

PRESIDENT OF THE ACADEMY

Marcia K. McNutt

EDITOR-IN-CHIEF

May R. Berenbaum

ASSOCIATE EDITORS

Huda Akil
Angela M. Gronenborn
Philippa Marrack
Catherine J. Murphy
Dolores R. Piperno
Natasha V. Raikhel
Peter J. Rossky
Christine E. Seidman
Neil H. Shubin
B. L. Turner II
Stephen T. Warren
Mary C. Waters
David A. Weitz

EDITORIAL BOARD

Animal, Nutritional, and Applied Microbial Sciences

Stephen M. Beverley
David L. Denlinger
Caroline S. Harwood
Xiang-Jin Meng
Lynn M. Riddiford
L. David Sibley
John R. Speakman
Thomas E. Spencer

Anthropology

Patricia L. Crown
Richard G. Klein
C. Owen Lovejoy
Joyce Marcus
James F. O'Connell
Elsa M. Redmond
Charles Stanish
Polly Wiessner
Melinda A. Zeder

Applied Mathematical Sciences

Peter J. Bickel
David L. Donoho
Donald B. Rubin
James A. Sethian
Bin Yu

Applied Physical Sciences

Gabriel Aeppli
Zachary Fisk
Daan Frenkel
Christopher Jarzynski
Mehran Kardar
Risto M. Nieminen
Angel Rubio

Astronomy

Neta A. Bahcall

Biochemistry

Natalie G. Ahn
Marlene Belfort
Michael R. Botchan
F. Ulrich Hartl
Alberto R. Kornblitt
Stephen C. Kowalczykowski

Kiyoshi Mizuuchi
Brenda A. Schulman
James A. Wells

Biophysics and Computational Biology

David Baker
Adriaan Bax
Axel T. Brunger
William F. DeGrado
Yale E. Goldman
Barry H. Honig
James H. Hurley
Robert Langer
Michael Levitt
Karolin Luger
Susan Marqusee
J. Andrew McCammon
Peter B. Moore
Joseph D. Puglisi
John W. Sedat
Michael F. Summers

Cellular and Developmental Biology

Helen M. Blau
Denis Duboule
Lawrence S. Goldstein
Rebecca Heald
Tina M. Henkin
Brigid L. M. Hogan
Roeland Nusse
Michael Rossbach
Janet Rossant
Gertrud M. Schüpbach

Cellular and Molecular Neuroscience

Nancy Y. Ip
Liquan Luo
Jeremy Nathans
Carla J. Shatz
Hee-Sup Shin
Joseph S. Takahashi

Chemistry

Lia Addadi
Joanna Aizenberg
Stephen J. Benkovic
Marcetta Y. Darensbourg
Joseph S. Francisco
Tobin J. Marks
Chad A. Mirkin
Monica Olvera de la Cruz
Amy C. Rosenzweig
Peter J. Stang

Computer and Information Sciences

William H. Press

Earth, Atmospheric, and Planetary Sciences

Donald E. Canfield
Thure E. Cerling
W. G. Ernst
Jean Jouzel
Michael Manga
A. R. Ravishankara
Lisa Tauxe
Mark H. Thieme

Economic Sciences

Anne C. Case
Matthew O. Jackson
Jose A. Scheinkman

Engineering Sciences

Alexis T. Bell
James J. Collins
Pablo G. Debenedetti
Evelyn L. Hu
Yonggang Huang
Rakesh K. Jain
Klavs F. Jensen
Sang Yup Lee
Jens Nielsen
John A. Rogers

Environmental Sciences and Ecology

Zhisheng An
Edward F. DeLong
Robert E. Dickinson
James A. Estes
Mary K. Firestone
Susan P. Harrison
Alan Hastings
David M. Karl
Nancy Knowlton
Simon A. Levin
Pablo A. Marquet
François M. M. Morel
Mary Power
Andrea Rinaldo

Evolutionary Biology

W. Ford Doolittle
Scott V. Edwards
Marcus W. Feldman
Douglas J. Futuyma
Raghavendra Gadagkar
Hopi E. Hoekstra
David Jablonski
Richard E. Lenski
Bruce R. Levin
Nancy A. Moran
Gene E. Robinson
Douglas W. Schemske
Nils C. Stenseth
Joan E. Strassmann

Genetics

Hugo Bellen
John Carlson
Louise T. Chow
Iva S. Greenwald
Mary-Claire King
Douglas E. Koshland
John R. Pringle
Jasper Rine
Rodney Rothstein
Matthew P. Scott
Allan C. Spradling
Anne M. Villeneuve
Graham C. Walker
Mariana F. Wolfner

Human Environmental Sciences

Arun Agrawal
Ruth S. DeFries
Susan Hanson
Diana M. Liverman
Robert J. Scholes
Karen C. Seto
B. L. Turner II
Arild Underdal
David Zilberman

Immunology and Inflammation

Robert L. Coffman

Peter Cresswell
K. Christopher Garcia
Lewis L. Lanier
Tak Wah Mak
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

Anton J. Berns
James E. Cleaver
Joseph L. Goldstein
Tony Hunter
Peter A. Jones
Karen E. Nelson
Carol L. Prives
Owen N. Witte

Medical Physiology and Metabolism

Myles A. Brown
Christopher K. Glass
Barbara B. Kahn
C. Ronald Kahn
Robert J. Lefkowitz
David J. Mangelsdorf
Andrew R. Marks
Gerald I. Shulman

Microbial Biology

Yuan Chang
John M. Coffin
R. John Collier
Jorge E. Galan
Stephen P. Goff
E. Peter Greenberg
Diane E. Griffin
Ralph R. Isberg
Malcolm A. Martin
Richard P. Novick
Michael B. A. Oldstone
Peter Palese
Lalita Ramakrishnan
Thomas E. Shenk
Thomas J. Silhavy

