

PRESIDENT OF THE ACADEMY

Ralph J. Cicerone

EDITOR-IN-CHIEF

Randy Schekman

ASSOCIATE EDITORS

David Chandler
Alan Fersht
Jack Halpern
Dolores R. Piperno
Solomon H. Snyder
B. L. Turner II
Peter K. Vogt
Susan R. Wessler

EDITORIAL BOARD

Animal, Nutritional, and Applied Microbial Sciences

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

Anthropology

Richard G. Klein
C. Owen Lovejoy
James F. O'Connell

Applied Mathematical Sciences

Peter J. Bickel
David L. Donoho
Stephen E. Fienberg

Applied Physical Sciences

Francisco de la Cruz
Jerry P. Gollub
Tom C. Lubensky
David A. Weitz

Astronomy

Neta A. Bahcall

Biochemistry

Michael R. Botchan
Jennifer A. Doudna
Edward D. Korn
Stephen C. Kowalczykowski
John Kuriyan
Michael A. Marletta
Kiyoshi Mizuuchi
Charles M. Radding
Venkatraman Ramakrishnan
Tom A. Rapoport
James A. Wells
William T. Wickner

Biophysics and Computational Biology

David Baker
Adriaan Bax
Axel T. Brunger
William A. Eaton
Angela M. Gronenborn
Barry H. Honig
Robert Langer
Michael Levitt
Gregory A. Petsko
John W. Sedat

Cellular and Developmental Biology

C. David Allis
Donald D. Brown

Eric H. Davidson
Brigid L. M. Hogan
Eric N. Olson
Michael Rosbash
David D. Sabatini
Gertrud M. Schüpbach

Cellular and Molecular Neuroscience

David E. Clapham
Pietro V. De Camilli
Richard L. Huganir
L. L. Iversen
Yuh-Nung Jan
Eve Marder
Jeremy Nathans
Charles F. Stevens
Thomas C. Südhof
Joseph S. Takahashi

Chemistry

Stephen J. Benkovic
Harry B. Gray
Michael L. Klein
Raphael D. Levine
Tobin J. Marks
Jerrold Meinwald
David A. Tirrell
Nicholas J. Turro

Computer and Information Sciences

Butler W. Lampson
William H. Press

Economic Sciences

Roy Radner
Jose A. Scheinkman

Engineering Sciences

Alexis T. Bell
Mark E. Davis
Mildred S. Dresselhaus
Evelyn L. Hu
William R. Schowalter

Environmental Sciences and Ecology

Robert E. Dickinson
Paul G. Falkowski
David M. Karl
Robert May
William W. Murdoch
David W. Schindler

Evolutionary Biology

Francisco J. Ayala
May R. Berenbaum
Sean B. Carroll
W. Ford Doolittle
Douglas J. Futuyma
Daniel L. Hartl
Richard E. Lenski
Masatoshi Nei
Gene E. Robinson

Genetics

Kathryn V. Anderson
Thomas W. Cline
Stanley N. Cohen
Barry Ganetzky
Iva S. Greenwald
Jeffrey C. Hall

Philip C. Hanawalt
Mary-Claire King
Jasper Rine
Reed B. Wickner

Geology

Thure E. Cerling
W. G. Ernst
Andrew H. Knoll

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

Dennis A. Carson
C. Thomas Caskey
Joseph L. Goldstein
Mark T. Groudine
Tony Hunter
Philip W. Majerus
Inder M. Verma
Owen N. Witte

Medical Physiology and Metabolism

Robert J. Lefkowitz
David J. Mangelsdorf
Salvador Moncada
David W. Russell

Microbial Biology

John M. Coffin
R. John Collier
Emil C. Gotschlich
E. Peter Greenberg
Diane E. Griffin
Peter M. Howley
Ralph R. Isberg
Elliott D. Kieff
Robert A. Lamb
Peter Palese
Thomas E. Shenk

Thomas J. Silhavy
Thomas E. Wellems

Physics

Curtis G. Callan, Jr.
Anthony Leggett
Paul C. Martin

Physiology and Pharmacology

Richard W. Aldrich
Susan G. Amara
David Julius
Arthur Karlin
Ramón Latorre

Plant Biology

David Baulcombe
Anthony R. Cashmore
Maarten J. Chrispeels
Enrico Coen
Joseph R. Ecker
Robert Haselkorn
June B. Nasrallah

Plant, Soil, and Microbial Sciences

James C. Carrington
Vicki L. Chandler
Brian J. Staskawicz

Psychological and Cognitive Sciences

Wilson S. Geisler
J. Anthony Movshon
Dale Purves
Edward E. Smith

Social and Political Sciences

Alejandro Portes
Brian Skyrms
Kenneth W. Wachter

Sustainability Science

Barry R. Bloom
William C. Clark
Partha Sarathi Dasgupta
Robert W. Kates
Pamela A. Matson
Elinor Ostrom
Stephen Polasky
Hans Joachim Schellnhuber

Systems Biology

Marc W. Kirschner
Wing Hung Wong

Systems Neuroscience

Thomas D. Albright
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. Authors must recommend three appropriate Editorial Board members, three NAS members who are expert in the paper's scientific area, and five qualified referees. No Academy member sponsor is required.

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

Correspondence: PNAS, 700 11th Street, NW, Suite 450, Washington, DC 20001 USA. 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 and 106–108, 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, 700 11th Street, NW, Suite 450, 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, 700 11th Street, NW, Suite 450, 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. **2011 Rates:** US, individual—\$375 (first class delivery available at a surcharge of \$375); non-US, individual—\$585; US/non-US, institutional online only, \$1,305–7,215. 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 two 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 US, \$50 non-US. 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 80% post-consumer recycled paper effective Volume 107, 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

Jenna Al-Malawi

Josiah W. Armour

Teresa V. Callahan

Victoria Chihos

Ryan Conley

Ali C. Guio

Amanda Hopkins

Andrew Huber

Benjamin Jipson

Meredith C. Jones

Etta Kavanagh

Jacob Kendall-Taylor

Jeffrey King

Kay McLaughlin

Kathryn Murphy

Tom Myers

Jennifer Nelson

Matthew Parks

May B. Piotrowski

Dane Secor

Mitchell Sipus

Production Manager

Dana M. Compton

Production Staff

Kelly A. Gerrity

Sophie Mohin

Kelly A. Newton

Kat Rodenhizer

Audrey Springer

Marketing Manager

Mark Chesnek

Marketing Staff

Jennifer Bradley

Media Staff

Sola Ayeni-Biu

Ann Griswold

Todd Johnston

Jenny Ruth Morber

Prashant Nair

Ashley Truxon

Senior Finance Officer

Janice Guzman

Business Staff

Metina Booze

Corey P. Colwill

Lesli H. Martin

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.