

# COLD SPRING HARBOR SYMPOSIA ON QUANTITATIVE BIOLOGY

## VOLUME LXXIX

### Cognition

[symposium.cshlp.org](http://symposium.cshlp.org)

Symposium organizers and Proceedings editors: Cori Bargmann (*The Rockefeller University*),  
Daphne Bavelier (*University of Geneva, Switzerland, and University of Rochester*),  
Terrence Sejnowski (*The Salk Institute for Biological Studies*), and David Stewart  
and Bruce Stillman (*Cold Spring Harbor Laboratory*)

COLD SPRING HARBOR LABORATORY PRESS

2014

## COLD SPRING HARBOR SYMPOSIA ON QUANTITATIVE BIOLOGY VOLUME LXXIX

© 2014 by Cold Spring Harbor Laboratory Press  
International Standard Book Number 978-1-621821-26-7 (cloth)  
International Standard Book Number 978-1-621821-27-4 (paper)  
International Standard Serial Number 0091-7451  
Library of Congress Catalog Card Number 34-8174

*Printed in the United States of America*  
*All rights reserved*  
*COLD SPRING HARBOR SYMPOSIA ON QUANTITATIVE BIOLOGY*  
*Founded in 1933 by*  
REGINALD G. HARRIS  
*Director of the Biological Laboratory 1924 to 1936*  
*Previous Symposia Volumes*

- |   |  |
|---|--|
| I (1933) Surface Phenomena  | XXXIX (1974) Tumor Viruses   |
| II (1934) Aspects of Growth   | XL (1975) The Synapse  |
| III (1935) Photochemical Reactions  | XLI (1976) Origins of Lymphocyte Diversity                                   |
| IV (1936) Excitation Phenomena  | XLII (1977) Chromatin  |
| V (1937) Internal Secretions  | XLIII (1978) DNA: Replication and Recombination                              |
| VI (1938) Protein Chemistry   | XLIV (1979) Viral Oncogenes  |
| VII (1939) Biological Oxidations  | XLV (1980) Movable Genetic Elements  |
| VIII (1940) Permeability and the Nature of Cell Membranes                                 | XLVI (1981) Organization of the Cytoplasm                                    |
| IX (1941) Genes and Chromosomes: Structure and Organization                               | XLVII (1982) Structures of DNA   |
| X (1942) The Relation of Hormones to Development  | XLVIII (1983) Molecular Neurobiology   |
| XI (1946) Heredity and Variation in Microorganisms  | XLIX (1984) Recombination at the DNA Level                                   |
| XII (1947) Nucleic Acids and Nucleoproteins   | L (1985) Molecular Biology of Development                                    |
| XIII (1948) Biological Applications of Tracer Elements                                    | LI (1986) Molecular Biology of Homo sapiens                                  |
| XIV (1949) Amino Acids and Proteins   | LII (1987) Evolution of Catalytic Function                                   |
| XV (1950) Origin and Evolution of Man   | LIII (1988) Molecular Biology of Signal Transduction                         |
| XVI (1951) Genes and Mutations  | LIV (1989) Immunological Recognition   |
| XVII (1952) The Neuron  | LV (1990) The Brain  |
| XVIII (1953) Viruses  | LVI (1991) The Cell Cycle  |
| XIX (1954) The Mammalian Fetus: Physiological Aspects of Development                      | LVII (1992) The Cell Surface   |
| XX (1955) Population Genetics: The Nature and Causes of Genetic Variability in Population | LVIII (1993) DNA and Chromosomes   |
| XXI (1956) Genetic Mechanisms: Structure and Function                                     | LVIX (1994) The Molecular Genetics of Cancer                                 |
| XXII (1957) Population Studies: Animal Ecology and Demography                             | LX (1995) Protein Kinesis: The Dynamics of Protein Trafficking and Stability |
| XXIII (1958) Exchange of Genetic Material: Mechanism and Consequences                     | LXI (1996) Function & Dysfunction in the Nervous System                      |
| XXIV (1959) Genetics and Twentieth Century Darwinism                                      | LXII (1997) Pattern Formation during Development                             |
| XXV (1960) Biological Clocks  | LXIII (1998) Mechanisms of Transcription                                     |
| XXVI (1961) Cellular Regulatory Mechanisms  | LXIV (1999) Signaling and Gene Expression in the Immune System               |
| XXVII (1962) Basic Mechanisms in Animal Virus Biology                                     | LXV (2000) Biological Responses to DNA Damage                                |
| XXVIII (1963) Synthesis and Structure of Macromolecules                                   | LXVI (2001) The Ribosome   |
| XXIX (1964) Human Genetics  | LXVII (2002) The Cardiovascular System                                       |
| XXX (1965) Sensory Receptors  | LXVIII (2003) The Genome of Homo sapiens                                     |
| XXXI (1966) The Genetic Code  | LXIX (2004) Epigenetics  |
| XXXII (1967) Antibodies   | LXX (2005) Molecular Approaches to Controlling Cancer                        |
| XXXIII (1968) Replication of DNA in Microorganisms  | LXXI (2006) Regulatory RNAs  |
| XXXIV (1969) The Mechanism of Protein Synthesis   | LXXII (2007) Clocks and Rhythms  |
| XXXV (1970) Transcription of Genetic Material   | LXXIII (2008) Control and Regulation of Stem Cells                           |
| XXXVI (1971) Structure and Function of Proteins at the Three-dimensional Level            | LXXIV (2009) Evolution: The Molecular Landscape                              |
| XXXVII (1972) The Mechanism of Muscle Contraction   | LXXV (2010) Nuclear Organization and Function                                |
| XXXVIII (1973) Chromosome Structure and Function  | LXXVI (2011) Metabolism and Disease  |
|   | LXXVII (2012) The Biology of Plants  |
|   | LXXVIII (2013) Immunity and Tolerance  |

**Front cover (paperback):** Image by James Whitaker, Cold Spring Harbor Laboratory. Watermark inspired by Santiago Ramón y Cajal (1852–1934), a distinguished Spanish neuroscientist who, together with Italian Camillo Golgi, won the Nobel Prize in Physiology or Medicine in 1906 “in recognition of their work on the structure of the nervous system.”

