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Klaus Groschner
Wolfgang F. Graier
Christoph Romanin *Editors*

Store-Operated Ca^{2+} Entry (SOCE) Pathways

Emerging Signaling Concepts in Human (Patho)physiology

Second Edition

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Editors
Klaus Groschner
Institute of Biophysics
Medical University of Graz
Graz, Austria

Wolfgang F. Graier
Institute of Molecular Biology and Biochemistry
Medical University of Graz
Graz, Austria

Christoph Romanin
Institute of Biophysics
Johannes Kepler University Linz
Linz, Austria

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Preface

A brief recapitulation of the overwhelming recent progress in our understanding of Ca^{2+} signaling and (patho)physiological processes linked to or associated with depletion/refilling of the cells' sarcoplasmic/endoplasmic reticulum led us to initiate the compilation of a second edition, an update of this book, less than 5 years after the release of the first edition. We kept the original structure to address the key issues of (1) fundamental mechanistic concepts, (2) cross talk between organelle and cell compartments, and (3) molecular and cellular (patho)physiology of these processes. Each of these sections has not only been significantly updated by amendatory, detailed information complementing the previous topics and chapters but also extended by entirely novel aspects addressed in separate, new chapters. Among these important extensions of the scope are the recently gained information on the molecular structure of the STIM–Orai machinery at the atomic resolution level (Chap. 2), novel insights into the supramolecular domain organization of the STIM–Orai coupling machinery (Chap. 5), the recent developments in STIM–Orai optogenetics (Chap. 7), novel insights into the structure and function of membrane (in particular plasma membrane)-endoplasmic reticulum contact sites (Chaps. 15, 17), as well as recently gained knowledge on the role of SOCE in cancer (Chaps. 30, 31). In turn, a few other aspects were found better suitable for combined synopsis within a single chapter such as integrative aspects of cardiovascular disease and therapy (Chap. 24).

Overall, we hope that this second edition may be inspiring and supportive by its comprehensive and timely information on the SOCE phenomenon for both students and advanced colleagues who focus on SOCE-related aspects of cellular Ca^{2+} homeostasis. Even more, we hope that this updated compilation of current expertise in SOCE signaling will serve as an influential knowledge base to further groundbreaking developments in this steadily growing field of cell biology/pathophysiology.

Graz, Austria — Klaus Groschner
Graz, Austria — Wolfgang F. Graier
Linz, Austria — Christoph Romanin

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Graz, Austria — Klaus Groschner
Graz, Austria — Wolfgang F. Graier
Linz, Austria — Christoph Romanin

Contents

Editors Biography

Klaus Groschner studied pharmacy at the School of Pharmacy, University of Graz, Austria. He completed his PhD studies at the Department of Pharmacodynamics in Graz and received part of his postdoctoral education at the University of Miami, Florida, USA, studying electrophysiology and cell biology. In 1990, he became an assistant professor at the Department of Pharmacology and Toxicology and received his habilitation in pharmacology and toxicology along with promotion to associate professor in 1993. Until 2011, he was head of a research unit for physiology and pharmacology of membrane transport at the Institute of Pharmaceutical Sciences at the University of Graz. Since 2012, he is full professor and chairman at the Institute of Biophysics at the Medical University of Graz.

Wolfgang F. Graier studied pharmacy at the University of Graz, Austria, and received his PhD in pharmacology at the Department of Pharmacology and Toxicology, University of Graz. In 1993–1994, he was a postdoctoral research fellow, analyzing physiology and membrane biophysics at the Dalton Cardiovascular Research Center, University of Missouri, Columbia, USA. In 1994, he became an assistant professor at the Department of Medical Biochemistry, University of Graz. In 1995, he became associate professor (habilitation) in biochemical pharmacology and in physiology in 2001 at the Department of Medical Biochemistry, University of Graz. Since 2009, he is full professor for molecular biology and chairman of the Institute of Molecular Biology and Biochemistry at the Medical University of Graz. Since 2015, he is also head of the Nikon Center of Excellence for Super-Resolution Microscopy: *Cells and Organelles* that is part of BioTechMed, the concerted research platform of the Medical University of Graz, the University of Graz, and the Graz University of Technology. In 2016, he cofounded a spin-off company named Next Generation Fluorescence Imaging or NGFI (www.ngfi.eu).

