



Professor Dr. Geoffrey Burnstock (1929–2020)

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Professor Geoffrey Burnstock, a great luminary in science and the founder of our field of purinergic signalling, sadly but peacefully died in Melbourne, Australia, on the 2nd of June, 2020, at the age of 91. He had retired at the age of 88, in October 2017, when, after 42 years in London, he decided to fulfill his wife's and family's desire to move back to Australia, where, in 1959, he had been appointed Senior Lecturer at Melbourne University, his first important academic engagement.

Geoffrey Burnstock grew up in London where he was born on May 10, 1929. After completing his secondary education at Greenford County Grammar School in 1946, he did his National service with the Air Force in 1947. In 1953, he completed a BSc degree at King's College, University of London, majoring in mathematics and physics. He subsequently completed a PhD at King's College and University College London in the field of zoology, studying gut motility in fish (1957). This turned out to be a great start for the young scientist as his first paper ever was published in *Nature*.

In 1956, he moved to the Physiology Department at the National Institute for Medical Research in Mill Hill, London, as a postdoctoral fellow with Wilhelm Feldberg (1956–1957). There, he developed a novel technique for recording membrane activities from smooth muscle, the “sucrose gap technique.” This led to a position with Edith Bulbring in the Department of Pharmacology at Oxford University (1957–1959). A Rockefeller Travelling Fellowship allowed him to work for a year with Clifford Ladd Prosser at the Physiology Department, University of Illinois, USA.

He then had to decide whether to take up an offer for a job in the USA or to return to Oxford as a Research Fellow. But he rather moved to Melbourne, Australia, in 1959 where he took up the position of Senior Lecturer in the Department of Zoology. Reasons for this were his good relations with Australian people in Oxford whose positive approach to new initiatives “give it a go” he found attractive but also the fact that his wife Nomi (nee Hirschfeld) whom he had married in 1957 had lived in nearby New Zealand. In Melbourne, he followed a successful career moving on to Reader in Physiological Zoology in 1962 and finally to Professor of Zoology and Chairman of Department (1964–1975) (Fig. 1). During this time, his three daughters Aviva, Tamara, and Diana were born.

By that time, he had made major scientific breakthroughs and established the basic mechanisms of purinergic signalling. In spite of the repeated criticisms he had received for his provoking idea that ATP functions as an extracellular signalling molecule and neurotransmitter, he was honored by attractive offers from the USA, Canada, England, and also Australia. In 1975, he finally decided to move back to England and take the prestigious chair of Anatomy and Physiology at University College London (UCL) (later renamed Anatomy and Developmental Biology), previously headed by John Zachary Young, his former PhD supervisor and one of the most influential biologists of the twentieth century. He stayed there until 1997. During that time, he also held the position of Contract Professor at the University of Siena (1985–1987) and the University of Milan (1993–

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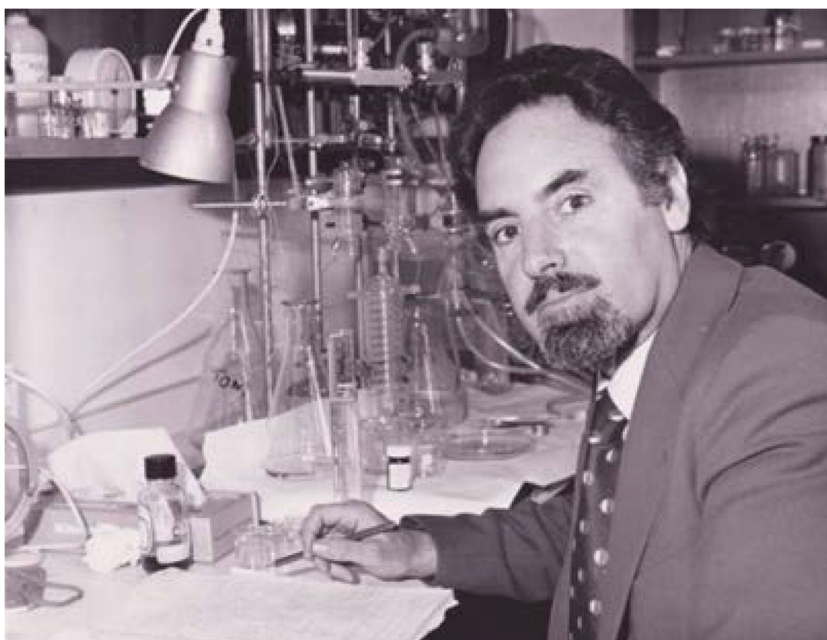
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Fig. 1 Geoff Burnstock in the laboratory in Melbourne, Australia, ca. 1969



1994) and was visiting professor at the Department of Pharmacology, University of California, Los Angeles (1970); at the Institute of Experimental Medicine, Hungarian Academy of Science (1983); and at the Royal Society of Medicine Foundation, NY, USA (1988). He also served as Vice-Dean of the Faculty of Medical Sciences (UCL 1980–1983) and as convener at the Centre for Neuroscience, UCL (from 1979).

After formally retiring at the age of 68 from his Chair at UCL, he moved with postdocs and PhD students to the Royal Free Medical School in Hampstead (London) where he could continue his scientific work and where he became Director of the Autonomic Neuroscience Institute, Royal Free & University College London (1974–2004) and later President of the Autonomic Neuroscience Center, Royal Free & University College Medical School (2004–2017). This brought him into closer contact with clinicians working in the hospital, including experts in cancer, skin, bladder, and vascular diseases, all fields of great interest to him. While still publishing at high rate in his 80s, the Royal Free Medical School asked him twice to retire and give up the office which he still held. The first time when he was asked to leave, he fought bitterly for a possibility to carry on and asked friends and colleagues from all over the world to help him out convincing the Dean to let him stay. Within a couple of days, the Dean's office was submerged by hundreds of letters from academics and people working in companies and foundations begging the Dean to let Geoff stay. This allowed him to gain a handful of years but later on, in 2015, he lost the battle. During his time in London, he had kept close ties to Australia, and he held both British and Australian citizenship. In 2017, he returned to Melbourne. His affiliation with the Department

of Pharmacology and Therapeutics, University of Melbourne, and his status as Honorary Professorial Fellow of the Florey Institute of Neuroscience and Mental Health allowed him to keep his collaborative and journal work as well as his worldwide contacts until his death.