Authorization to photocopy items for internal or personal use, or the internal or personal use of specific clients, is granted by Cold Spring Harbor Laboratory Press, provided that the appropriate fee is paid directly to the Copyright Clearance Center (CCC). Write or call CCC at 222 Rosewood Drive, Danvers, MA 01923 (508-750-8400) for information about fees and regulations. Prior to photocopying items for educational classroom use, contact CCC at the above address. Additional information on CCC can be obtained at CCC Online at [www.copyright.com](http://www.copyright.com).

For a complete catalog of all Cold Spring Harbor Laboratory Press publications, visit our website [www.cshlpress.org](http://www.cshlpress.org).

Online access: Please visit our companion website at [symposium.cshlp.org](http://symposium.cshlp.org). For access questions, please contact Cold Spring Harbor Laboratory Press at [cshpress@cshl.edu](mailto:cshpress@cshl.edu).

## Symposium Participants

- ABDUS-SABOOR, ISHMAIL, Weill Cornell Medical College in Qatar, Doha, Qatar
- ABRAHAM, ANNA, Kuwait University, Safat, Kuwait
- AGETSUMA, MASAKAZU, Osaka University, Ibaraki, Japan
- AHRENS, MISHA, Janelia Farm, Howard Hughes Medical Institute, Ashburn, Virginia
- AHRENS, SANDRA, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- AKRAMI, ATHENA, Princeton University, Howard Hughes Medical Institute, Princeton, New Jersey
- ANDERSON, DAVID, Caltech/Howard Hughes Medical Institute, Pasadena, California
- ANGELAKI, DORA, Baylor College of Medicine, Houston, Texas
- ANOKHIN, KONSTANTIN, Kurchatov Institute National Research Center, Moscow, Russia
- ANSELM, FRANCESCA, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- APERGIS-SCHOUTE, ANNEMIEKE, University of Cambridge, Cambridge, United Kingdom
- ARAI, YOSHIO, University of Pittsburgh, Pittsburgh, Pennsylvania
- AVERY, MICHAEL, Salk Institute, San Diego, California
- AXEL, RICHARD, Columbia University, New York, New York
- BANDYOPADHYAY, ARKARUP, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- BAO, ZHIRONG, Sloan-Kettering Institute, New York, New York
- BARBASH, SHAHAR, Hebrew University of Jerusalem, Jerusalem, Israel
- BARGMANN, CORI, The Rockefeller University, New York, New York
- BATCHELOR, ALEXANDRA, Harvard University, Cambridge, Massachusetts
- BATSCHING, SOPHIE, University Würzburg, Würzburg, Germany
- BAVELIER, DAPHNE, University of Geneva, Geneva, Switzerland and University of Rochester, Rochester, New York
- BENDESKY, ANDRES, Harvard University, Cambridge, Massachusetts
- BHANDAWAT, VIKAS, Duke University, Durham, North Carolina
- BIRNBAUM, REBECCA, Lieber Institute for Brain Development, Johns Hopkins, Baltimore, Maryland
- BOBOILA, CRISTIAN, Columbia University, New York, New York
- BOLDING, KEVIN, Duke University, Durham, North Carolina
- BONNER, MICHAEL, University of Pennsylvania, Philadelphia, Pennsylvania
- BORGES MONROY, REBECA, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- BORST, ALEXANDER, Max Planck Institute of Neurobiology, Martinsried, Germany
- BRAATEN, DOUGLAS, The New York Academy of Sciences, New York, New York
- BRODY, CARLOS, Princeton University, Princeton, New Jersey
- BRUSH, ELEANOR, Princeton University, Princeton, New Jersey
- BUZSÁKI, GYÖRGY, New York University, Langone Medical Center, New York, New York
- CARCEA, IOANA, New York University Medical School, New York, New York
- CARDOSO-LEITE, PEDRO, University of Geneva, Geneva, Switzerland
- CARNIOL, KAREN, *Cell*, Cambridge, Massachusetts
- CARRASCO, MARISA, New York University, New York, New York
- CAZAKOFF, BRITTANY, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- CHAE, HONG GOO, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- CHANG, DONG-SEON, Max Planck Institute for Biological Cybernetics, Tübingen, Germany
- CHARTARIFSKY, LITAL, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- CHEN, XIUYE, Harvard University, Cambridge, Massachusetts
- CHOUARD, TANGUY, *Nature*, London, United Kingdom
- CHUN, MARVIN, Yale University, New Haven, Connecticut
- CHURCHLAND, ANNE, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- CHURCHLAND, MARK, Columbia University, New York, New York
- CHURCHLAND, PATRICIA, University of California, San Diego, La Jolla, California
- COEN, PHILIP, Princeton University, Princeton, New Jersey
- DAN, YANG, University of California, Berkeley, Berkeley, California
- DANG, CHUNG, Fred Hutchinson Cancer Research Center, Seattle, Washington
- DANIELS, BRYAN, University of Wisconsin–Madison, Madison, Wisconsin
- DASGUPTA, SHAMIK, University of Oxford, Oxford, United Kingdom
- DAVID, KAREN, National Institutes of Health/National Institute of Neurological Disorders and Stroke, Bethesda, Maryland
- DEISSEROTH, KARL, Stanford University, Stanford, California
- DELEVICH, KRISTEN, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- DESIMONE, ROBERT, Massachusetts Institute of Technology/McGovern Institute for Brain Research, Cambridge, Massachusetts
- DEVINENI, ANITA, Columbia University, New York, New York
- DICARLO, JAMES, McGovern Institute for Brain Research/Massachusetts Institute of Technology, Cambridge, Massachusetts
- DICKERSON, MICHAEL, Southwest Baptist University, Springfield, Missouri
- DOBOSIEWICZ, MAY, The Rockefeller University, New York, New York
- DUAN, CHUNYU, Princeton University, Princeton, New Jersey
- DUBNAU, JOSH, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- DUBOWITZ, LILLI, London, United Kingdom
- DUBOWITZ, VICTOR, University of London, London, United Kingdom
- DULAC, CATHERINE, Howard Hughes Medical Institute/Harvard University, Cambridge, Massachusetts
- EBIHARA, AKINORI, The Rockefeller University, New York, New York
- ECKMEIER, DENNIS, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- EMERY, VIRGINIA OLGA, Dartmouth Medical School, Bow, New Hampshire
- EMMONS, SCOTT, Albert Einstein College of Medicine, Bronx, New York
- ERLICH, JEFFREY, Princeton University, Princeton, New Jersey
- FARNSWORTH, BRYN, Uppsala University, Uppsala, Sweden
- FASSHI, ARASH, International School for Advanced Studies (ISAS/ SISSA), Trieste, Italy
- FEE, MICHAEL, Massachusetts Institute of Technology, Cambridge, Massachusetts
- FERNALD, RUSSELL, Stanford University, Stanford, California
- FISCHER, JAN, University of Zurich, Zollikon, Switzerland
- FISCHLER, WALTER, Columbia University, New York, New York
- FISHMAN, ZVI, Columbia University, New York, New York
- FLAVELL, STEVEN, Howard Hughes Medical Institute/Rockefeller University, New York, New York
- FRANK, LOREN, University of California, San Francisco, San Francisco, California
- FRANKS, KEVIN, Duke University, Durham, North Carolina
- FREEMAN, JEREMY, Howard Hughes Medical Institute, Ashburn, Virginia
- FREIWALD, WINRICH, The Rockefeller University, New York City, New York

