

PRESIDENT OF THE ACADEMY

Ralph J. Cicerone

EDITOR-IN-CHIEF

Randy Schekman

ASSOCIATE EDITORS

William C. Clark
Alan Fersht
Jack Halpern
Jeremy A. Sabloff
Solomon H. Snyder
Peter K. Vogt
Susan R. Wessler

SPECIAL FEATURE EDITOR

Fred W. McLafferty

EDITORIAL BOARD

Animal, Nutritional, and Applied Microbial Sciences

David L. Denlinger
R. Michael Roberts
Linda J. Saif
Ryuzo Yanagimachi

Anthropology

Richard G. Klein
Dolores R. Piperno
Alan Walker

Applied Mathematical Sciences

Peter J. Bickel

Applied Physical Sciences

David Chandler
Noel A. Clark
Francisco de la Cruz

Astronomy

Geoffrey W. Marcy

Biochemistry

Edward D. Korn
John Kuriyan
Alan M. Lambowitz
Michael A. Marletta
Kiyoshi Mizuuchi
Charles M. Radding
Venkatraman Ramakrishnan
Tom A. Rapoport
Peter Walter
James A. Wells
William T. Wickner

Biophysics and Computational Biology

David Baker
Adriaan Bax
Charles R. Cantor
William A. Eaton
Barry H. Honig
Robert Langer
Michael Levitt
Gregory A. Petsko

Cellular and Developmental Biology

Eric H. Davidson
John B. Gurdon
Eric N. Olson
Michael Rosbash
David D. Sabatini
Gertrud M. Schüpbach
Robert Tjian

Cellular and Molecular Neuroscience

Pietro V. De Camilli
Richard L. Haganir
L. L. Iversen
Yuh Nung Jan
Jeremy Nathans
Charles F. Stevens
Thomas C. Südhof
Joseph S. Takahashi
Charles S. Zuker

Chemistry

Stephen J. Benkovic
Harry B. Gray
Raphael D. Levine
Jerrold Meinwald
Mark A. Ratner
Nicholas J. Turro

Computer and Information Sciences

William H. Press

Economic Sciences

Avinash K. Dixit

Engineering Sciences

Anthony G. Evans

Environmental Sciences and Ecology

James H. Brown
Christopher B. Field
David M. Karl
Robert May
David W. Schindler

Evolutionary Biology

Francisco J. Ayala
May R. Berenbaum
W. Ford Doolittle
Douglas J. Futuyma
Daniel L. Hartl
Masatoshi Nei
Tomoko Ohta

Genetics

Kathryn V. Anderson
Thomas W. Cline
Stanley N. Cohen
Stanley Fields
Iva S. Greenwald
Jeffrey C. Hall
Philip C. Hanawalt

Rudolf Jaenisch
Jasper Rine
Reed B. Wickner

Geology

W. G. Ernst
James P. Kennett

Geophysics

Mark H. Thiemens

Human Environmental Sciences

Ruth S. DeFries
Susan Hanson

Immunology

Peter Cresswell
Douglas T. Fearon
Tak Wah Mak
Philippa Marrack
William E. Paul
Ralph M. Steinman
Tadatsugu Taniguchi
Arthur Weiss

Mathematics

Richard V. Kadison
Robion C. Kirby

Medical Genetics, Hematology, and Oncology

Joseph L. Goldstein
Mark T. Groudine
Tony Hunter
Philip W. Majerus
David C. Page
Stanley B. Prusiner
Craig B. Thompson
Inder M. Verma
Robert H. Waterston

Medical Physiology and Metabolism

Michael S. Brown
Charles A. Dinarello
Robert J. Lefkowitz
Salvador Moncada

Microbial Biology

John M. Coffin
R. John Collier
Emil C. Gotschlich
E. Peter Greenberg

Diane E. Griffin
Peter M. Howley
Elliott D. Kieff
Robert A. Lamb
Peter Palese
Thomas E. Shenk
Thomas J. Silhavy
Thomas E. Wellems

Physics

Anthony Leggett
Paul C. Martin
José N. Onuchic

Physiology and Pharmacology

Susan G. Amara
David Julius
Ramon Latorre

Plant Biology

Anthony R. Cashmore
Maarten J. Chrispeels
Enrico Coen
Jeffery L. Dangl
Joseph R. Ecker
Robert Haselkorn
June B. Nasrallah

Plant, Soil, and Microbial Sciences

Roger N. Beachy
Brian J. Staskawicz
M. S. Swaminathan

Psychology

Dale Purves
Edward E. Smith

Social and Political Sciences

Alejandro Portes
Brian Skyrms

Sustainability Science

Barry R. Bloom
Partha Sarathi Dasgupta
Robert W. Kates
Pamela A. Matson
Elinor Ostrom
Hans Joachim Schellnhuber
B. L. Turner II

Systems Neuroscience

Robert Desimone
Fred H. Gage
Charles D. Gilbert
Marcus E. Raichle
Leslie G. Ungerleider

Submission to PNAS

Authors (members and nonmembers) may submit their manuscripts directly to PNAS at www.pnascentral.org. In a cover letter or in the online submission form, authors must recommend 3 appropriate Editorial Board members, 3 NAS members who are expert in the paper's scientific area, and 5 qualified referees. **Submission is open to all authors** and no Academy member sponsor is required.

PNAS (ISSN-0027-8424) is published weekly in print by the National Academy of Sciences.

Correspondence: PNAS, 500 Fifth Street, NW, NAS 340, Washington, DC 20001 USA or 2101 Constitution Avenue, NW, NAS 340, Washington, DC 20418 USA (for courier or express mail). E-mail: PNAS@nas.edu.