Physics

Curtis G. Callan Jr.
J. C. Seamus Davis
Anthony Leggett
Herbert Levine
Bernard F. Schutz

Physiology and Pharmacology

Richard W. Aldrich
Susan G. Amara
Francisco Bezanilla
Donald W. Pfaff
Nieng Yan

Plant Biology

David Baulcombe
Philip N. Benfey

Dominique Bergmann
Gloria M. Coruzzi
Joseph R. Ecker
Stephen P. Long
June B. Nasrallah
Krishna K. Niyogi
Julian I. Schroeder
Douglas E. Soltis

Plant, Soil, and Microbial Sciences

Julia Bailey-Serres
James A. Birchler
Vicki L. Chandler
Sean Cutler
Richard A. Dixon
Sheng Yang He
Donald R. Ort
Craig S. Pikaard
Pamela C. Ronald
Qifa Zhang

Psychological and Cognitive Sciences

Renee Baillargeon
Martin S. Banks
Randall Engle
Susan T. Fiske
Michael S. Gazzaniga
Susan Gelman
David J. Heeger
Barbara Landau
Jennifer Richeson
Henry L. Roediger
Elke U. Weber
Timothy D. Wilson

Social and Political Sciences

Richard D. Alba
Dalton Conley
Mark Granovetter
David D. Laitin
Ronald Lee
Margaret Levi
Douglas S. Massey
Adrian Raftery
Stephen W. Raudenbush
Kenneth W. Wachter

Sustainability Science

Arun Agrawal
Gregory P. Asner
William C. Clark
Ruth S. DeFries
Carl Folke
Susan Hanson
Diana M. Liverman
Bonnie J. McCay
Hans Joachim Schellnhuber
Karen C. Seto
B. L. Turner II
Arild Underdal
David Zilberman

Systems Neuroscience

Thomas D. Albright
Emery N. Brown
Charles D. Gilbert
Michael E. Goldberg
David J. Heeger
Tony Movshon
Marcus E. Raichle
Terrence J. Sejnowski
Peter L. Strick

PNAS is published weekly by the National Academy of Sciences, 500 Fifth Street, NW, NAS 338, Washington, DC 20001.

ISSN 1091-6490 (Online)

ISSN 0027-8424 (Print)

Correspondence: PNAS, 500 Fifth Street, NW, NAS 338, Washington, DC 20001. 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 106–118, copyright as a collective work only; author(s) retains copyright to individual articles. **Requests for Permission:** See <https://www.pnas.org/page/about/rights-permissions> for details. Address requests to reproduce material published in Volumes 1–89 to the original author(s); email other requests to PNASpermissions@nas.edu, or PNAS Permissions Editor, 500 Fifth Street, NW, NAS 338, Washington, DC 20001. 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, fax 978-750-4470, or <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. For subscription help, email pnas.subs@sheridan.com, phone 717-632-3535, or visit <https://www.pnas.org/page/subscriptions/subscribers>. **2021 Rates:** Individual online only, \$235; institutional online only, \$535–9,060. Subscriptions are on a calendar-year basis. **International Subscribers:** Sales agent information can be found at <https://www.pnas.org/page/subscriptions/subs-faq#contact>. **Change of Address:** PNAS, Subscriber Services, PO Box 465, Hanover, PA 17331. Phone 717-632-3535, email pnas.subs@sheridan.com. Please send notification 6 weeks in advance and list the old and new addresses.

PNAS is published online at <https://www.pnas.org>.

PNAS STAFF

Publisher

Kenneth R. Fulton

Executive Editor

Diane M. Sullenberger

Deputy Executive Editor

Daniel H. Salsbury

Managing Editor

Emma P. Shumeyko

Associate Managing Editor, Editorial Board Services

Etta Kavanagh

Assistant Managing Editors

Josiah W. Armour

Andrew Schroeder

Senior Recruiting Editor

David Stopak

Recruiting Editors

Meredith L. Bastian

Zan M. Dodson

Editorial Ethics Manager

Yael Fitzpatrick

Front Matter Editor

Gene Russo

Senior Editorial

Coordinators

James B. Allison

Daniela Torres Checo

Pablo Luis Clemente

Jeffrey King

Jacob D. Svobodny

Editorial Staff

Emille Beller

Michael Casini

Zella Christensen

Emily A. Densmore

Alvin Deskins

Abigail Fox

Abi Franklin

Hannah M. Gardner

Barbara Gillen

Isaac Hersh

Amy McDermott

Kiefer McDowell

Meghan Ramil

Linda Sjostrom

Lilli Sutton

Evelyn Waugh

Digital Product

Manager

Michael S. Hardesty

Product Staff

Nazifa Jan

Kat Rodenhizer

Production Manager

Sharon Jane Chua

Production Accounts

Specialist

Audrey Springer

Production Staff

Delaney Cruickshank

Chloe Fells

Jennifer H. Nguyen

Subscription Specialist

Kay McLaughlin

Marketing/Data Analytics

Manager

Kirsten Ronald

Marketing Assistant

Gerald Allen

Media and Communications

Manager

Prashant Nair

Media Staff

Sarah Dargen

Matthew Hardcastle

Melissa Suran

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.

Competing Interest

All authors, members, referees, and editors must disclose any association that poses a competing interest in connection with the manuscript. Authors must acknowledge all funding sources supporting the work. See <https://www.pnas.org/page/authors/competing-interest> for details.

Information for Authors

Please see the complete Information for Authors at <https://www.pnas.org>.

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