In addition to all this, Geoff Burnstock held numerous editorial appointments. In particular, he was editor-in-chief of *Autonomic Neuroscience* and of *Purinergic Signalling*, a journal which he founded in 2004 and which was of central importance for the development of research in the field. His administrative duties were plentiful, and he acted as consultant and adviser to a large number of pharmaceutical companies. All this could not detract him from research. He was leader of the field until his death (see Figs. 2, 3, and 4 and Tables 1 and 2).

Major scientific achievements

From the very beginning, Geoff's approach to science was to explore systems with an unbiased, multidisciplinary, and "out of the box" attitude. He was proud of questioning tradition. His investigations were based on intuition, factual information based on a broad and thorough literature search, and on the use of techniques that he imported from many different fields including anatomy, histology, electrophysiology, and pharmacology to challenge scientific dogmas, discard or corroborate new hypotheses, and pose new fundamental biological questions. In this respect, he must be considered one of the pioneers of a multi-disciplinary research approach that has become so popular today. As a result of his unconventional approaches disrespecting prevailing dogmas and disregarding



Fig. 2 Geoff Burnstock among purine researchers in London 2007



Fig. 3 Geoff Burnstock surrounded by purine researchers in Bonn at the International Conference Purines 2014



Fig. 4 Geoff Burnstock leading an ever-growing international purine research community (at the International Conference Purines 2014 in Bonn, Germany)

fundamental beliefs, however, several of Geoff's radical hypotheses had encountered resistance, rejection, and even condemnation by part of the scientific establishment.

His first major finding was the discovery of autonomic neurotransmission in the early 1960s involving none of the two main transmitters known at the time, acetylcholine and noradrenaline. Specifically, he observed that rapid hyperpolarization of intestinal smooth muscle cells remained after inhibiting classical transmission with adrenergic and cholinergic blockers, which he attributed to non-adrenergic, non-cholinergic (NANC) inhibitory nerves. He soon extended this finding to the urinary bladder and blood vessels and showed that the transmitter involved was the purine nucleotide ATP, which led him to name this new type of neurotransmission "purinergic." In 1972, he published in the journal *Pharmacological Reviews* his most famous article, "Purinergic Nerves," which was followed, in 1978, by his second most famous paper recognizing the existence of distinct receptors for the purine nucleotides ATP and ADP, and of receptors for their breakdown product, the purine nucleoside adenosine. He presciently raised the possibility that other nucleotides served a similar function, which was confirmed many years later.

These initial studies were received with massive skepticism and encountered severe resistance by large parts of the scientific community. The concept of purinergic transmission was rejected on the grounds that ATP was too ubiquitous a molecule to be a neurotransmitter. Moreover, it was very hard to believe at those times that a rather primitive molecule involved in metabolism and energy production inside cells could also act highly selectively on the cell surface fulfilling key roles in cell-to-cell communication. Geoff was attacked and ridiculed at international meetings, and several scientists even stated they would "devote their lives to destroying the purinergic hypothesis."

Despite this, Geoff tenaciously pursued his ideas and convictions and kept performing work to provide more and more evidence. The purinergic hypothesis slowly started to grow, also thanks to Geoff's passionate ability to convince young scientists to join the field.

Finally, in the early 1990s, several important discoveries definitively accredited the purinergic hypothesis. Together

with his old friend Eric Barnard, with whom he had been a PhD student at University College London in the early 1950s, Geoff cloned the first G protein-coupled receptor for ATP (P2Y₁), and at about the same time, David Julius in San Francisco cloned the P2Y₂ receptor. A year later, the first two ATP-gated ionotropic receptors (P2X₁ and P2X₂) were cloned. Within a very short period, seven P2X and eight P2Y receptor subtypes were cloned and characterized, clearly highlighting the existence of two distinct families of P2 receptors previously predicted by Geoff Burnstock. Since then, the purinergic hypothesis flourished throughout the world, also thanks to Geoff's ability to infuse enthusiasm on the topic and attract people to the field. As a result of the studies performed in the last 20 years, several therapeutic opportunities based on the modulation of the purinergic system are becoming reality. Among other therapeutic purinergic concepts, Geoff sustained the idea of P2X₃ antagonists for treating pain, inflammation, and other conditions: Gefapixant (after Geoff) is currently in clinical trial for the treatment of chronic cough. Hopefully, there will be others of Geoff's ideas coming to fruition in the future.

A second unconventional hypothesis that encountered strong resistance among scientists was Geoff's 1976 Commentary in *Neuroscience* entitled "Do some nerve cells release more than one transmitter?" In this paper, Geoff collected a number of examples from both invertebrates and vertebrates going against the then firmly established belief that one nerve could only release one transmitter. Geoff's commentary prompted research in the area and contributed to fostering the concept of co-transmission, according to which all nerves in both the peripheral and central nervous systems utilize more than one transmitter. This included ATP, which is indeed co-stored with classical transmitters like acetylcholine and noradrenaline at many synapses.

Public recognition

Throughout his career, Geoff Burnstock received numerous honors, awards, memberships in scientific societies, medals, or keynote lectures (Tables 1 and 2). Of the impressive list,