- FUKUNAGA, IZUMI, National Institute for Medical Research, London, United Kingdom
- FULLER, GREGORY, Johns Hopkins University, Baltimore, Maryland
- GANN, ALEX, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- GARBE, DAVID, University of Pennsylvania, Philadelphia, Pennsylvania
- GARCIA DA SILVA, PEDRO, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- GARDNER, DANIEL, Weill Cornell Medical College, New York, New York
- GARDNER, ESTHER, New York University School of Medicine, New York, New York
- GAZZALEY, ADAM, University of California, San Francisco, San Francisco, California
- GHOSH, SANCHARI, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- GLIMCHER, PAUL, New York University, New York, New York
- GOARD, MICHAEL, Massachusetts Institute of Technology, Cambridge, Massachusetts
- GOLDEN, JAMES, Cornell University, Ithaca, New York
- GOLDSTEIN, ANN, *Neuron*, Cambridge, Massachusetts
- GRAYBIEL, ANN, Massachusetts Institute of Technology, Cambridge, Massachusetts
- GREENE, JOSHUA, Rockefeller University, New York, New York
- GROPPE, DAVID, Feinstein Institute for Medical Research, Manhasset, New York
- GU, YIRAN, New York University, New York, New York
- GU, ZIRONG, Cincinnati Childrens Hospital Medical Center, Cincinnati, Ohio
- GUTNISKY, DIEGO, Janelia Farm Research Campus, Ashburn, Virginia
- HANGYA, BALAZS, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- HANSEN, CELIA, University of California, San Francisco, San Francisco, California
- HARRIS, HILA, Weizmann Institute of Science, Rehovot, Israel
- HATTORI, DAISUKE, Columbia University, New York, New York
- HECK, DETLEF, University of Tennessee Health Science Center, Memphis, Tennessee
- HIROKAWA, JUNYA, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- HOCEVAR BREZAVSCEK, ANA, The Rockefeller University, New York, New York
- HOEKSTRA, HOPI, Harvard University, Cambridge, Massachusetts
- HONG, INGIE, Johns Hopkins Medical Institute, Baltimore, Maryland
- HOUSE, PATRICK, Stanford University, Stanford, California
- HUGHES, VIRGINIA, *National Geographic*, *Popular Science*, *MATTER*, Brooklyn, New York
- HURTADO-LÓPEZ, JULIÁN, Universidad Autónoma de Occidente, Cali, Colombia
- IWASAKI, KENICHI, University of Michigan, Ann Arbor, Michigan
- JAKIMO, ALAN, Hofstra University, Hempstead, New York
- JARAMILLO, SANTIAGO, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- JESSELL, THOMAS, Columbia University/Hammer Health Sciences Center, New York, New York
- JIANG, PING, University of Helsinki, Helsinki, Finland
- JIN, XIN, Rockefeller University, New York, New York
- JITSUKI, SUSUMU, Yokohama City University, Yokohama, Japan
- JONES, ADAM, National Institute of Mental Health/National Institutes of Health, Bethesda, Maryland
- KAHN, KEVIN, Johns Hopkins University, Baltimore, Maryland
- KANWISHER, NANCY, Massachusetts Institute of Technology, Cambridge, Massachusetts
- KARSH, NOAM, University of Haifa, Haifa, Israel
- KAUFMAN, MATTHEW, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- KEANE, BRIAN, Rutgers University, Piscataway, New Jersey
- KEBSCHULL, JUSTUS, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- KENNEDY, ANN, Columbia University, New York, New York
- KEPECS, ADAM, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- KERR, MATTHEW, Johns Hopkins University, Baltimore, Maryland
- KIM, JINEUN, Korea Advanced Institute of Science and Technology, Daejeon-si, South Korea
- KIM, JOSHUA, Massachusetts Institute of Technology, Boston, Massachusetts
- KIM, YONGSOO, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- KLEINFELD, DAVID, University of California, San Diego, La Jolla, California
- KOENIG, SEBASTIAN, Universität Würzburg, Würzburg, Germany
- KORFF, RICKI, Cornell University, Ithaca, New York
- KOTTMANN, ANDREAS, City College of New York, New York, New York
- KRISHNAN, KEERTHI, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- KRISTAN, JR., WILLIAM, University of California, San Diego, La Jolla, California
- KRUG, LISA, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- KUBIE, JOHN, State University of New York Downstate Medical Center, Brooklyn, New York
- KUCHIBHOTLA, KISHORE, New York University School of Medicine, New York, New York
- KUHL, PATRICIA, University of Washington, Seattle, Washington
- KUMAR, VIVEK, University of Texas Southwestern Medical Center, Dallas, Texas
- LARA, ANTONIO, Columbia University, New York, New York
- LARGE, ADAM, University of Pittsburgh, Pittsburgh, Pennsylvania
- LAU, BILLY, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- LEDoux, JOSEPH, New York University, New York, New York
- LEE, EUNJEONG, National Institute of Mental Health/National Institutes of Health, Bethesda, Maryland
- LEE, HYE YOUNG, University of California, San Francisco, San Francisco, California
- LEE, RAY, Princeton University, Princeton, New Jersey
- LI, BO, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- LI, JENNIFER, Harvard University, Cambridge, Massachusetts
- LIU, HAIXIN, State University of New York at Stony Brook, Stony Brook, New York
- LO, SHIH-CHING, Genentech Inc., South San Francisco, California
- LOCKERY, SHAWN, University of Oregon, Eugene, Oregon
- LOEHFELM, ALINE, University of Saarland, Saarbrücken, Germany
- LONDON, BRIAN, Columbia University, New York, New York
- LOSITSKY, OLGA, Princeton University, Princeton, New Jersey
- LUO CLAYTON, ALICE, Simons Foundation, New York, New York
- LVOVSKAYA, SVETLANA, University of Texas Southwestern Medical Center, Dallas, Texas
- LYON, GHOLSON, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- MACHADO, TIMOTHY, Columbia University, New York, New York
- MAFFEI, ARIANNA, State University of New York at Stony Brook, Stony Brook, New York
- MAINEN, ZACHARY, Champalimaud Neuroscience Programme, Lisbon, Portugal
- MALAIA, EVIE, University of Texas at Arlington, Arlington, Texas
- MARASCO, PAUL, Lerner Research Institute, Cleveland Clinic, Cleveland, Ohio
- MARDER, EVE, Brandeis University, Waltham, Massachusetts
- MARLIN, BIANCA, New York University School of Medicine, New York, New York
- MASSET, PAUL, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- MATHURU, AJAY, Institute of Molecular and Cell Biology, Singapore, Singapore
- MAZZUCATO, LUCA, State University of New York at Stony Brook, Stony Brook, New York
- MCCOMBIE, RICHARD, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York
- MCKINSEY, GABRIEL, University of California, San Francisco, San Francisco, California
- MEHTA, ASHESH, Feinstein Institute for Medical Research, Great Neck, New York
- MEISTER, MARKUS, California Institute of Technology, Pasadena, California

