

PRESIDENT OF THE ACADEMY

Marcia K. McNutt

EDITOR-IN-CHIEF

Inder M. Verma

ASSOCIATE EDITORS

Richard Eisenberg
Alan Fersht
Dolores R. Piperno
Natasha V. Raikhel
Christine E. Seidman
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

Stephen M. Beverley
David L. Denlinger
John J. Eppig
Caroline S. Harwood
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
Donald J. Geman
Donald B. Rubin
James A. Sethian

Applied Physical Sciences

Matthew P. Fisher
Zachary Fisk
Angel Rubio
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
Brenda A. Schulman
James A. Wells

Biophysics and Computational Biology

David Baker
Adriaan Bax
Axel T. Brunger
Angela M. Gronenborn
Barry H. Honig
Robert Langer
Michael Levitt
J. Andrew McCammon
Peter B. Moore
Gregory A. Petsko
Joseph D. Puglisi
John W. Sedat
Michael F. Summers

Cellular and Developmental Biology

Denis Duboule
Brigid L. M. Hogan

Satyajit Mayor
Roeland Nusse
Eric N. Olson
Michael Rosbash
Gertrud M. Schüpbach

Cellular and Molecular Neuroscience

David E. Clapham
Nancy Y. Ip
Yuh-Nung Jan
Jeremy Nathans
Charles F. Stevens
Joseph S. Takahashi
Gina Turriano

Chemistry

Stephen J. Benkovic
Harry B. Gray
Jack Halpern
Michael L. Klein
Raphael D. Levine
Thomas E. Mallouk
Tobin J. Marks
Jerrold Meinwald
Catherine J. Murphy
Peter J. Rossky

Computer and Information Sciences

William H. Press
Eva Tardos

Earth, Atmospheric, and Planetary Sciences

Donald E. Canfield
Thure E. Cerling
W. G. Ernst
A. R. Ravishankara
Lisa Tauxe
Mark H. Thiemens

Economic Sciences

Paul R. Milgrom
Roy Radner
Jose A. Scheinkman

Engineering Sciences

Alexis T. Bell
James J. Collins
Mark E. Davis
Pablo G. Debenedetti
James A. Dumesic
Evelyn L. Hu
Rakesh K. Jain
John A. Rogers
John H. Seinfeld

Environmental Sciences and Ecology

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

Evolutionary Biology

May R. Berenbaum
Andrew G. Clark
W. Ford Doolittle
Douglas J. Futuyma
Daniel L. Hartl
David M. Hillis
David Jablonski
Richard E. Lenski
Gene E. Robinson

Joan E. Strassmann
Nils C. Stenseth

Genetics

Kathryn V. Anderson
Sue Biggins
John Carlson
Iva S. Greenwald
Philip C. Hanawalt
Mary-Claire King
Douglas E. Koshland
Jasper Rine
Allan C. Spradling

Human Environmental Sciences

Anthony J. Bebbington
Ruth S. DeFries
Susan Hanson
Emilio F. Moran
B. L. Turner II

Immunology and Inflammation

Robert L. Coffman
Peter Cresswell
K. Christopher Garcia
Christopher C. Goodnow
Tak Wah Mak
Philippa Marrack
Ruslan Medzhitov
Carl F. Nathan
Lawrence Steinman
Tadatsugu Taniguchi
Arthur Weiss

Mathematics

Robion C. Kirby
Kenneth A. Ribet
Srinivasa S. R. Varadhan

Medical Genetics, Hematology, and Oncology

Dennis A. Carson
C. Thomas Caskey
James E. Cleaver
Joseph L. Goldstein
Mark T. Groudine
Tony Hunter
Carol L. Prives
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
Ralph R. Isberg
Elliott D. Kieff
Michael B. A. Oldstone
Peter Palese
Lalita Ramakrishnan
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
Arthur Karlin
Ramón Latorre
Gail Mandel

Plant Biology

David Baulcombe
Philip N. Benfey
Caroline Dean
Joseph R. Ecker
June B. Nasrallah
Krishna K. Niyogi
Julian I. Schroeder

Plant, Soil, and Microbial Sciences

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

Psychological and Cognitive Sciences

Marlene Behrmann
Randolph Blake
Susan T. Fiske
Michael S. Gazzaniga
Susan Gelman
Dale Purves

Social and Political Sciences

Adrian Raftery
Stephen W. Raudenbush
Kenneth W. Wachter
Mary C. Waters

Sustainability Science

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

Systems Neuroscience

Huda Akil
Thomas D. Albright
Robert Desimone
Fred H. Gage
Charles D. Gilbert
Tony Movshon
Marcus E. Raichle
Peter L. Strick
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 106–114, 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. **2018 Rates:** Individual online only, \$235; institutional online only, \$525–8,880. 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

Senior Recruiting Editor

David Stopak

Recruiting Editor

Jennifer Robinson

Front Matter Editor

Gene Russo

Editorial Managers

Etta Kavanagh

Jacob Kendall-Taylor

Assistant Editorial Managers

Josiah W. Armour

Kathryn Murphy DeTura

Editorial Staff

James B. Allison

Carolyn M. Beans

Daniela Torres Checo

Pablo Luis Clemente

Brianna Costache

Abigail Fox

Samantha Fuller

Jenny Geyer

Julia Glueck

Rose Hallett

Elizabeth Huhn

Jeffrey King

Rachel Laney

Tom Myers

Andrew Schroeder

Megan E. Shuler

Jacob D. Svobodny

Rachel VanValkenburg

Rocio Vidal-Ronchas

Senior Production Manager

Midori Baer

Production Staff

Delaney Cruickshank

Elizabeth Griffith

Benjamin Jipson

Kat Rodenhizer

Audrey Springer

Senior Marketing Associate

Nasreen Hosein

Subscription Specialist

Kay McLaughlin

Media and Communications Manager

Prashant Nair

Media Staff

Leigh Cooper

Brian M. Doctrow

Taylor Gedeon

Chris Samoray

Senior Financial and Administrative Officer

Anton L. Bandy

Business Staff

Kim Mann

Vilija B. Teel

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 at www.pnas.org in PNAS Early Edition.

The articles in PNAS report original research by independent authors and have not been endorsed by the National Academies.