Table 1 Honors of Geoffrey Burnstock

1970	Royal Society of Victoria Silver Medal
1971	Fellow of the Australian Academy of Science (FAA)
1974	Scientific Fellow of the Zoological Society of London
1983	Visiting Professor, Institute of Experimental Medicine, Hungarian Academy of Science
1984	Honorary Member of the Erik K. Ferström Symposium on Neural Regulation of Brain Circulation: Effects of Neurotransmitters and Neuromodulators, Lund
1985–1987	Contract Professor, University of Siena, Italy
1986	Fellow of the Royal Society (FRS)
1987	Honorary Member of the Royal College of Physicians (MRCP)
1988	Visiting Professor, Royal Society of Medicine Foundation, New York, USA
1989	Special Award and Sculpture presented at the NIH Conference, Bethesda, Maryland, September 18, 1989, “For the Concept of Purinergic Transmission”
1992	Member of Academia Europaea
1993	Foreign Member of the Russian Society of Neuropathology
1993–1994	Contract Professor, University of Milan, Italy
1995–1998	President, International Neurovegetative Society
1995–2000	Foundation President, International Society for Autonomic Neuroscience (ISAN)
1995	Fellow of University College London
1996	Phoenix Science Prize
1997	Honorary Member of the Australasian Society of Clinical and Experimental Pharmacologists and Toxicologists (ASCEPT)
1998	President (Medicine), British Association
1998	Honorary Fellow of the Anatomical Society of Great Britain and Ireland
1998	Invitation to the House of Lord by the Earl and Countess of Munster to Celebrate Skeletal and Osteoporosis Research
1998	Founder Fellow, Academy of Medical Sciences
1998	Honorary Fellow of the Royal College of Surgeons of England (FRCS)
2000	Honorary Fellow of the Royal College of Physicians (FRCP)
2000	Janssen Award for “Lifetime Achievement in Digestive Sciences” in San Diego
2000	Royal Society Royal Medal
2002	Doctor Honoris Causa, University of Antwerp, Belgium
2003	Honorary Member of the Physiological Society
2004	Correspondent Academician of the Real Academia Nacional de Farmacia, Spain
2004	Honorary Fellow of the British Pharmacological Society
2006	Honorary Professorial Research Fellow, Mental Health Research Institute of Victoria, Australia
2006	Honorary Membership of the Hungarian Society of Experimental and Clinical Pharmacology
2007	Doctor Honoris Causa, Goethe-Universität (Frankfurt)
2008	Honorary Member of the Australian Physiological Society
2009	Copernicus Gold Medal, Ferrara
2009	The British Neuroscience Association. Annual Award for “Outstanding Contribution to British Neuroscience”
2010	The Gaddum Memorial Award
2011	Doctor Honoris Causa, University of Leipzig
2011	The Geoffrey Burnstock Prize for Neuroscience (UCL)
2012	The Erasmus Medal (Academia Europaea)
2012	Star Reviewer, The American Physiological Society
2013	Honorary Membership of the Good Practice in Traditional Chinese Medicine Research Association (GP-TCM RA)
2014	Honorary Membership of the German Purine Club
2016	Honorary Professor of Chengdu University of Traditional Chinese Medicine
2018	The Australian Academy of Science Macfarlane Burnet Medal & Lecture
2018	The Companion of the Order of Australia (AC) (equivalent to the British Knighthood)

Table 2 Special named or invited lectures

1968	Special Lecture, “The Autonomic Neuromuscular Junction,” International Union of Physiological Sciences (IUPS), Washington
1970	Special Lecture Series, “Autonomic Neuroeffector Systems,” UCLA, Los Angeles
1971	The Brailsford Robertson Memorial Lecture, Adelaide
1972	The Australian Physiology and Pharmacology Society Invited Lecture, Adelaide
1972	Invited Lecture to Arts Directors Club, Melbourne
1976	The West Memorial Lecture, University College, Cardiff
1976	The Third Otto Krayer Lecture, “Autonomic Neuromuscular Interactions,” Harvard University
1976	The Slovak Academy of Sciences Invited Lecture, Bratislava
1976	The South African Physiology and Pharmacology Societies’ Invited Lecture, Durban
1977	Inaugural Lecture, Chair of Anatomy, Department of Anatomy and Embryology, University College London
1978	The Guest Lecturer for the First Biomedical Research Forum, University of Michigan
1979	The Synthelabo Lecture, Paris
1979	The British Physiological Society “Review Lecture,” Birmingham
1980	The Cumings Memorial Lecture, The Migraine Trust Third International Symposium, London
1980	The Hypertension Artérielle et Système Nerveux Inserm Lecture, Paris
1981	The Plenary Lecture, The Norwegian Physiological Society, Myrdal
1981	The 1981 Guest Lecture in Series “The Mechanism of Drug Action,” Ann Arbor
1981	The American Gastroenterological Association Memorial Lecture, New York
1982	The Schueler Distinguished Lecture in Pharmacology, Tulane University, New Orleans
1982	Invited Lecture, Dutch Society for Gastroenterology, Veldhoven
1982	Visiting Professor and Guest Speaker of the First Surgical Clinic University of Athens
1983	The Guest Lecture, British Association for Rheumatology and Rehabilitation, UCH, London
1983	Invited Lecture, Hungarian Academy of Science, Budapest
1983	The Third Anatomical Society of Great Britain and Ireland Review Lecture, “The Autonomic Nervous System: Current Developments and Future Directions,” Cardiff
1983	Invited Lecture, “Autonomic Revolution: Neurotransmitters, Cotransmitter, Neuromodulators and Tropic Factors,” Heidelberg
1984	Invited Lecture, “Autonomic Neuroeffector Mechanisms: New Links with Disease,” Kantonsspital, Basel
1985	The First Ulf von Euler Lecture in Physiology, Stockholm
1985	Lecture Series on “Autonomic Neuroeffector Systems in Development and Disease,” “Contract Professor,” University of Siena
1985	He CIBA-GEIGY Guest Lecture, Medical Research Society, London
1985	The Guest Lecture, Bayliss & Starling Society, “Peptidergic Control of the Vascular System,” London
1986	The First John T. Shepherd Lecture, “Mechanisms of Vasodilatation,” Mayo Clinic, Rochester
1986	The Harold Lamport Lecture in Physiology, Seattle
1987	The Biomedical Review Lecture, Liverpool
1987	The Sadashiv M. Kirpekar Memorial Lecture, Health Science Centre at Brooklyn, New York
1987	The Invited Lecture, International Medical Society of Paraplegia, Stoke Mandeville
1987	The Plenary Lecture, Xth International Congress of Pharmacology, Sydney
1987	The Oliver-Sharpay Lecture, Royal College of Physicians, London
1987	The Review Lecture, Clinical Autonomic Research Society, London
1987	The Ariëns Lecture, “Purinergic Receptors,” Utrecht
1988	Keynote Lecture, IBRO Neuroscience Workshop for Young Scientists, Nairobi
1988	Plenary Lecture, British Pharmaceutical Society Conference, Aberdeen
1988	ICI/Physiological Sciences Prize Lecture “Changing Concepts of the Autonomic Nervous System,” Manchester
1988	Special Guest Lecture, Joint Meeting of Canadian and American Pain Societies, Toronto
1988	Distinguished Neuroscience Lecture, “Dual Control of Local Blood Flow by Nerves and Endothelial Cells,” University of Toronto
1988	Special Neuroscience Seminar, Colorado State University
1989	Special Invited Lecture, “Autonomic Neuroeffector Mechanisms, Recent Developments,” Japanese Pharmacological Society, Kyoto
1990	The Heymans Memorial Lecture, “Co-transmission,” Ghent
1990	Review Lecture, Società Italiana di Fisiologia, “Autonomic Nervous System: the 30 Years after Sir Henry Dale,” Florence
1990	State of the Art Lecture, 13th Scientific Meeting of the International Society of Hypertension, Montreal