Christoph Romanin studied chemistry at the Graz University of Technology, Austria, and completed his doctoral studies at the Department of Pharmacology and Toxicology, University of Graz. In 1986, he started with a postdoc position at

the Institute of Biophysics of the Johannes Kepler University Linz, Austria, where he became professor in biophysics (habilitation) in 1993 and served as an associate professor since 1997. In 2001, he was a guest researcher at the National Institute on Aging (NIA) of the NIH in Bethesda, USA. Currently, he is vice-chairman of the institute and head of the Ion Channel Group at the Institute of Biophysics in Linz, Austria.

List of Contributors

Eunüs S. Ali Department of Medical Biochemistry, School of Medicine, Flinders University, Adelaide, SA, Australia

Centre for Neuroscience, School of Medicine, Flinders University, Adelaide, SA, Australia

Indu S. Ambudkar Secretory Physiology Section, Molecular Physiology and Therapeutics Branch, National Institute of Dental and Craniofacial Research – NIDCR, National Institutes of Health – NIH, Bethesda, MD, USA

Greg J. Barritt Department of Medical Biochemistry, School of Medicine, Flinders University, Adelaide, SA, Australia

Centre for Neuroscience, School of Medicine, Flinders University, Adelaide, SA, Australia

Fiona Bartoli Inserm UMR S1180, University Paris-Sud, Université Paris-Saclay, Châtenay-Malabry, France

Alexis Bavencoffe Department of Integrative Biology and Pharmacology, McGovern Medical School, The University of Texas Health Science Center at Houston, Houston, TX, USA

Lothar A. Blatter Department of Physiology & Biophysics, Rush University Medical Center, Chicago, IL, USA

Dora Bodnar Epithelial Signaling and Transport Section, Molecular Physiology and Therapeutics Branch, National Institute of Dental and Craniofacial Research – NIDCR, National Institute of Health – NIH, Bethesda, MD, USA

Sunitha Bollimuntha Department of Biomedical Sciences, School of Medicine and Health Sciences, University of North Dakota, Grand Forks, ND, USA

Martin D. Bootman School of Life, Health and Chemical Sciences, The Open University, Milton Keynes, UK

Xiangyu Cai Department of Cellular and Molecular Physiology, The Pennsylvania State University College of Medicine, Hershey, PA, USA

Woo Young Chung Epithelial Signaling and Transport Section, Molecular Physiology and Therapeutics Branch, NIDCR, NIH, Bethesda, MD, USA

Nicolas Demaurex Department of Cell Physiology and Metabolism, University of Geneva, Geneva 4, Switzerland

Isabella Derler Institute of Biophysics, Johannes Kepler University Linz, Linz, Austria

Hayley Dingsdale School of Biosciences, Cardiff University, Cardiff, UK

Petra Eder Department of Internal Medicine I, Comprehensive Heart Failure Center Würzburg, University Hospital Würzburg, Würzburg, Germany

A. Mark Evans Centre for Integrative Physiology, College of Medicine and Veterinary Medicine, University of Edinburgh, Edinburgh, UK

Marc Fahrner Institute of Biophysics, Johannes Kepler University Linz, Linz, Austria

Nicola Fameli Institute of Biophysics, Medical University of Graz, Graz, Austria

Department of Anesthesiology, Pharmacology, and Therapeutics, University of British Columbia, Vancouver, BC, Canada

Qingping Feng Department of Physiology and Pharmacology, Schulich School of Medicine and Dentistry, Western University, London, ON, Canada

