

## 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 Turrigiano

### 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  
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  
Mark T. Groudine  
Tony Hunter  
Carol L. Prives  
Gregg L. Semenza  
Owen N. Witte

### Medical Physiology and Metabolism

Joseph L. Goldstein  
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](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 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](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 PNAS, 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). **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](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. **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).

## 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-Ronchias

### Senior Production Manager

Midori Baer

### Production Staff

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

### Financial 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](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 at [www.pnas.org](http://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.