Table 2 (continued)

1990	The Du Pont Lecture, “Update on Autonomic Transmitters: Their Possible Implications in Pain,” Oxford
1991	The Rheumatology Lecture, Bloomsbury
1991	Plenary Lecture, “Determinants of Signal Transmission in Healthy and Diseased Autonomic Neuromuscular Junctions,” Satellite Symposium of 14th International Diabetes Federation Congress, New York
1992	The Preclinical Guest Lecture, Cardiff
1992	Opening Lecture, “Physiological and Pathological Roles of Purines: An Update,” Purines ‘92: Pharmacology and Clinical Applications, Milan
1992	Basic Research Lecture, “Fundamental Aspects of GI Motility” at the First United European Gastroenterology Week, Athens
1992	Guest Lecture, “Purinergic Mechanisms in Local Control of the Vasculature,” Association Française des Pharmacologistes, Montpellier
1992	Special Seminar, “Vascular Cross Talk,” Tulane Medical School, New Orleans
1993	Knight Visiting Professor Lecture, The Miami Project to Cure Paralysis, Miami
1994	Keynote Lecture, Medical Research Forum “Endothelial Control of Vascular Tone; Interactions with Neural Mechanisms,” UCL and RFHMS, London
1994	Invited Lecture, “Purinergic Mechanisms: Therapeutic Potential,” GLAXO Institute of Molecular Biology, Geneva
1994	The Charnock Bradley Lecture, Royal (Dick) School of Veterinary Studies, University of Edinburgh, Edinburgh
1995	The C. Ladd Prosser Lecture, University of Illinois, Urbana, USA
1995	Invited Lecture, “Adrenergic Systems, 100 Years after the Discovery of Adrenaline,” Polish Academy of Sciences, Cracow
1995	Chairman of Ciba Foundation Symposium, “P2 Purinoceptors: Localization Function and Transduction Mechanisms,” London
1995	The Plenary Lecture, “Autonomic Neurotransmission: 60 Years since Sir Henry Dale,” Clinical Autonomic Research Society, London
1995	The Opening Plenary Lecture, “Autonomic Neurotransmission,” 1st Asia-Pacific Anatomical Conference, Singapore
1996	The Overseas Lecture, “Purinergic Receptors,” Australian Neuroscience Society, Adelaide
1997	Plenary Lecture, “Purinergic Signalling: Historical Overview and Current Developments,” American Society for Pharmacology & Experimental Therapeutics (ASPET), San Diego
1997	Plenary Lecture, “Purinergic Signalling Including Interactions with Peptides,” 1st European Opioid Conference, Guildford
1997	The Keynote Lecture, “Purinergic Signalling,” Annual Meeting of the Japanese Society of Smooth Muscle Research, Osaka
1998	Presidential Address (as President of the Medical Sciences Section of the British Association), “Bridging the Gaps Between Basic Science, Clinical Medicine and the Pharmaceutical Industry”, Cardiff
1998	The First Bengt Falck Lecture, Lund
1998	The Magnes Memorial Lecture “Local Mechanisms Controlling Vascular Tone,” Israel Society for Physiology and Pharmacology, Ma’ale Hachanisha, Israel
1998	The Medical Science Review Lecture, Sheffield
1999	The J.Z. Young Lecture, “Autonomic Neurotransmission: 60 Years since Sir Henry Dale,” Oxford
1999	The Distinguished Guest Lecture, “Autonomic Neurotransmission in Health and Disease,” Royal College of Surgeons of Ireland, Dublin
1999	The G.W. Harris Prize Lecture, “Purinergic Signalling,” The Physiological Society, UK. London
1999	The Rocha e Silva Award Lecture, Brazilian Society of Pharmacology and Experimental Therapeutics Annual Meeting, Caxambu, Brazil
1999	The Distinguished Lecture in Pharmacology, “Autonomic Neurotransmission Including Purinergic Signalling,” Northwestern University Medical School, Chicago
1999	The Louis D’Agrosa Memorial Lecture, “Purinergic Signalling,” School of Medicine, St. Louis University, St. Louis
2000	The Neuroscience Society Lecture, Göteborg
2000	Public Lecture, “The Expanding Field of Purinergic Signalling,” sponsored by the Royal Society of Victoria and Monash University, Melbourne
2000	Purines 2000, Opening Lecture Madrid
2001	Horace Davenport Distinguished Lecturer 2001, American Physiological Society, Orlando, USA
2001	Ludwig Robert Müller Memorial Lecture, “Neurotransmitters of the Gut.” The Third European Federation of Autonomic Societies (EFAS) Meeting, Erlangen, Germany
2001	The Sherrington Lecture, “Purinergic Signalling,” Liverpool
2001	Dahlemer Cell Biology Colloquium Lecture, Berlin
2002	Special Lecture, “Roles of ATP in the Nervous System,” The Third International Symposium on the Study of Brain Function, Fukuoka, Japan
2002	Plenary Speaker, “Purinergic Signalling,” XIVth World Congress of Pharmacology (IUPHAR), San Francisco, USA
2002	Plenary Speaker, “Vascular Neuroeffector Mechanisms: The Next 30 Years,” 10th International Symposium on Vascular Neuroeffector Mechanisms, Lake Tahoe, California, USA
2003	Neuroscience Distinguished Lecturer, Toronto, Canada
2003	The Stevenson Memorial Lecture, London, Ontario, Canada
2004	The Winsbury White Lecture, Royal Society of Medicine, London, UK
2004	The First Annual Burnstock Lecture, University of North Carolina, USA
2004	Inaugural Lecture upon Election to the Real Academia Nacional de Farmacia, Spain, Madrid
2005	Plenary Lecture, “Purinergic Mechanosensory Transduction and Visceral Pain,” 4th Congress of International Society for Autonomic Neuroscience (ISAN), Marseille
2005	The Rand Medal Lecture, Australian Society for Clinical and Experimental Pharmacologists and Toxicologists (ASCEPT), Melbourne, Australia
2005	Guest Lecturer, Discipline Integration Seminar Series, University of Surrey
2006	The Lo Yuk Tong Foundation Lecture, University of Hong Kong
2006	Public Lecture in Medical Lecture Series, University of Brunei Darussalam
2006	The Plenary Lecture, “Purinergic Signalling: Past, Present and Future,” 8th International Symposium on Adenosine and Adenine Nucleotides, Ferrara
2006	Lecture Given at the Hungarian Academy of Science upon Award of Honorary Membership of the Hungarian Society of Experimental and Clinical Pharmacology, Budapest