Maud Frieden Department of Cell Physiology and Metabolism, University of Geneva, Geneva, Switzerland

Donald L. Gill Department of Cellular and Molecular Physiology, The Pennsylvania State University College of Medicine, Hershey, PA, USA

Wolfgang F. Graier Institute of Molecular Biology and Biochemistry, Medical University of Graz, Graz, Austria

Klaus Groschner Institute of Biophysics, Medical University of Graz, Graz, Austria

Aparna Gudlur Division of Signalling and Gene Expression, La Jolla Institute for Allergy & Immunology, La Jolla, CA, USA

Daniele Guido Department of Cell Physiology and Metabolism, University of Geneva, Geneva 4, Switzerland

Yousang Gwack Department of Physiology, David Geffen School of Medicine at UCLA, Los Angeles, CA, USA

Lee Haynes The Physiological Laboratory, Department of Cellular and Molecular Physiology, The University of Liverpool, Liverpool, UK

Patrick G. Hogan Division of Signalling and Gene Expression, La Jolla Institute for Allergy & Immunology, La Jolla, CA, USA

Jeong Hee Hong Department of Physiology, College of Medicine, Gachon University, Yeonsu-gu, Incheon City, Korea

Yun Huang Center for Epigenetics and Disease Prevention, Institute of Biosciences and Technology, Texas A&M University, Houston, TX, USA

Archana Jha Epithelial Signaling and Transport Section, Molecular Physiology and Therapeutics Branch, National Institute of Dental and Craniofacial Research – NIDCR, National Institute of Health – NIH, Bethesda, MD, USA

Kiho Lee Department of Animal and Poultry Sciences, Virginia Tech, Blacksburg, VA, USA

Natalia A. Loktionova Department of Cellular and Molecular Physiology, The Pennsylvania State University College of Medicine, Hershey, PA, USA

Jose J. Lopez Cell Physiology Research Group, Department of Physiology, University of Extremadura, Cáceres, Spain

Gyorgy Lur Department of Neurobiology, Yale School of Medicine, New Haven, CT, USA

Guolin Ma Center for Translational Cancer Research, Institute of Biosciences and Technology, Texas A&M University Health Science Center, Houston, TX, USA

Zoltan Machaty Department of Animal Sciences, Lilly Hall of Life Sciences, Purdue University, West Lafayette, IN, USA

Roland Malli Institute of Molecular Biology and Biochemistry, Medical University of Graz, Graz, Austria

Rajender K. Motiani Systems Biology Group, CSIR-Institute of Genomics and Integrative Biology, New Delhi, India

Shmuel Muallem Epithelial Signaling and Transport Section, Molecular Physiology and Therapeutics Branch, National Institute of Dental and Craniofacial Research – NIDCR, National Institute of Health – NIH, Bethesda, MD, USA

Martin Muik Institute of Biophysics, Johannes Kepler University Linz, Linz, Austria

Barbara A. Niemeyer Molecular Biophysics, Center for Integrative Physiology and Molecular Medicine, Saarland University, Homburg, Germany

Robert M. Nwokonko Department of Cellular and Molecular Physiology, The Pennsylvania State University College of Medicine, Hershey, PA, USA

Emmanuel Okeke The Physiological Laboratory, Department of Cellular and Molecular Physiology, The University of Liverpool, Liverpool, UK

Hwei Ling Ong Secretory Physiology Section, Molecular Physiology and Therapeutics Branch, National Institute of Dental and Craniofacial Research – NIDCR, National Institutes of Health – NIH, Bethesda, MD, USA

Jonathan Pacheco Instituto de Fisiología Celular, Universidad Nacional Autónoma de México, Ciudad Universitaria, México, DF, México

Biswaranjan Pani Department of Biomedical Sciences, School of Medicine and Health Sciences, University of North Dakota, Grand Forks, ND, USA

Natalia Prevarskaya Laboratory of Excellence, Ion Channels Science and Therapeutics, Université Lille I Sciences et Technologies, Villeneuve d'Ascq, France

