



BRITISH
PHARMACOLOGICAL
SOCIETY

BJP

British Journal
of Pharmacology

VOLUME 172 NUMBER 23 December 2015

www.brjpharmacol.org
ISSN 0007-1188 ISSN 1476-5381

WILEY
Blackwell

BJP

British Journal of Pharmacology

Editor-in-Chief

J.C. (Ian) McGrath *Glasgow, UK & Sydney, Australia*

Senior Editors

Amrita Ahluwalia *London, UK*
Michael J. Curtis *London, UK*
James Docherty *Dublin, Ireland*

Mark Gienbycz *Calgary, Canada*
Daniel Hoyer *Melbourne, Australia*
Paul Insel *La Jolla, USA*

Angelo A. Izzo *Naples, Italy*
David MacEwan *Liverpool, UK*
Clare Stanford *London, UK*
Susan Wonnacott *Bath, UK*

Reviews Editor

Stephen Alexander *Nottingham, UK*

Senior Online Editor

Annette Gilchrist *Downers Grove, USA*

Press Editors

Y.S. Bakhle
Caroline Wedmore

Editorial Board

Ruth Andrew *Edinburgh, UK*
Alexis Bailey *Guildford, UK*
Chris Bailey *Bath, UK*
Phillip Beart *Melbourne, Australia*
Tamás Bíró *Budapest, Hungary*
Heather Bradshaw *Bloomington, USA*
Keith Brain *Birmingham, UK*
James Alexander Brock *Melbourne, Australia*
John Challiss *Leicester, UK*
Diana Chow *Houston, USA*
Macdonald Christie *Sydney, Australia*
Sandy Clanachan *Edmonton, Canada*
John Cryan *Cork, Ireland*
Anthony Davenport *Cambridge, UK*
Jo De Mey *Odense, Denmark*
Martin Diener *Giessen, Germany*
Peter Doris *Houston, USA*
Pedro D'Orléans-Juste *Sherbrooke, Canada*
Grant Drummond *Clayton, Australia*
Claire Edwards *Oxford, UK*
Michael Emerson *London, UK*
Liana Fattore *Cagliari, Italy*
Peter Ferdinandy *Szeged, Hungary*
Anthony Ford *San Mateo, USA*
Chris George *Cardiff, UK*
Heather Giles *London, UK*
Derek Gilroy *London, UK*
Gary Gintant *Illinois, USA*
Michelle Glass *Auckland, New Zealand*
Fiona Gribble *Cambridge, UK*
John Hartley *London, UK*
Deborah L. Hay *Auckland, New Zealand*

Miles Houslay *London, UK*
Jackie Hunter *Weston, UK*
Ryuji Inoue *Fukuoka, Japan*
Paul Insel *San Diego, USA*
Angelo A. Izzo *Naples, Italy*
Yong Ji *Nanjing, China*
Marcel Jiménez *Barcelona, Spain*
Eamonn Kelly *Bristol, UK*
Melanie Kelly *Halifax, Canada*
Terry Kenakin *Durham, USA*
Dave Kendall *Nottingham, UK*
Charles Kennedy *Glasgow, UK*
Simon Kennedy *Glasgow, UK*
Chris Langmead *Welwyn Garden City, UK*
Rebecca Lever *London, UK*
Eliot Lilley *Redhill, UK*
Jon Lundberg *Stockholm, Sweden*
Mhairi Macrae *Glasgow, UK*
Karen McCloskey *Belfast, UK*
Barbara McDermott *Belfast, UK*
Alister McNeish *Reading, UK*
Olivier Micheau *Dijon, France*
Paula Moreira *Coimbra, Portugal*
Maria Moro *Madrid, Spain*
Fiona Murray *San Diego, USA*
Anne Negre-Salvayre *Toulouse, France*
Janet Nicholson *Biberach an der Riss, Germany*
Eliot Ohlstein *Pennsylvania, USA*
Saoirse O'Sullivan *Nottingham, UK*
Hiroshi Ozaki *Tokyo, Japan*
Reynold Panettieri Jr *Philadelphia, USA*
Andreas Papapetropoulos *Athens, Greece*

Clare Parish *Melbourne, Australia*
Adam Pawson *Edinburgh, UK*
Ray Penn *Baltimore, USA*
John Peters *Dundee, UK*
Roger Phillips *Bradford, UK*
Michael Pugsley *Jersey City, USA*
Susan Pyne *Strathclyde, UK*
Jelena Radulovic *Chicago, USA*
Patrick Sexton *Monash, Australia*
Chris Sobey *Monash, Australia*
Michael Spedding *Suresnes, France*
Beata Sperlagh *Budapest, Hungary*
Shiva Sruti *Pittsburgh, USA*
Katarzyna Starowicz *Krakow, Poland*
Barbara Stefanska *Quebec, Canada*
Gary Stephens *Reading, UK*
Csaba Szabo *Budapest, Hungary*
Kenneth Takeda *Strasbourg, France*
Paolo Tammaro *Oxford, UK*
Anna Teti *L'Aquila, Italy*
David Thwaites *Newcastle upon Tyne, UK*
Ekaterini Tiligada *Athens, Greece*
Jean-Pierre Valentin *Macclesfield, UK*
Paul Vanhoutte *Hong Kong, China*
Christopher Vaughan *Sydney, Australia*
Harald Wajant *Würzburg, Germany*
Julia Walker *Durham, USA*
Xin Wang *Manchester, UK*
Nina Weber *Amsterdam, the Netherlands*
James Whiteford *London, UK*
Baofeng Yang *Heilongjiang, China*

The *British Journal of Pharmacology* is a broad-based journal giving leading international coverage of all aspects of experimental pharmacology. The Editorial Board represents a wide range of expertise and ensures that well-presented work is published as promptly as possible, consistent with maintaining the overall quality of the journal.

Disclaimer

The Publisher, British Pharmacological Society and Editors cannot be held responsible for errors or any consequences arising from the use of information contained in this journal; the views and opinions expressed do not necessarily reflect those of the Publisher, British Pharmacological Society and Editors. Neither does the publication of advertisements constitute any endorsement by the Publisher, British Pharmacological Society and Editors of the products advertised.

Copyright and Copying

Copyright © 2015 The British Pharmacological Society. All rights reserved. No part of this publication may be reproduced, stored or transmitted in any form or by any means without the prior permission in writing from the copyright holder. Authorization to copy items for internal and personal use is granted by the copyright holder for libraries and other users registered with their local Reproduction Rights Organisation (RRO), e.g. Copyright Clearance Center (CCC), 222 Rosewood Drive, Danvers, MA 01923, USA (www.copyright.com), provided the appropriate fee is paid directly to the RRO. This consent does not extend to other kinds of copying, such as copying for general distribution for advertising or promotional purposes, for creating new collective works, or for resale. Special requests should be addressed to: permissions@wiley.com.