Table 2 (continued)

2007	Opening Lecture, “Endothelium: The Determinant of Cardiovascular Health and Disease,” International Workshop, Cracow
2007	The Daniel Percy 2007 Public Lecture, “Purinergic Signalling: Past, Present and Future,” McMaster University, Hamilton, Canada
2007	Opening Lecture in Pharmacology, University of Lisbon, Portugal
2008	Astra Zeneca 2008 Seminar, University of Manchester, Manchester
2008	The Tony Birmingham Lecture, School of Biomedical Sciences, Nottingham University, Nottingham
2008	Invited Lecture to Open the IV Symposium Covian, University of São Paulo, School of Medicine, Ribeirão Preto, Brazil
2008	Opening Plenary Lecture, Purines 2008, Copenhagen
2009	Special Lecture, “Workshop: Purinergic Signalling,” Kazan
2009	The Copernicus Gold Medal Lecture (Lectio Magistralis), Ferrara
2009	The Opening (Plenary) Lecture, Purines 2009 Meeting, Fukuoka
2009	Invited Speaker, “Overview of the Pathophysiology of Purinergic Signalling,” Federation of European Physiological Societies (FEPS) Meeting, Ljubljana, Slovenia
2010	The Opening (Plenary) Lecture, “The Therapeutic Potential of Purinergic Signalling,” Purines 2010 International Meeting, Tarragona
2010	The Urology Foundation Guest Lecture, “Therapeutic Potential of Purinergic Signalling for Disorders in the Urinary Tract,” Manchester
2010	The Opening (Plenary) Lecture, The First Brazilian Purine Club Meeting, Aguas de Lindoia
2010	The Opening (Plenary) Lecture, The 2nd UK Purine Club Meeting, Nottingham
2010	The Opening Lecture, Symposium “ATP and Purinergic Signalling in Physiology and Chronic Disease,” Maastricht
2010	The Biofor Lecture, Bilbao
2011	The Opening (Plenary) Lecture, The 4th Joint German-Italian Purine Club Meeting, Bonn
2011	Special Lecture on the Occasion of my Award of Dr. Honoris Causa from the University of Leipzig
2011	The Opening Plenary Lecture, Joint International Society of Autonomic Neuroscience (ISAN)/American Autonomic Society (AAS) Meeting, Buzios, Brazil
2011	The Gaddum Memorial Award Lecture, British Pharmacological Society, London
2012	The Erasmus Medal Lecture, Academia Europaea, Bergen, Norway
2012	The Opening (Plenary) Lecture, The 2nd Sino-German International Symposium on “Purinergic Signalling, Pain and Acupuncture,” Chengdu, China
2012	The Opening Lecture, “The Birth and Postnatal Development of Purinergic Signalling,” Purines 2012 International Meeting, Fukuoka
2013	The Opening (Plenary) Lecture, The Annual Meeting of the Japanese Pharmacological Society, Fukuoka, Japan
2013	Invited Special Lecture, The Meeting of the Keio Medical Society, Tokyo
2013	The 2013 Paton Prize Lecture (at International Union of Physiological Sciences (IUPS) Meeting), Birmingham
2013	Keynote Lecture (Associated with Appointment as Honorary Member of GP-TCMRA, 2nd GP-TCMRA Meeting, Graz, Austria)
2013	The Opening (Plenary) Lecture, The 5th Joint German-Italian Purine Club Meeting, Rimini, Italy
2013	The Krogh Seminar, “Purinergic Signalling: Pathophysiology and Therapeutic Potential,” Copenhagen, Denmark
2014	The Opening Lecture at the International Symposium: Purinergic Frontiers: From Basic Science to Clinical Challenges, Madrid, Spain
2014	The Opening Plenary Lecture at Purines 2014, Bonn, Germany
2015	Keynote Talk at the Hippocrates Symposium, Salzburg, Austria
2015	The Opening Lecture at the 5th Brazilian Purine Club Meeting, São Sebastião, Brazil
2015	The Plenary Lecture at the 6th Joint German-Italian Purine Club Meeting, Hamburg, Germany
2016	The Opening Lecture at the German Medical Acupuncture Society Meeting, Bad Nauheim, Germany
2016	Keynote Lecture at Neurology 2016, London, UK
2017	Opening Lecture at the 7th Joint Italian-German Purine Club Meeting in Rome, Italy
2017	Opening Lecture at the 2nd Sino-German Symposium on Purinergic Signalling, Pain and Acupuncture in Leipzig, Germany
2018	Opening Lecture at the 1st Chinese Purine Club Meeting in Chengdu, China

only a few examples can be mentioned here: Royal Society of Victoria Silver Medal (1970); Fellow of the Australian Academy of Science (FAA) (1971); Fellow of the Royal Society (FRS) (1986); Honorary Member of the Royal College of Physicians (MRCP) (1987); Member of Academia Europaea (1992); Foreign Member of the Russian Society of Neuropathology (1993); Fellow of University College London (1995); Founder Member of The Academy of Medical Sciences (1998); Honorary Fellow of the Royal College of Surgeons of England (FRCS) (1999); Honorary Fellow of the Royal College of Physicians (FRCP) (2000); Royal Society Royal Medal (2000); Correspondent Academician of the Real Academia Nacional de Farmacia, Spain (2003); Honorary Member of the Physiological Society (2003); Honorary Fellow of the Pharmacological