Inserm U1003, Equipe Labellisée par la Ligue Nationale Contre le Cancer, Université de Sciences et Technologies de Lille (USTL), Villeneuve d'Ascq, France

James W. Putney The Signal Transduction Laboratory, Department of Health and Human Services, National Institute of Environmental Health Sciences – NIH, Research Triangle Park, NC, USA

Katja Rietdorf School of Life, Health and Chemical Sciences, The Open University, Milton Keynes, UK

Abigaël Ritaine Laboratory of Excellence, Ion Channels Science and Therapeutics, Université Lille I Sciences et Technologies, Villeneuve d'Ascq, France

Inserm U1003, Equipe Labellisée par la Ligue Nationale Contre le Cancer, Université de Sciences et Technologies de Lille (USTL), Villeneuve d'Ascq, France

Christoph Romanin Institute of Biophysics, Johannes Kepler University Linz, Linz, Austria

Juan A. Rosado Cell Physiology Research Group, Department of Physiology, University of Extremadura, Cáceres, Spain

Grigori Y. Rychkov School of Medicine, The University of Adelaide, Adelaide, SA, Australia

South Australian Health and Medical Research Institute, Adelaide, SA, Australia

Jessica Sabourin Inserm UMR S1180, University Paris-Sud, Université Paris-Saclay, Châtenay-Malabry, France

Gines M. Salido Cell Physiology Research Group, Department of Physiology, University of Extremadura, Cáceres, Spain

Sophie Saüc Department of Cell Physiology and Metabolism, University of Geneva, Geneva, Switzerland

Rainer Schindl Institute of Biophysics, Johannes Kepler University Linz, Linz, Austria

George Shapovalov Laboratory of Excellence, Ion Channels Science and Therapeutics, Université Lille I Sciences et Technologies, Villeneuve d'Ascq, France

Inserm U1003, Equipe Labellisée par la Ligue Nationale Contre le Cancer, Université de Sciences et Technologies de Lille (USTL), Villeneuve d'Ascq, France

Niroj Shrestha Institute of Biophysics, Medical University of Graz, Graz, Austria

Brij B. Singh Department of Biomedical Sciences, School of Medicine and Health Sciences, University of North Dakota, Grand Forks, ND, USA

András Spät Laboratory of Molecular Physiology, Hungarian Academy of Sciences, Budapest, Hungary

Department of Physiology, Semmelweis University, Budapest, Hungary

Sonal Srikanth Department of Physiology, David Geffen School of Medicine at UCLA, Los Angeles, CA, USA

Peter B. Stathopulos Department of Physiology and Pharmacology, Schulich School of Medicine and Dentistry, Western University, London, ON, Canada

Zuoming Sun Department of Molecular Immunology, Beckman Research Institute of the City of Hope, Duarte, CA, USA

Gergö Szanda Department of Physiology, Semmelweis University, Budapest, Hungary

Jyoti Tanwar Systems Biology Group, CSIR-Institute of Genomics and Integrative Biology, New Delhi, India

Alexei V. Tepikin The Physiological Laboratory, Department of Cellular and Molecular Physiology, Institute of Translational Medicine, University of Liverpool, Liverpool, UK

Jin-bin Tian Department of Integrative Biology and Pharmacology, McGovern Medical School, The University of Texas Health Science Center at Houston, Houston, TX, USA

Mohamed Trebak Department of Cellular and Molecular Physiology, The Pennsylvania State University College of Medicine, Hershey, PA, USA

Luis Vaca Instituto de Fisiología Celular, Universidad Nacional Autónoma de México, Ciudad Universitaria, México, DF, México

Cornelis van Breemen Department of Anesthesiology, Pharmacology and Therapeutics, The University of British Columbia, Vancouver, BC, Canada

Chunmin Wang Vivere Health, Houston, TX, USA

Youjun Wang Beijing Key Laboratory of Gene Resources and Molecular Development, College of Life Sciences, Beijing Normal University, Beijing, People's Republic of China