SYMPOSIUM PARTICIPANTS

- MICHELY, JULIA, University of Saarland, Saarbrücken, Germany  
 MIZUNO, KEIKO, Kings College London, London, United Kingdom  
 MOORE, JEFFREY, University of California, San Diego, La Jolla, California  
 MOVSHON, J. ANTHONY, New York University, New York, New York  
 MU, YU, Janelia Farm Research Campus, Howard Hughes Medical Institute, Ashburn, Virginia  
 MURAYAMA, MASANORI, RIKEN, Wako, Japan  
 MURRAY, ANDREW, Columbia University, New York, New York  
 NAGAYAMA, SHIN, University of Texas, Houston, Houston, Texas  
 NAKAJIMA, MIHO, The Rockefeller University, New York, New York  
 NAKAYAMA, HIROFUMI, The Rockefeller University, New York, New York  
 NALBANTIAN, SUZANNE, Brookville, New York  
 NARAIN, CHARVY, *Nature Neuroscience*, London, United Kingdom  
 NEFTCI, EMRE, University of California, San Diego, La Jolla, California  
 NEMES, ADRIANA, Columbia University, New York, New York  
 NESTLER, ERIC, Mount Sinai University, New York, New York  
 NEUNUEBEL, JOSHUA, Howard Hughes Medical Institute, Janelia Farms Research Campus, Ashburn, Virginia  
 NIV, YAEL, Princeton University, Princeton, New Jersey  
 NIZAMI, LANCE, Independent Research Scholar, Palo Alto, California  
 NOROVICH, AMY, Columbia University, New York, New York  
 NUNES RAPOSO, DAVID, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 OBOTI, LIVIO, Children's National Health System, Washington, D.C.  
 ODOEMENE, KACHI, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 OKA, YUKI, Columbia University, New York, New York  
 O'RAWE, JASON, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 OSWALD, ANNE-MARIE, University of Pittsburgh, Pittsburgh, Pennsylvania  
 OTAZU, GONZALO, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 PACHITARIU, MARIUS, University College London, London, United Kingdom  
 PATEL, GAURAV, Columbia University/New York State Psychiatric Institute, New York, New York  
 PEIKON, IAN, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 PENZO, MARIO, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 PI, HYUN JAE, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 POLLOCK, MILA, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 PORCIELLO, GIUSEPPINA, Sapienza University, Rome, Italy  
 POUGET, ALEXANDRE, University of Geneva, Geneva, Switzerland and University of Rochester, Rochester, New York  
 PREUSCHOFF, KERSTIN, École Polytechnique Fédérale de Lausanne, Lausanne, Switzerland  
 PUNZI, GIOVANNA, Lieber Institute for Brain Development, Baltimore, Maryland  
 QIAO, MU, Harvard University, Cambridge, Massachusetts  
 RAMÍREZ-MORENO, DAVID, Universidad Autónoma de Occidente, Cali, Colombia  
 RANADE, SACHIN, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 REARDON, THOMAS, Columbia University, New York, New York  
 REDONDO, ROGER, Howard Hughes Medical Institute, Massachusetts Institute of Technology, Cambridge, Massachusetts  
 REID, ASHLAN, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 REIMERS, MARK, Virginia Commonwealth University, Richmond, Virginia  
 REYNOLDS, JOHN, The Salk Institute, La Jolla, California  
 ROBERT, JASON, Arizona State University, Tempe, Arizona  
 ROBSON, DREW, Harvard University, Cambridge, Massachusetts  
 ROMO, RANULFO, Universidad Nacional Autónoma de México (UNAM), Mexico City, Mexico  
 ROOS, ANNERINE, Stellenbosch University, Cape Town, South Africa  
 ROOT, CORY, Columbia University, New York, New York  