Society (2004); Honorary Professorial Research Fellow, Mental Health Research Institute of Victoria, Australia (2006); Honorary Membership of the Hungarian Society of Experimental and Clinical Pharmacology (2006); Honorary Member of the Australian Physiological Society (2008); Copernicus Gold Medal, Ferrara (2009) (see Fig. 5); The British Neuroscience Association Annual Award for “Outstanding Contribution to British Neuroscience” (2009); Honorary Professor of Chendu University of Traditional Chinese Medicine (2016); The Australian Academy of Science Macfarlane Burnet Medal and Lecture (2018); The Companion of the Order of Australia (AC) (equivalent to British Knighthood) (2018). In 2018, he was also appointed to the 2018 Queen’s Birthday Honors (Australia), for eminent service to biological sciences in the field of pharmacology and

Fig. 5 Professor Burnstock receiving the Copernicus Gold Medal in Ferrara, Italy, in 2009. On the far right, Prof. Francesco Di Virgilio



toxicology as an academic, author and mentor, through pioneering research into purinergic signalling pathways in mammalian systems and through medical research. He

received three honorary doctorates, Doctor Honoris Causa, University of Antwerp (2002); Doctor Honoris Causa Goethe-University (Frankfurt am Main) (2007) (see Fig. 6);

Fig. 6 At Frankfurt University on the occasion of the Honorary Doctorate Award to Geoff Burnstock in 2007



and Doctor Honoris Causa University of Leipzig (2011). Several times, he was nominated for the Nobel Prize, and he definitely would have deserved it.

A personal view: Maria Abbraccio (Milan, Italy)

I have been very lucky to have been exposed to Geoff's passionate teaching and coaching for more than 30 years. I first met Geoff in 1987 in Pisa, at an Italian Research Council physiological meeting. I was working on adenosine in the brain and I was fascinated by Geoff's free mind and infectious enthusiasm, to the point that I decided to start working on ATP receptors. I communicated this decision to Geoff a couple of years later (1990) in Yamanaka, Japan, on the occasion of one of the old purine meetings, when I also approached him to ask his opinion on the possibility of establishing an international Purine Club. Geoff enthusiastically sustained both ideas and invited me to join his lab in London for a sabbatical leave, which I did in 1992–93. We performed together several wonderful experiments to show the role of ATP in CNS glial cells and got to know each other much better. Besides being an excellent scientist and mentor, Geoff was also an extraordinary human being. On Saturdays, he used to invite some of his collaborators to his home to spend the day with him and his family. I was staying in London together with my young son, and the two of us had a wonderful time together with Geoff, Nomi, and their two daughters (the ones living in London, since the third one had remained in Australia). Whenever possible, we were joined by my husband Angelo, who is a scientist as well, which stimulated our science discussions even more. We used to spend part of the time working, mostly writing the papers that we did not have time to write during the very busy weeks in the lab, but also chatting, watching TV (cricket, in particular, that he and Nomi liked a lot), cooking, and spending time in the garden.

It was incredible how Geoff could switch from science to any other topic with the same easiness and enthusiasm. He used to say that "there is no difference between talking science and talking about our hobbies or things that we like, because science is part of our life". I have been always struck by Geoff's limitless and profound desire of (and admiration for) knowledge. He had a genuine interest in people and was always open to listen and learn from them. And, despite declaring himself an avowed agnostic, he approached life, nature, and people with the same profound (and almost religious) respect and love.

During the London period, we strengthened the idea of the Purine Club that was then formalized in 1994 on the occasion of another purine meeting in Philadelphia. Since then, our collaboration and friendship has never come to an end. In

the following years, I used to spend summer weeks in Geoff's lab in London, again performing experiments, discussing science, and organizing scientific meetings together. With years, I saw him growing older but keeping the same energy, the same genuine excitement and astonishment in front of any new discovery. He kept studying for his entire life, he had an immense culture, he was the founder of our field, yet it was not unusual to see him at scientific meetings taking notes of what young speakers were saying, always eager to learn something new.

I have learned a lot from Geoff. He taught me to recognize my own strengths and weaknesses, in order to capitalize on the first and work on the second ones. He helped me overcoming obstacles and affirming my ideas by tenaciously and honestly working on them without giving up. In this respect, his story was quite reassuring and a seminal example because it was the clear-cut demonstration that if you work well, sooner or later people are going to recognize your work. He has been one of the most influential persons in my life, and I will never forget him. Nor will Alex and Angelo and the entire purinergic community worldwide.

A personal view: Kenneth A. Jacobson (Bethesda, USA)

I first met Geoff in Australia in 1987 at International Union of Basic and Clinical Pharmacology (IUPHAR) international congress. Having been impressed with his keynote, opening lecture in the Sydney Opera House on the central role of extracellular purines (ATP and adenosine) in biology, I approached him to express my interest. There were only a handful of papers published by that time on ATP in cell signalling. I decided after our discussion to begin work on P2 receptors (for nucleotides), in addition to adenosine receptors, which I was already heavily involved in by then. The science of adenosine receptors (John Daly and others) and ATP receptors (Burnstock) developed on parallel tracks, gaining momentum in the 1970s, and Burnstock was the first to unify both classes in the context of purinergic signalling. Adenosine receptors were designated as P1 and ATP receptors as P2. In 1985, he and Charles Kennedy proposed a further division of ATP receptors into P2X (ion channels) and P2Y (metabotropic) receptors. Charles Kennedy has now taken over the editorship of Purinergic Signalling (journal started by Geoff).