Shufan Wen Center for Translational Cancer Research, Institute of Biosciences and Technology, Texas A&M University, Houston, TX, USA

Jin Seok Woo Department of Physiology, David Geffen School of Medicine at UCLA, Los Angeles, CA, USA

Dongki Yang Department of Physiology, College of Medicine, Gachon University, Yeonsu-gu, Incheon City, Korea

Lu Zhang Department of Animal Sciences, Lilly Hall of Life Sciences, Purdue University, West Lafayette, IN, USA

Yandong Zhou Department of Cellular and Molecular Physiology, The Pennsylvania State University College of Medicine, Hershey, PA, USA

Yubin Zhou Center for Translational Cancer Research, Institute of Biosciences and Technology, Texas A&M University Health Science Center, Houston, TX, USA

Department of Medical Physiology, College of Medicine, Texas A&M University Health Science Center, Houston, TX, USA

Jinhui Zhu Department of Physiology and Pharmacology, Schulich School of Medicine and Dentistry, Western University, London, ON, Canada

Michael Xi Zhu Department of Integrative Biology and Pharmacology, McGovern Medical School, The University of Texas Health Science Center at Houston, Houston, TX, USA

Abbreviations

α-SNAP	α-Soluble NSF attachment protein
$\Delta\Psi_m$	Mitochondrial membrane potential
σ1R	Sigma-1 receptor
–/–	Double knockout
+TIP	Plus-end-tracking protein
$[Ca^{2+}]$	Ca^{2+} concentration
$[Ca^{2+}]_{cyt}/[Ca^{2+}]_c$	Cytosolic Ca^{2+} concentration
$[Ca^{2+}]_{ER}$	Free Ca^{2+} concentration of the ER
$[Ca^{2+}]_i$	Intracellular free Ca^{2+} concentration
$[Na^+]_{ns}$	Sodium concentration within the nanospace
2-APB	2-Aminoethoxydiphenyl borate
aa	Amino acid
AA	Arachidonic acid
ABCA	ATP-binding cassette subfamily A member
AC	Adenylyl cyclase
AD	Alzheimer's disease
ADPKD	Autosomal dominant polycystic kidney disease
AM	Atrial myocyte
Ang II	Angiotensin II
ANT	Adenine nucleotide translocase
APC	Adenomatous polyposis coli
APP	Amyloid precursor protein
ARC	Arachidonate-regulated Ca^{2+} channel
Arf6	ADP-ribosylation factor 6
AtCRY2	*Arabidopsis thaliana* cryptochrome 2
ATF6	Activating transcription factor 6
ATP	Adenosine triphosphate
ATXN1	Ataxin 1
BACCS	Blue light-activated Ca^{2+} channel switch
bFGF	Basic fibroblast growth factor
BHQ	2,5-Di-(tert-butyl)-1,4-benzohydroquinone
BKCas	Big conductance Ca^{2+}-activated K^+ channels