 ROTHSCHILD, GIDEON, University of California, San Francisco, San Francisco, California  
 RUSHWORTH, MATTHEW, University of Oxford, Oxford, United Kingdom  
 SABES, PHILLIP, University of California, San Francisco, San Francisco, California  
 SANDERS, JOSHUA, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 SASSE, SOFIA, University of Münster, Münster, Germany  
 SCHAEFER, ANDREAS, MRC National Institute for Medical Research, London, United Kingdom  
 SCHAEFER, ANNE, Icahn School of Medicine at Mount Sinai, New York, New York  
 SCHUCK, NICOLAS, Princeton University, Princeton, New Jersey  
 SCHWARTZ, EDMUND, Columbia University, New York, New York  
 SEELY, JEFFREY, Columbia University, New York, New York  
 SEJNOWSKI, TERRENCE, The Salk Institute for Biological Studies, La Jolla, California  
 SELIMI, FEKRUIE, INSERM, Paris, France  
 SHADLEN, MICHAEL, Columbia College of Physicians and Surgeons, New York, New York  
 SHANKAR, SHRUTI, Temasek Life Sciences, Singapore, Singapore  
 SHEA, STEPHEN, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 SHEPPARD, JOHN, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 SHYKIND, BENJAMIN, Weill Cornell Medical College in Qatar, Doha, Qatar  
 SIMONCELLI, EERO, New York University, New York, New York  
 SINGER, EMILY, Simons Foundation/*Quanta Magazine*, New York, New York  
 SLIFKIN, ANDREW, Cleveland State University, Cleveland, Ohio  
 SOSULSKI, DARA, University College London, London, United Kingdom  
 SRIDHARAN, DEVARAJAN, Stanford University School of Medicine, Stanford, California  
 STEPHENSON-JONES, MARCUS, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 STEWART, DAVID, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 STILLMAN, BRUCE, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 STIX, GARY, *Scientific American*, New York, New York  
 STRINGER, CARSEN, University College London, London, United Kingdom  
 STRYKER, MICHAEL, University of California, San Francisco, San Francisco, California  
 SVOBODA, KAREL, Howard Hughes Medical Institute, Ashburn, Virginia  
 SWARTZ, JEROME, Huntington, New York  
 SWARTZ GORDON, SHANAH, Lloyd Harbor, New York  
 TADA, HIROBUMI, Yokohama City University, School of Medicine, Yokohama, Japan  
 TALLEY, EDMUND, National Institutes of Health, Rockville, Maryland  
 TOEPFER, FRANZISKA, University of Würzburg, Würzburg, Germany  
 TONEGAWA, SUSUMU, RIKEN Brain Science Institute and Massachusetts Institute of Technology, Saitama, Japan  
 TUCCILARONE, JASON, Cold Spring Harbor Labs, Cold Spring Harbor, New York  
 UNDERWOOD, EMILY, Science, Washington, D.C.  
 UNNIKRISHNAN, M.K., Manipal College of Pharmaceutical Sciences, Manipal, India  
 UPSON, SANDRA, Scientific American Mind, New York, New York  
 URSINI, GIANLUCA, Lieber Institute for Brain Development, Baltimore, Maryland  
 VAUGHAN, ALEXANDER, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 VENTIMIGLIA, DONOVAN, Rockefeller University, New York, New York  
 VENTURINI, RITA, Champalimaud Foundation, Lisbon, Portugal  
 VILANKAR, KEDARNATH, Cornell University, Ithaca, New York  
 WANG, BOR-SHUN, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York  
 WEBER, FRANZ, University of California, Berkeley, Berkeley, California  
 WEKSELBLATT, JOSEPH, University of Oregon, Eugene, Oregon  
 WIGLER, MICHAEL, Cold Spring Harbor Laboratory, Cold Spring Harbor, New York

