

## PRESIDENT OF THE ACADEMY

Ralph J. Cicerone

## EDITOR-IN-CHIEF

Inder M. Verma

## ASSOCIATE EDITORS

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

## 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

### Applied Mathematical Sciences

Peter J. Bickel  
David L. Donoho

### 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  
John Kuriyan  
Michael A. Marletta  
Kiyoshi Mizuuchi  
Dinshaw Patel  
Charles M. Radding  
Venkatraman Ramakrishnan  
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  
David D. Sabatini  
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  
Eve Marder  
Jeremy Nathans  
Charles F. Stevens  
Thomas C. Südhof  
Joseph S. Takahashi

### 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

Thure E. Cerling  
W. G. Ernst  
Mark H. Thiemens

### Economic Sciences

Roy Radner  
Jose A. Scheinkman

### Engineering Sciences

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

### Environmental Sciences and Ecology

Edward F. DeLong  
Robert E. Dickinson  
David M. Karl  
Simon A. Levin  
Robert May  
François M. Morel  
William W. Murdoch  
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 Š. 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

### 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

### Medical Genetics, Hematology, and Oncology

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

### Medical Physiology and Metabolism

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

### Microbial Biology

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  
Peter Palese  
Thomas E. Shenk

Thomas J. Silhavy  
Thomas E. Wellemes

### Physics

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  
Natasha V. Raikhel

### Plant, Soil, and Microbial Sciences

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

### Psychological and Cognitive Sciences

Susan T. Fiske  
Michael S. Gazzaniga  
Wilson S. Geisler  
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  
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](http://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, 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 106–111, copyright as a collective work only; author(s) retains copyright to individual articles. **Requests for Permission:** See [www.pnas.org/misc/rightperm.shtml](http://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](http://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 National Academy of Sciences, P.O. Box 936110, Atlanta, GA 31193-6110 USA. For subscription help, email [pnas.subs@sheridan.com](mailto:pnas.subs@sheridan.com), phone 717-632-3535, or visit [www.pnas.org/subscriptions](http://www.pnas.org/subscriptions). **2014 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](http://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](mailto: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](mailto:pnas.subs@sheridan.com) or call 717-632-3535.

**Single Copies:** \$40 per issue in the US, \$50 non-US. To order, email [pnas.subs@sheridan.com](mailto: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](http://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

### 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

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

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

Rachel Howard

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](http://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](http://www.pnas.org).

## PNAS Online

PNAS articles are published daily online at [www.pnas.org](http://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.