BTP2	*N*-[4-[3,5-Bis(trifluoromethyl)-1H-pyrazol-1-yl]phenyl]-4-methyl-1,2,3-thiadiazole-5-carboxamide
Ca^{2+}	Calcium
CAD	Channel-activating domain
CaM	Calmodulin
CaMK	Ca^{2+}-/CaM-dependent protein kinase
cAMP	Cyclic adenosine monophosphate
CaN	Calcineurin
CAPE	Caffeic acid phenethyl ester
CAR	Ca^{2+} accumulation region
CASK	Ca^{2+}-/CaM-dependent serine protein kinase
cat-SOC	Cation store-operated channel
Cav-1	Caveolin-1
CAX	Ca^{2+}/hydrogen exchanger
CC	Coiled coil
CCE	Capacitative Ca^{2+} entry
CCh	Carbachol
CDC42	Cell division control protein 42 homolog
CDI	Ca^{2+}-dependent inactivation
cER	Cortical endoplasmic reticulum
CFP	Cyan fluorescent protein
CGD	Chronic granulomatous disease
cGMP	Cyclic guanosine monophosphate
CIRB	CaM- and IP_3R-binding site
CK1	Casein kinase 1
Cl^-	Chloride
CLEM	Correlative light and electron microscopy
CM	Cardiac myocyte
CnA	Catalytic A subunit of calcineurin
CnB	Calcineurin B
Co-IP	Co-immunoprecipitation
COX	Cyclooxygenase
CPA	Cyclopiazonic acid
CPAE	Calf pulmonary endothelial cell
CRAC	Ca^{2+} release-activated Ca^{2+} channel
CRACR2A	CRAC regulator 2A
CREB	cAMP response element-binding transcription factor
CRMP2	Collapsin response mediator protein-2
cRNA	Complementary RNA
CRYs	Cryptochromes
CSQ	Calsequestrin
CTID	C-terminal inhibitory domain
DAG	Diacylglycerol
DAPC	Dystrophin-associated protein complex
DBD	DNA-binding domain

DC	Dendritic cell
DCX	Doublecortin
DHPR	Dihydropyridine receptor
DKO	Double knockout
dLNs	Draining lymph nodes
DMD	Duchenne muscular dystrophy
DN	Dominant negative
DTS	Dense tubular system
DVF	Divalent-free
DYRK	Dual-specificity tyrosine phosphorylation-regulated kinase
EAE	Experimental autoimmune encephalomyelitis
EB1	End-binding 1 protein
EC	Endothelial cell
ECC	Excitation–contraction coupling
ECCE	Excitation-coupled Ca^{2+} entry
ECM	Extracellular matrix
EDCF	Endothelium-derived contracting factor
EDL	Extensor digitorum longus
EDRF	Endothelium-derived relaxing factor
EE	Early endosome
EGFR	Epidermal growth factor receptor
EGTA	Ethylene glycol-bis(β-aminoethyl ether)-*N*,*N*,*N*′,*N*′-tetraacetic
EMRE	Essential MCU regulator
En	Endosome
eNOS	Endothelial NO synthase (NOS III)
EPAC	Exchange protein directly activated by cAMP
ER	Endoplasmic reticulum
E_{rev}	Reversal potential
ERM	Ezrin–radixin–moesin
ESCRT	Endosomal sorting complex required for transport
E-Syt	Extended synaptotagmin
ET-1	Endothelin 1
ETC	Excitation–transcription coupling
ETON	Extended transmembrane Orai1 N-terminal
EVH1	Ena (Enabled)/VASP (vasodilator-stimulated phosphoprotein) homology 1
FAD	Familial Alzheimer's disease
FAK	Focal adhesion kinase
FCCP	Carbonyl cyanide 4-(trifluoromethoxy)phenylhydrazone
FCDI	Fast Ca^{+2}-dependent inactivation
FF	Diphenylalanine
FFAT	Acidic tract motif
FGF2	Fibroblast growth factor 2
FKBP	FK506-binding protein