SYMPOSIUM PARTICIPANTS

WITKOWSKI, JAN, Cold Spring Harbor Laboratory, Cold Spring Harbor,  
New York  
WOLFE, GLENN, University of Toronto, Toronto, Canada  
WOLPERT, DANIEL, University of Cambridge, Cambridge  
WONG, LI CHIN, New York University School of Medicine, New York,  
New York  
XIONG, QIAOJIE, Cold Spring Harbor Laboratory, Cold Spring Harbor,  
New York  
YAMAZAKI, DAISUKE, University of Tokyo, Bunkyo-ku, Japan  
YANG, ZHENGHONG, University of Würzburg, Würzburg, Germany  
YATES, DARRAN, *Nature Reviews Neuroscience*, London, United  
Kingdom

YU, C. RON, Stowers Institute for Medical Research, Kansas City,  
Missouri  
YU, KAI, Cold Spring Harbor Laboratory, New York, New York  
ZADOR, TONY, Cold Spring Harbor Laboratory, Cold Spring Harbor,  
New York  
ZANDBELT, BRAM, Vanderbilt University, Nashville, Tennessee  
ZHANG, BYOUNGTAK, Seoul National University, Seoul, South Korea  
ZHAO, BUYUN, University of Cambridge, Cambridge, United Kingdom  
ZHONG, CHUN, Johns Hopkins University, Baltimore, Maryland  
ZHOU, CHUAN, Howard Hughes Medical Institute, Janelia Farms,  
Ashburn, Virginia



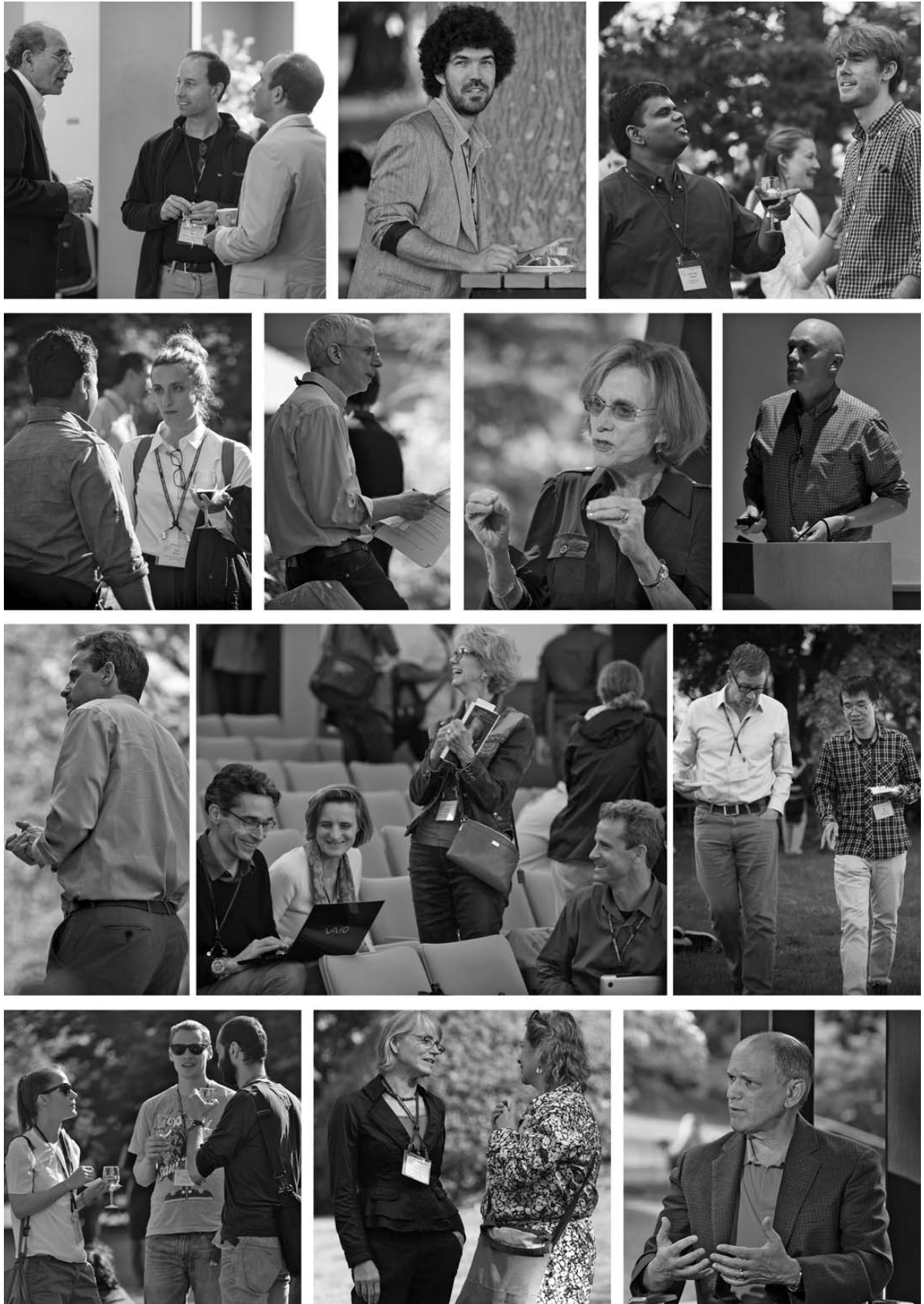


Row 1: A. Loehfelm, S. Batsching; K. Svoboda, B. Stillman; G. Buzsáki, J. Kubie, S. Tonegawa  
Row 2: D. Stewart, C. Bargmann; Y. Mu, K. Kuchibhotla, K. Chen, B. Marlin; P. Churchland  
Row 3: C. Narain, D. Yates; A.F. Ebihara, G. Otazu; C. Duan, A. Akrami  
Row 4: R. Axel; T. Zador; B. Marlin; G. Turner