Geoff told me that the turning point in his concept of purinergic signalling was at the time of the international conference in 1989 on adenosine and P2 receptors that John Daly and I organized in Bethesda, at which event we gave Burnstock an award for "the concept of purinergic transmission". For > 20 years, Burnstock was doubted by most pharmacologists, who believed that ATP only had a role inside the

cell, and any observation of its activity outside the cell must be an artifact. His ideas were not only contested by other scientists, it reached the point of being ridiculed—and sessions were held in international conferences for the expressed goal of proving Burnstock wrong. The final vindication and acceleration of research in the field came with the cloning of the P2Y₁ receptor in 1993 (with Eric Barnard) and beginning a year later the first P2X receptors. In fact, the purinergic system is as fundamental and vast (or more so) in biology than the cholinergic system that has been studied for many decades longer. It is a dramatic example of having to be persistent with one's well-grounded scientific ideas that violate conventional wisdom.

Geoff was encouraging to many other scientists who wanted to contribute to the purinergic field, and he was beloved by his colleagues and an inspiration in the field. He took a particular interest in our lab's work through the 1990s and even supported a postdoc in our lab in 1994 for the purpose of doing the first molecular modeling of P2Y receptors. I appreciated his feedback on ideas for future research. I once approached him enthusiastically about an idea related to the autonomic nervous system—but not in the purinergic realm. Amusingly, his reaction was blunt: “Ken, don't do it—it's not interesting.” In hindsight, he was right. Although not a chemist, he was aware that having ligands for these receptors was key to progress in the field and eventually leading to drug candidates. Among other therapeutic concepts based on P2 receptors, he nurtured the idea of P2X₃ receptor antagonists for treating pain and other conditions. This idea is now coming to fruition with the clinical studies of a P2X₃ antagonist by Merck (originally from Anthony Ford at Afferent) that is initially being tested for treatment of chronic cough. The drug is called Gefapixant (after Geoff). There are many more of Burnstock's ideas that are yet to come to fruition. His passing is the end of an era. He will be missed!

A personal view: Christa Müller (Bonn, Germany)

In 1989, during my postdoctoral stay at the NIH in Bethesda, MD, USA, in John W. Daly's laboratory, I got the chance to attend the international *Conference on Purine Nucleosides and Nucleotides in Cell Signalling* which took place in Bethesda. I was completely new to the field of purinergic signalling having just started to work on adenosine A_{2B} receptor antagonists. All of a sudden, a huge new universe opened up, all based on Geoff Burnstock's radical discoveries: signalling by nucleotides such as ATP acting on extracellular membrane proteins! And virtually no drugs or tool compounds, at least no potent or selective ones, were available to study these receptors, of which subfamilies,

ionotropic P2X, and metabotropic P2Y receptors, each with a number of subtypes, were proposed to exist. This appeared like an unlimited playing field for a young medicinal chemist. Next to my first scientific role model, John Daly, I had discovered a new hero, Geoff Burnstock. And at that conference, both of my science heroes received prizes, John for pioneering research on the biology and chemistry of adenosine, and Geoff for the concept of purinergic transmission. I was hanging on every of Geoff's words and decided to try to find a future possibility to work on ligands for nucleotide-activated P2 purinergic receptors.

Since then, I saw Geoff at each of the international purine conferences, mostly presenting the opening lecture, which was always a special highlight. Over the past 30 years, I met Geoff on quite a number of occasions, and with getting to know him better, my admiration has exponentially grown. Geoff Burnstock was not only an exceptional scientist with a unique approach, he was human through and through. I want to highlight a few of his prominent qualities which impressed me deeply.

The storyteller

Geoff's seminars and talks always provided an extremely broad overview of the field including aspects of biology, physiology, pharmacology, medicine, and even chemistry. He was an excellent speaker, enthusiastic and explicit, highly convincing, and always entertaining with a good sense of British as well as Australian humor. He used to enrich his scientific talks with anecdotes, new ones or new versions each time, and it never became boring listening to him.

When I now reread his autobiography entitled “Against the Odds”, I was laughing aloud again and again. I recommend everybody to read it to have fun and to learn a lot—for science and for life.

The reader

Geoff Burnstock probably read more scientific articles than most other scientists I know. And he did not only read them, but analyzed their contents and summarized what he had learned, putting it into new context and presenting it in form of highly valuable review articles, which led to the development of new scientific directions and research fields. I remember that I was extremely proud when he sent me postcards in the old days asking for reprints of my articles (me—a young, unknown medicinal chemist!). However, he not only read scientific literature, but you could also have deep discussions with him on books of fiction, and he would share with me a list of his favorite novels, which will still take me years to read.

The educator, advisor, and facilitator

In 2008, when I asked Geoff whether he would be willing to support our translational research consortium *Neuroallianz*, generously funded by the German Federal Ministry of Education and Research (BMBF), by becoming a member of the Strategic Advisory Board, he did not hesitate a second and immediately answered (unconditionally) “yes”. *Neuroallianz* focused on the development of innovative therapeutics and diagnostics for neurogenerative diseases aiming at the translation of basic research to marketed products in collaboration with pharmaceutical industry. For about 10 years, Geoff traveled to North-Rhine-Westphalia on a regular basis to share his wisdom and knowledge, provide guidance, and promote our projects, some of which resulted in the development of (pre)clinical candidates for purinergic targets. Geoff was able to listen attentively, to draw the right conclusions, and to formulate criticism clearly, but always gently and politely. His main driving force and chief aim was to promote science. And he was an optimist: “After what could be regarded as a setback, it can turn out for the best” (cited after his autobiography).

Geoff was an outstanding scientist, and he had the heart in the right place. We will sorely miss him.

