, full day joint presentations from teams of collaborating theorists and experimentalists presenting the state of a field and the evolution of their collaboration, research seminars, and laboratory visits. The final afternoon is devoted to an open discussion with the students, ranging widely across concerns about planning for graduate school applications, the daily life of a scientist, strategies for choosing thesis topics, and more. We had 24 students, with 8 recruited from the enormous—and enormously diverse—undergraduate student body of the CUNY system, who also are funded to work in research groups at the Center over the remainder of the summer. The online version (during the pandemic) attracted 1000 students from around the world.

Adventures in the Theoretical Sciences The CUNY Graduate Center, Summer 2020.

In response to the COVID–19 crisis, which canceled summer schools around the world, I organized an informal online school. Topics included astrophysics, biophysics, condensed matter physics, machine learning, and quantum field theory, aimed at advanced undergraduates and beginning graduate students. Typical attendance was ~100 students, from all over the world.

Methods in Computational Neuroscience Marine Biological Laboratory, Summers 1991–2015.

The Marine Biological Laboratory has had a tradition of summer schools from the 1800s. In the late 1980s, they launched a course on computational neuroscience, and I participated for twenty-five years; my colleague Rob de Ruyter van Steveninck and I served as directors from 1998 through 2002. We structured the course around extended joint lectures from collaborating theorists and experimentalists; organized students into groups with mixed backgrounds (exactly half the students came from physics/math/engineering backgrounds and half from biology) to work on a series of difficult problem sets, helping to teach the skills required to cross disciplinary boundaries; and broke away from the traditional model of prerequisite lectures, jumping into exciting problems and filling in missing knowledge with individualized small group tutorials. This course has become the premier meeting ground for theorists and experimentalists with an interest in the brain, and the sense of community among students and faculty has been important for the field. Over decades, the average age of the lecturers has held fairly constant, not least because a number of former students now are faculty members.

Princeton Lectures on Biophysics NEC Research Institute, Summers 1991–95.

When I moved to the newly founded NEC Research Institute, many young physicists were interested in biological problems but there were few places to learn about them. We decided to have a series of one-week summer workshops, which ran more or less annually through the 1990s. I organized the first five, which started with a broad sampling of topics and then focused in successive years on problems ranging from the dynamics of single molecules to adaptation and learning in the brain. One especially lively session on vision was the subject of a news report in *Science* **261**, 982–984 (1993). These workshops were an early meeting ground for many physicists who have since established themselves as substantial contributors to the field.