Row 1: A. Kennedy, A. Batchelor; M. Carrasco, Y. Niv; D. Yates, N. Karsh  
Row 2: A. Goldstein, M. Shadlen; Y. Dan, J.A. Movshon; J. Witkowski, P. Churchland  
Row 3: E. Brush, V. Dubowitz; A. Loehfelm, S. Batsching, J. Michely; M. Stryker, D. Bavelier  
Row 4: S. Lockery, I. Carcea; R. Fernald, G. Mckinsey; V. Kumar, I. Abdus-Saboor





Row 1: R. Axel, M. Shadlen, P. Glimcher; P. House; K. Vilankar, J. Golden  
Row 2: S. Dasgupta, H. Harris; G. Stix; A. Graybiel; M. Rushworth  
Row 3: J. DiCarlo; A. Pouget, D. Bavelier, P. Churchland, J. DiCarlo; J. Reynolds, M. Gio  
Row 4: F. Toepfer, S. Koenig, L. Oboti; N. Kanwisher, M. Carrasco; E. Nestler



Row 1: G. Rothschild, M. Agetsuma; C. Brody, K. Svoboda, A. Pouget  
Row 2: S. Jaramillo, I. Carcea; G. Fuller, J. Wekselblatt, D. Heck; D. Anderson  
Row 3: A. Schaefer, F. Selimi; D. Gardner, D. Kleinfeld, R. Axel; M. Shadlen, D. Angelaki  
Row 4: D. Gardner; R. Lee, J. Kubie; J. Watson, H. Hoekstra, A. Gann





*Row 1:* J. Freeman, D. Gutnisky; A. Slifkin, K. David; D. Ramirez-Moreno, J. Hurtado-Lopez  
*Row 2:* A. Apergis-Schoute, B. Zhao, K. Deisseroth; O. Lositsky, P. Coen  
*Row 3:* Z. Fishman; Z. Mainen; H. Furukawa; J. LeDoux  
*Row 4:* R. Desimone, T. Sejnowski; D. Stewart, D. Kleinfeld



Row 1: G. Lyon, Y. Gu; A. Mathuru, E. Underwood; D. Wolpert

Row 2: Poster Session; Symposium Picnic; K. Deisseroth

Row 3: L. Frank, G. Buzsáki; A. Mathuru, A. Schaefer; A. Mehta, D. Gropp

Row 4: D. Sridharan; C. Narain, A. Gazzaley; P. Kuhl



## Foreword

The Laboratory selected the theme of Cognition for the 79th Symposium in this historic series largely because of the tremendous advances being made by neuroscientists and psychologists working on cognitive processes at scales varying from the molecular to whole-brain and theoretical studies. Previous Symposia that addressed the brain included the fourth Symposium on Excitation Phenomena (1936), The Neuron (1952), Sensory Receptors (1965), The Synapse (1975), Molecular Neurobiology (1983), The Brain (1990), and Function & Dysfunction in the Nervous System (1996), so a return to the general theme of neuroscience was long overdue. Furthermore, a number of national projects on brain function have been initiated over the last few years, including President Barack Obama's announcement of the BRAIN (Brain Research through Advancing Innovative Neurotechnologies) Initiative in April 2013, a collaborative research project akin to the Human Genome Project, with the ultimate goal of mapping the activity of every neuron in the brain by 2025. These projects and initiatives reflect the fact that many neuroscientists are increasingly optimistic that major obstacles in understanding brain function may be overcome through the use of new technologies and approaches, and that these advances may shed light on novel approaches to treat psychiatric, neurological, and neurodegenerative diseases.

The 2014 Symposium was designed to span a broad range of approaches toward increased understanding of cognitive processes in the brain including cell/molecular biology; developmental neurobiology; genetics and genomics; electrophysiological approaches; functional neuroimaging at cellular and whole-brain resolutions; computational neuroscience; behavioral, ethological, and psychophysical studies; and evolutionary/comparative neuroscience. The program of invited speakers was arranged to ensure that fundamental discoveries were balanced with approaches relevant to societal well-being, including a variety of stratagems for harnessing our increased understanding of brain function to improve treatment of mental illness and brain disorders. Speakers responded to the challenge of putting their own research, whether based on single-neuron studies, circuits, or whole-brain studies, into a broader context, allowing for a tremendous amount of cross talk across disciplines with much insight gained from this unusually broad meeting. This is one of the strengths of the Symposium, and the 2014 meeting was particularly successful in highlighting emerging connections between molecular/cellular networks and higher brain functions such as language and decision-making.

Opening night speakers included Richard Axel (Columbia University) on innate and learned responses to odors, Allison Doupe (University of California, San Francisco) on vocal motor plasticity, Matthew Rushworth (University of Oxford) on decision-making, and Patricia Kuhl (University of Washington) on language acquisition. One of the three Churchland neuroscientists who spoke at the Symposium, Patricia Churchland (University California, San Diego) addressed "The Brains Behind Morality" in an excellent Dorcas Cummings lecture for Laboratory friends, neighbors, and Symposium participants in advance of the annual dinner parties. Terry Sejnowski delivered a compelling and comprehensive summary that captured much of the research and discussions presented at the meeting.

This Symposium was attended by almost 300 scientists from both U.S. and international universities, and the program included 60 invited presentations, six short talks selected from the openly submitted abstracts on the basis of scientific merit, and 130 poster presentations. To disseminate the latest results and discussion of the Symposium to a wider audience, attendees were able to share many of the Symposium talks with their colleagues who were unable to attend using the Leading Strand video archive. A collection of interviews by Karen Carniol (*Cell*), Ann Goldstein (*Neuron*), Charvy Narain (*Nature Neuroscience*), Gary Stix (*Scientific American*), and Jan Witkowski (CSHL Banbury Center) with leading experts in the field were arranged during the Symposium, distributed from the Cold Spring Harbor Symposium interviews website, and available in edited form in this volume.

