

PRESIDENT OF THE ACADEMY
Ralph J. Cicerone

EDITOR-IN-CHIEF
Inder M. Verma

ASSOCIATE EDITORS

Richard Eisenberg
Alan Fersht
Dolores R. Piperno
Natasha V. Raikhel
Neil H. Shubin
Solomon H. Snyder
B. L. Turner II
Peter K. Vogt
Stephen T. Warren
David A. Weitz

EDITORIAL BOARD

Animal, Nutritional, and Applied Microbial Sciences

David L. Denlinger
John J. Eppig
R. Michael Roberts
Linda J. Saif

Anthropology

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

Applied Mathematical Sciences

Peter J. Bickel
David L. Donoho
James A. Sethian

Applied Physical Sciences

David D. Awschalom
Francisco de la Cruz
Zachary Fisk
John D. Weeks

Astronomy

Neta A. Bahcall

Biochemistry

Michael R. Botchan
F. Ulrich Hartl
Edward D. Korn
Stephen C. Kowalczykowski
Michael A. Marletta
Kiyoshi Mizuuchi
Dimshaw Patel
Charles M. Radding
Venkatraman Ramakrishnan
Brenda A. Schulman
James A. Wells

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

Eric H. Davidson
Brigid L. M. Hogan
Eric N. Olson
Michael Rosbash

Gertrud M. Schüpbach
Richard A. Young

Cellular and Molecular Neuroscience

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

Chemistry

Stephen J. Benkovic
Harry B. Gray
Jack Halpern
Michael L. Klein
Raphael D. Levine
Tobin J. Marks
Jerrold Meinwald
Peter J. Rossky
David A. Tirrell

Computer and Information Sciences

Butler W. Lampson
William H. Press

Earth, Atmospheric, and Planetary Sciences

Donald E. Canfield
Thure E. Cerling
W. G. Ernst
Mark H. Thieme

Economic Sciences

Roy Radner
Jose A. Scheinkman

Engineering Sciences

Alexis T. Bell
Mark E. Davis
Pablo G. Debenedetti
Mildred S. Dresselhaus
James A. Dumesic
Evelyn L. Hu
John H. Seinfeld

Environmental Sciences and Ecology

Edward F. DeLong
Robert E. Dickinson
David M. Karl
Nancy Knowlton
Simon A. Levin
Robert May
François M. Morel
William W. Murdoch
Mary Power
Andrea Rinaldo
David W. Schindler

Evolutionary Biology

May R. Berenbaum
James H. Brown
W. Ford Doolittle
Douglas J. Futuyma
Daniel L. Hartl
David M. Hillis
David Jablonski
Richard E. Lenski
Masatoshi Nei
Gene E. Robinson

Genetics

Kathryn V. Anderson
Stanley N. Cohen

Barry Ganetzky
Iva S. Greenwald
Jeffrey C. Hall
Philip C. Hanawalt
Mary-Claire King
Douglas E. Koshland
Jasper Rine
Allan C. Spradling
Reed B. Wickner

Human Environmental Sciences

Ruth S. DeFries
Susan Hanson
B. L. Turner II

Immunology and Inflammation

Robert L. Coffman
Peter Cresswell
Douglas T. Fearon
K. Christopher Garcia
Tak Wah Mak
Philippa Marrack
Ruslan Medzhitov
Carl F. Nathan
William E. Paul
Tadatsugu Taniguchi
Arthur Weiss

Mathematics

Richard V. Kadison
Robion C. Kirby
Kenneth A. Ribet
Srinivasa S. R. Varadhan

Medical Genetics, Hematology, and Oncology

Dennis A. Carson
C. Thomas Caskey
James E. Cleaver
Mark T. Groudine
Tony Hunter
Philip W. Majerus
Gregg L. Semenza
Owen N. Witte