A personal view: Herbert Zimmermann (Frankfurt am Main, Germany)

I first met Geoff Burnstock at a meeting on the “Cholinergic Synapse” held in Žinkovy Castle, Czechoslovakia in 1978. Eric Barnard with whom Burnstock later cloned the first ATP receptor was also there. At this meeting, Geoff reported on the ultrastructure of autonomic cholinergic nerves and their relation to smooth muscle—but not on purinergic signalling. During this time, I was mainly interested in synaptic vesicle turnover and biochemistry at the cholinergic synapse and the vesicular storage of acetylcholine and ATP. We had no idea what vesicular ATP could be good for. Was it to help storing acetylcholine? At that time, I worked at the Max-Planck-Institute of Biophysical Chemistry in Göttingen and I have to admit that I had heard little of Geoff’s work on smooth muscle and on ATP as a neurotransmitter in NANC nerves. I also do not know whether my talk made any impression on him. It was only later when we became good friends.

My approach to the purinergic signalling system resulted from my interest in vesicular ATP and the extracellular fate of released ATP, taking a biochemical approach. Together with colleagues of the Max-Planck-Institute for Psychiatry in Munich, I had organized a first international symposium on ectoenzymes in 1984 on Ringberg Castle in Upper Bavaria. Of central importance for pushing forward the research on ectonucleotidases was the “International Workshop on Ecto-

ATPases” organized by Liselotte Plesner from Aarhus, Denmark in Mar del Plata, Argentina. In those days, Geoff did not attend ectonucleotidase meetings. My first congress purely related to purinergic signalling was the “5th International Symposium on Adenosine and Adenine Nucleotides. From Molecular Biology to Integrative Physiology” organized by Luiz Belardinelli and Amir Pelleg in Philadelphia in 1994. I fully became aware of the many facets of this signalling pathway. The first P2 receptors had just been cloned. Whereas I reported the molecular characterization of ecto-5'-nucleotidase and our first attempts to isolate an ecto-ATPase, Geoff stood out with multiple presentations. In a certain way, with my interest in extracellular hydrolysis, I bridged the gap between the ATP side and the adenosine side of purinergic signalling, two fields that have been quarreling for quite some time. There I also met Maria Abbracchio. Now new connections were established by those who “believed in ATP,” and with several European colleagues, we discussed the possibility of applying for a grant with Program Biomed 2 of the European Commission. We managed to submit in 1995, and in 1996, we succeeded in raising a substantial amount of money (then, before the introduction of the Euro as a common currency, issued as ECU). I acted as coordinator. Project leaders besides myself were Maria Pia Abbracchio from the Instituto die Science Farmacologiche Facolta'die Farmacia, Universita'degli Studi di Milano; Geoffrey Burnstock from the Autonomic Neuroscience Institute des University College London; Edith Heilbronn from the Department of Neurochemistry and Neurotoxicology Stockholm University; Maria Teresa Miras-Portugal from the Dipartimento de Bioquimica y Biologica Molecular der Universidad Complutense, Madrid; Ana Sebastião from the Laboratory of Pharmacology, Gulbenkian Institute of Science, Lisbon; and Klaus Starke from the Institute of Pharmacology, Freiburg University. The project ran for 3 years, involved several workshops in Frankfurt am Main and Milan, and formed the basis for the future close interaction of European researchers in the purinergic field as well as the development of close friendships. Later, I had the pleasure to serve as Associate Editor on Geoff’s journal *Purinergic Signalling* for many years.

Many conferences followed, now integrating purinergic receptors, release, ectonucleotidases, and physiology and pathophysiology. I have particularly lovely mementos of the meetings organized by our Italian colleagues in Chieti, Milano, Camerino, or Ferrara. Geoff was the undisputed leader of the field, always presenting the introductory lecture with impressive overviews of the field. But he also listened to all the other lectures, staying to the very end. Needless to say that the hospitality of our Italian friends further stimulated social interactions. The Series of Italian-German and German-Italian purine meetings continued until recently, and Geoff was always our guest of honor, and also, the meetings Maria Teresa

Fig. 7 Geoff Burnstock and his wife Nomi enjoying a holiday in New Zealand (2011)



Miras-Portugal held in Madrid where Geoff always was guest of honor and the conference organized by Kazuhide Inoue in Fukuoka, Japan.

I have very fond memories of the meeting on “Purinergic Signalling in Neuron-Glia Interactions” which Douglas Fields from the National Institutes of Health, Bethesda, Maryland, organized in 2005 in London. Afterwards, Geoff invited some of us to his house. We relaxed in his wonderful garden and I also tried out his indoor-heated swimming pool.

I am very grateful to Geoff for presenting (together with other colleagues of the field) a lecture at the symposium, which was organized by the Faculty of Biosciences in 2004 at the occasion of my 60th birthday. We had him in Frankfurt again in 2007 when we were honored to award him the title of a “Doctor honoris causa”.

During all these meetings, Geoff was accompanied by his wife Nomi. Gifted with artistic talents, Nomi always took the opportunity to explore the cultural sites of the surroundings. Often, she was accompanied by my wife Margret. The two went on very well together. Following many previous invitations to New Zealand, we finally managed to visit Geoff and Nomi in January 2011, first in their summerhouse near Wellington where the two used to escape from the cold and moist winters in London (Fig. 7). There Geoff had time to follow his hobbies, carving and painting driftwood, reading, or doing his daily share at a jigsaw puzzle to train his gray cells. But he also ran the journal *Purinergic Signalling* and other international research duties. Geoff and Nomi took us for a few days through the Crook Street to the wonderful Abel

Tasman National Park on the South Island. From there, we started our New Zealand round trip and visited them afterwards in Australia in their Melbourne flat. When the two were for a lecture in Bad Nauheim near Frankfurt, we took the opportunity to visit them and to take them to the Taunus mountains where one has an impressive view of Frankfurt.

These are only some of the occasions where we could experience the friendship and generosity of Geoff and Nomi. Throughout all the years I knew Geoff, I always admired his tremendous curiosity which did not cease with increasing age, his enthusiasm for research that inspired young scientists, and his fairness and politeness in scientific dispute. We still keep two pieces of driftwood he had grafted in New Zealand and a wonderful piece of ceramics made by Nomi. We miss him.

Compliance with ethical standards

Conflicts of interest Maria P. Abbraccio declares that she has no conflict of interest.

Kenneth A. Jacobson declares that he has no conflict of interest.

Christa E. Müller declares that she has no conflict of interest.

Herbert Zimmermann declares that he has no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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