We thank Val Pakaluk, Mary Smith, Ed Campodonico, and his staff in the Meetings & Courses Program for their assistance in organizing and running the Symposium, and John Inglis and his staff at Cold Spring Harbor Laboratory Press, particularly Inez Sialiano and Jan Argentine.

Cori Bargmann  
Daphne Bavelier  
Terrence Sejnowski  
David Stewart  
Bruce Stillman

## Sponsors

Funded in part by Forest Laboratories and The Swartz Foundation.

Contributions from the following companies provide core support for the Cold Spring Harbor meetings program.

### **Corporate Sponsors**

Agilent Technologies  
Bristol-Myers Squibb Company  
Genentech  
Life Technologies (part of Thermo Fisher Scientific)  
New England BioLabs

### **Plant Corporate Associates**

Monsanto Company  
DuPont/Pioneer Hi-Bred International

### **Foundations**

HudsonAlpha Institute for Biotechnology

# Contents

Symposium Participants	v
Foreword	xv
<b>Physiology of Cognition</b>	
A Neural Circuit That Controls Cortical State, Plasticity, and the Gain of Sensory Responses in Mouse <i>Michael P. Stryker</i>	1
Diverse Effects of Conditioned Threat Stimuli on Behavior <i>Justin M. Moscarello and Joseph LeDoux</i>	11
Animal-to-Animal Variability in Neuromodulation and Circuit Function <i>Albert W. Hamood and Eve Marder</i>	21
The Brainstem Oscillator for Whisking and the Case for Breathing as the Master Clock for Oro-facial Motor Actions <i>David Kleinfeld, Jeffrey D. Moore, Fan Wang, and Martin Deschênes</i>	29
<b>Neural Syntax and Substrates</b>	
Emergence of Cognition from Action <i>György Buzsáki, Adrien Peyrache, and John Kubie</i>	41
Dynamic Hippocampal Circuits Support Learning- and Memory-Guided Behaviors <i>Emily B. Anderson, Irene Grossrubatscher, and Loren Frank</i>	51
Identification and Manipulation of Memory Engram Cells <i>Xu Liu, Steve Ramirez, Roger L. Redondo, and Susumu Tonegawa</i>	59
<b>Movement and Motor Control</b>	
A Dynamical Basis Set for Generating Reaches <i>Mark M. Churchland and John P. Cunningham</i>	67
Internal and External Feedback Circuits for Skilled Forelimb Movement <i>Eiman Azim, Andrew J.P. Fink, and Thomas M. Jessell</i>	81
Computations in Sensorimotor Learning <i>Daniel M. Wolpert</i>	93
<b>Visual Perception and Neural Computation</b>	
Neural Mechanisms Underlying Visual Object Recognition <i>Arash Afraz, Daniel L.K. Yamins, and James J. DiCarlo</i>	99
The Macaque Face Patch System: A Window into Object Representation <i>Doris Tsao</i>	109
Representation of Naturalistic Image Structure in the Primate Visual Cortex <i>J. Anthony Movshon and Eero P. Simoncelli</i>	115
<b>Eye Movement and Motion Perception</b>	
The Influence of Gaze Control on Visual Perception: Eye Movements and Visual Stability <i>Rebecca M. Krock and Tirin Moore</i>	123
Neural Circuits for Motion Vision in the Fly <i>Alexander Borst</i>	131
How Optic Flow and Inertial Cues Improve Motion Perception <i>Dora E. Angelaki</i>	141
<b>Attention and Value</b>	
How Attention Affects Spatial Resolution <i>Marisa Carrasco and Antoine Barbot</i>	149
Causal Model Comparison Shows That Human Representation Learning Is Not Bayesian <i>Andra Geana and Yael Niv</i>	161

**Perceptual Judgment and Decision-Making**

Understanding of the Hows and Whys of Decision-Making: From Expected Utility to Divisive Normalization <i>Paul Glimcher</i>	169
Spontaneous Decisions and Free Will: Empirical Results and Philosophical Considerations <i>Joana Rigato, Masayoshi Murakami, and Zachary Mainen</i>	177
Predicting the Accuracy of a Decision: A Neural Mechanism of Confidence <i>Christopher R. Fetsch, Roozbeh Kiani, and Michael N. Shadlen</i>	185
Internal States and Behavioral Decision-Making: Toward an Integration of Emotion and Cognition <i>Ann Kennedy, Kenta Asahina, Eric Hoopfer, Hidehiko Inagaki, Yonil Jung, Hyosang Lee, Ryan Remedios, and David J. Anderson</i>	199

**Perception and Social Behavior**

Early Language Learning and the Social Brain <i>Patricia K. Kuhl</i>	211
Dopaminergic Dynamics Contributing to Social Behavior <i>Lisa A. Gunaydin and Karl Deisseroth</i>	221
Cognitive Skills Needed for Social Hierarchies <i>Russell D. Fernald</i>	229

**Summary**

Summary: Cognition in 2014 <i>Terrence J. Sejnowski</i>	237
---	-----

**Dorcas Cummings Lecture**

Patricia Smith Churchland	245
---------------------------	-----

**Conversations at the Symposium**

David Anderson	253
Dora Angelaki	255
Richard Axel	258
Cori Bargmann	260
Patricia Churchland	263
Karl Deisseroth	266
Robert Desimone	269
James DiCarlo	271
Adam Gazzaley	275
Ann Graybiel	277
Joseph LeDoux	279
Eric Nestler	282
Alexandre Pouget	285
Matthew Rushworth	288
Michael Shadlen	291
Karel Svoboda	293
Susumu Tonegawa	295
Daniel Wolpert	297
Tony Zador	299

<b>Author Index</b>	303
---------------------	-----

<b>Subject Index</b>	305
----------------------	-----