Medical Physiology and Metabolism

Joseph L. Goldstein
Robert J. Lefkowitz
David J. Mangelsdorf
David W. Russell

Microbial Biology

Carolina Barillas-Mury
John M. Coffin
R. John Collier
Stephen P. Goff
Emil C. Gotschlich
E. Peter Greenberg
Diane E. Griffin
Peter M. Howley
Ralph R. Isberg
Elliott D. Kieff
Robert A. Lamb
Michael B. A. Oldstone
Peter Palese
Thomas E. Shenk
Thomas J. Silhavy

Physics

William Bialek
Curtis G. Callan Jr.
Anthony Leggett
Herbert Levine
Boris I. Shraiman

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
Susan R. Wessler

Psychological and Cognitive Sciences

Randolph Blake
Susan T. Fiske
Michael S. Gazzaniga
Wilson S. Geisler
Susan Gelman
Dale Purves

Social and Political Sciences

Adrian Raftery
Kenneth W. Wachter
Mary C. Waters

Sustainability Science

Anthony J. Bebbington
Barry R. Bloom
F. Stuart Chapin III
William C. Clark
Ruth S. DeFries
Susan Hanson
Emilio F. Moran
Stephen Polasky
Hans Joachim Schellnhuber
B. L. Turner II

Systems Biology

Wing Hung Wong

Systems Neuroscience

Thomas D. Albright
Huda Akil
Robert Desimone
Fred H. Gage
Charles D. Gilbert
J. Anthony Movshon
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 by the National Academy of Sciences.

Correspondence: PNAS, 500 Fifth Street, NW, NAS 340, Washington, DC 20001 USA. Email: 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 106–112, 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); email other requests to PNASpermissions@nas.edu, fax 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 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.

Subscriptions: Send payments to PNAS, P.O. Box 936110, Atlanta, GA 31193-6110 USA. For subscription help, email pnas.subs@sheridan.com, phone 717-632-3535, or visit www.pnas.org/subscriptions. **2015 Rates:** Individual online only, \$235; institutional online only, \$495–8,365. Subscriptions are entered on a calendar-year basis.

International Subscribers: Sales agent information can be found online at www.pnas.org/site/subscriptions/orders.shtml. **Change of Address:** PNAS, Subscriber Services, PO Box 465, Hanover, PA 17331 USA. Phone 717-632-3535, email pnas.subs@sheridan.com. 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, email pnas.subs@sheridan.com or call 717-632-3535. **Canadian GST:** Registration Number R-133130880.

Postmaster: Send address changes to PNAS, Subscriber Services, PO Box 465, Hanover, PA 17331 USA. Periodicals postage paid at Washington, DC, and additional mailing offices.

PNAS is available online at www.pnas.org.

PNAS STAFF

Publisher

Kenneth R. Fulton

Executive Editor

Diane M. Sullenberger

Deputy Executive Editor

Daniel H. Salsbury

Publication Director

Dana M. Compton

Senior Recruiting Editor

David Stopak

Front Matter Editor

Gene Russo

Editorial Manager

Etta Kavanagh

Assistant Editorial Managers

Josiah W. Armour

Kathryn Murphy DeTura

Jacob Kendall-Taylor

Editorial Staff

James B. Allison

Sarah Appleby

Raven Baptiste

Teresa V. Callahan

Haley Campbell

Pablo Luis Clemente

Michael Deneen

Abigail Fox

Samantha Fuller

Allyson Heisler

Elizabeth Huhn

Jeffrey King

Tom Myers

Claudia Peng

Andrew Schroeder

Dane Secor

Megan E. Shuler

Heather Snijdewind

Jacob D. Svobodny

Associate Production Manager

Kelly Newton

Production Staff

Elizabeth Griffith

Benjamin Jipson

Kat Rodenhizer

Audrey Springer

Subscription Specialist

Kay McLaughlin

Marketing Manager

Brittany Campbell

Media and Communications Officer

Prashant Nair

Media Staff

Paul Gabrielsen

Jessica P. Johnson

Luwam A. Yeibio

Senior Finance Officer

Janice Guzman

Business Staff

Jessica Brokenburr

Shenine Shelton

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/site/authors/coi.xhtml 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 main text 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 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.