FRB	FKBP–rapamycin binding
FRET	Förster/fluorescence resonance energy transfer
GC-A	Guanylyl cyclase-A
GECAs	Genetically encoded Ca^{2+} actuators
GECIs	Genetically encoded Ca^{2+}-sensitive indicators
GEF	Guanine nucleotide exchange factor
GLP-1	Glucagon-like peptide 1
GLUT4	Glucose transporter 4
GPCR	G protein-coupled receptor
GPN	Glycyl-L-phenylalanine-2-naphthylamide
GqPCR	Gq protein-coupled receptor
Grx's	Glutaredoxins
GSH	Glutathione
GSK-3β	Glycogen synthase kinase 3β
GST	Glutathione S-transferase
H_2O_2	Hydrogen peroxide
H2S	Hydrogen sulfide
HAD	HIV-associated dementia
HCMD	High Ca^{2+} microdomain
HDAC	Histone deacetylase
hESC-CM	Human embryonic stem cell-derived cardiomyocyte
HF	Heart failure
HIV	Human immunodeficiency virus
HMGB1	High-mobility group box 1 protein
Hrs	Hepatocyte growth factor-regulated tyrosine kinase substrate
HSG	Human submandibular gland
HUVEC	Human umbilical vein EC
I_{CRAC}	Ca^{2+} release-activated Ca^{2+} current
IκB	Inhibitor of NF-κB
IKK	IκB kinase
IMM	Inner mitochondrial membrane
iNKT	Invariant natural killer T
IP_3	Inositol 1,4,5-trisphosphate
IP_3R	IP_3 receptor
IQGAP	IQ motif-containing GTPase-activating protein
IRE1	Inositol-requiring protein 1
IS	Immunological synapse
Iso	Isoproterenol
I_{SOC}	Store-operated Ca^{2+} current
ITAM	Immunoreceptor tyrosine-based activation motif
JNK	c-Jun N-terminal kinase
JP	Junctophilin
K^+	Potassium
KCa	Ca^{2+}-activated K^+ channel
KD	Knockdown

LB	Lewy body
LCK	Lymphocyte-specific protein tyrosine kinase
LOV	Light–oxygen–voltage sensing
LOXs	Lipoxygenases
LPS	Lipopolysaccharide
LRC	LTC_4-regulated Ca^{2+} channel
LRD	Lipid raft domain
LRRK2	Leucine-rich repeat kinase 2
LTC_4	Leukotriene C_4
LTCCs	L-type Ca^{2+} channels
MAM	Mitochondria-associated membrane
MAPK	Mitogen-activated protein kinase
MAPPER	Membrane-attached peripheral ER
MBP	Myelin basic protein
MCP-1	Monocyte chemoattractant protein-1
MCS	Membrane contact site
MCU	Mitochondrial Ca^{2+} uniporter
MCUP	Mitochondrial Ca^{2+} uniporter complex
MCUR1	Mitochondrial Ca^{2+} uniporter regulator 1
MEF	Mouse embryonic fibroblast
MEF2	Myocyte enhancer factor 2
MEK	Mitogen-activated protein kinase kinase
MG	Myasthenia gravis
MHC	Major histocompatibility complex
MICU	Mitochondrial calcium uptake
mitoNOS	Mitochondria-specific NO synthase
MLC	Myosin light chain
MLCK	Myosin light chain kinase
MMP	Matrix metalloproteinase
MORN	Membrane occupation and recognition nexus
MPF	M-phase promoting factor
MPTP	1-Methyl-4-phenyl-1,2,3,6-tetrahydropyridine
MRs	Mineralocorticoid receptors
MRF	Myogenic regulatory factor
mRFP	Mitochondrially targeted red fluorescent protein
MS	Multiple sclerosis
MT	Microtubule
Mwk mice	Moonwalker mice
Na^+	Sodium
NAADP	Nicotinic acid adenine dinucleotide phosphate
NAD(P)H	Nicotinamide adenine dinucleotide phosphate
NAFLD	Nonalcoholic fatty liver disease
NASH	Nonalcoholic steatohepatitis
NCKX	Na^+/Ca^{2+}–K^+ exchanger
NCX	Na^+/Ca^{2+} exchanger