Copyright: Volumes 90–105, copyright © 1993–2008 by the National Academy of Sciences of the United States of America, all rights reserved. Volumes 1–89, copyright as a collective work only; author(s) retains copyright to individual articles. **Requests for Permission:** See www.pnas.org/misc/rightperm.shtml for details. Address requests to reproduce material published in Volumes 1–89 to the original author(s); e-mail other requests to PNASpermissions@nas.edu, fax 1-202-334-2739, or PNAS Permissions Editor, 500 Fifth Street, NW, NAS 340, Washington, DC 20001 USA. Please cite the exact material to be reprinted and state specifically where it will be used. **Photocopies:** PNAS is registered with the Copyright Clearance Center (CCC), 222 Rosewood Drive, Danvers, MA 01923 USA, fax 1-978-750-4470, or www.copyright.com. Authorization to photocopy items for the internal or personal use of specific clients is granted by the National Academy of Sciences provided that the proper fee is paid directly to CCC. **Microforms:** Contact UMI at www.umi.com or P.O. Box 1346, Ann Arbor, MI 48106-1346 USA.

Advertising: Mark Chesnek, 500 Fifth Street, NW, NAS 340, Washington, DC 20001 USA. Phone 1-202-334-2696, fax 1-202-334-1346, e-mail mchesnek@nas.edu.

Subscriptions: Send payments to PNAS, c/o AIP, P.O. Box 503284, St. Louis, MO 63150-3284 USA. For subscription help, e-mail subs@aip.org, phone 1-516-576-2270, or visit www.pnas.org/subscriptions. **2009 Rates:** U.S., individual—\$340 (first class delivery available at a surcharge of \$285); U.S., institutional—\$2,095; non-U.S., individual—\$530; non-U.S., institutional—\$2,450. Subscriptions are entered on a calendar-year basis.

Exclusive Agent for Subscribers in Japan: USACO Corporation, 17-12 Higashi-Azabu, 2-Chome, Minato-ku, Tokyo 106-0044, Japan. Phone 81 3 3505 3256, fax 81 3 3505 6282, e-mail tokyo-sales@usaco.co.jp. **Change of Address:** PNAS, c/o AIP, Suite 1N01, 2 Huntington Quadrangle, Melville, NY 11747 USA. Phone 1-800-344-6902, fax 1-516-349-9704, e-mail subs@aip.org. Please send notification 6 weeks in advance and list the old and new addresses. **Claims:** Requests for replacement copies will not be honored more than 60 days after the issue date for domestic subscribers and not more than 90 days after the issue date for foreign subscribers. Claims will not be honored for more than 2 issues per calendar year for the same subscriber. To make a claim, e-mail subs@aip.org or call 1-800-344-6902. **Single Copies:** \$40 per issue in the U.S., \$50 non-U.S. To order, e-mail subs@aip.org or call 1-800-344-6902. **Canadian GST:** Registration Number R-133130880.

Postmaster: Send address changes to PNAS, c/o AIP, Suite 1N01, 2 Huntington Quadrangle, Melville, NY 11747 USA. Periodicals postage paid at Washington, DC, and additional mailing offices.

PNAS is available online at www.pnas.org.
PRINTED IN THE USA



Printed on acid-free paper effective Volume 84, Issue 1, and on 10% post-consumer recycled paper effective Volume 105, Issue 1. Printed with soy ink.

PNAS STAFF

Publisher

Kenneth R. Fulton

Executive Editor

Diane M. Sullenberger

Managing Editor

Daniel H. Salsbury

Recruiting Editor

David Stopak

Editorial Staff

James B. Allison
Josiah W. Armour
Maya Ellis Brown
Tom J. Colihan
Julia M. Diez d'Aux
Kathleen E. Dugan
Moses M. Jackson
Meredith C. Jones
Nicole Joy
Etta Kavanagh
Jacob Kendall-Taylor
Sarah Leamy
Megan Miller
Tom Myers
Jennifer Nelson
N. T. Ngo
May B. Piotrowski
Allison Ross
Benjamin Snow
Evella Trent-Deck

Production Manager

Dana M. Compton

Production Staff

Barbara A. Bacon
Sophie Mohin
Kelly A. Newton
Ariana B. Raveica
Siyuan Xie

Marketing Manager

Mark Chesnek

Marketing Staff

Jennifer Bradley

Media Staff

Carrie Arnold
Jonathan Lifland
Kaspar Mossman
Ashley Truxon

Finance Manager

Simone Marshall-Campbell

Business Staff

Juanita Culler
Julia A. Little
Sara Spizzirri

Authorship

Authorship should be limited to those who have contributed substantially to the work. Authors must indicate their specific contributions to the published work; this information will be published as a footnote to the paper. The corresponding author must have obtained permission from all authors for the submission of each version of the paper and for any change in authorship.

Conflict of Interest

All authors, members, referees, and editors must disclose any association that poses a conflict of interest in connection with the manuscript. Authors must acknowledge all funding sources supporting the work. See www.pnas.org/misc/coi.shtml for details.

Supporting Information

Authors may use Supporting Information to enhance their papers in PNAS by providing additional substantive material for online posting, but the print version of the paper must stand on its own merits.

Cover Images

Authors are encouraged to submit scientifically interesting and visually arresting images for the cover.

Information for Authors

Please see the complete Information for Authors, available online at www.pnas.org.

PNAS Online

PNAS articles are published daily online before print at www.pnas.org in PNAS Early Edition.

The articles in PNAS report original research by independent authors and do not necessarily represent the views of the National Academies.