NCXmito	Mitochondrial Na^+/Ca^{2+} exchanger
NPC1	Niemann–Pick type C protein 1
NFATs	Nuclear factor of activated T cells
NF-κB	Nuclear factor kappa-light-chain-enhancer of activated B cells
NIK	NF-κB-inducible kinase
NIR	Near infrared
$NKA\alpha_{2,3}$	Na^+/K^+-ATPase isoforms $\alpha_{2,3}$
NLS	Nuclear localization sequence
NMR	Nuclear magnetic resonance
nNOS	Neuronal nitric oxide synthase
NO	Nitric oxide
NOX	NADPH oxidase
NRON	Noncoding RNA repressor of NFAT
NSC	Cortical neural stem cell
$O_2^{\bullet-}$	Superoxide anion
OASF	Orai-activating small fragment
OMM	Outer mitochondrial membrane
ORP	Oxysterol-binding protein-related protein
ox-LDL	oxidized low-density lipoprotein
P2Y receptor	Purinergic G protein-coupled receptor
PA	Phosphatidic acid
PAEC	Porcine aortic endothelial cell
PAH	Pulmonary arterial hypertension
PAMs	Plasma membrane-associated membranes
PAR	Protease-activated receptor
PARP	Poly ADP ribose polymerase
PASMC	Pulmonary artery smooth muscle cell
PC	Polycystin
PD	Parkinson's disease
PDAC	Pancreatic ductal adenocarcinoma cell
PDGF	Platelet-derived growth factor
PDZ	PSD95–disc large–zonula occludens protein
PE	Phenylephrine
PERK	RNA-like ER kinase
Ph	Phagosome
PHR	Photolyase homology region
PhyBs	Phytochromes
PI	Phosphoinositide
PI4P	Phosphatidylinositol-4-phosphate
PIP_2	Phosphatidylinositol 4,5-bisphosphate
PKA	Protein kinase A
PKB/Akt	Protein kinase B
PKC	Protein kinase C
PKG	Protein kinase G
PLB	Phospholamban

PLC	Phospholipase C
PLN	Phospholamban
PM	Plasma membrane
PMCA	Plasma membrane Ca^{2+} ATPase
POST	Partner of STIM
PRD	Proline-rich domain
PS	Phosphatidylserine/presenilin
PTP1B	Protein tyrosine phosphatase 1B
RA	Rheumatoid arthritis
RAAS	Renin–angiotensin–aldosterone system
Rab 7	Ras-related protein 7
RasGRP1	Ras guanine nucleotide-releasing protein 1
RBL	Rat basophil leukemia
REG	Regulatory domain
RHD	Rel homology domain
RNAi	RNA interference
ROCs	Receptor-operated channels
ROCE	Receptor-operated Ca^{2+} entry
ROS	Reactive oxygen species
RR	Ruthenium red
RTKs	Receptor tyrosine kinases
RyR	Ryanodine receptor
S/ER	Sarcoplasmic/endoplasmic reticulum
S/P	Serine/proline rich
$S1^{CT}$	Soluble STIM1
S1P	Sphingosine-1-phosphate
SA node	Sinoatrial node
SACs	Stretch-activated cation channels
SACE	Stretch-activated Ca^{2+} entry
SAM	Sterile alpha motif
SARAF	SOC-associated regulatory factor
SCA	Spinocerebellar ataxia
SCD	Sudden cardiac death
$Scgd^{-/-}$ mice	δ-Sarcoglycan deleted mouse model for muscular dystrophy
SCID	Severe combined immune deficiency
SD	Sporadic Alzheimer's disease
SERCA	Sarcoplasmic/endoplasmic reticulum Ca^{2+}-ATPase
SF	Shape factor
SICE	Store-independent Ca^{2+} entry
SLP76	SH2 domain-containing leukocyte protein of 76 kDa
SMC	Smooth muscle cell
SMOCE	Second messenger-operated Ca^{2+} entry
SNAP25	Synaptosome-associated protein 25
SNARE	Soluble *N*-ethylmaleimide-sensitive factor attachment receptor
sNPF	Short neuropeptide F

SOAP	STIM1–Orai1 association pocket
SOAR	STIM1–Orai-activating region
SOC	Store-operated channel
SOCE	Store-operated Ca^{2+} entry
SOCIC	Store-operated Ca^{2+} influx complex
SOD	Superoxide dismutase
SPCA	Secretory pathway Ca^{2+}-ATPase
SPL	Subplasmalemmal
SR	Sarcoplasmic reticulum
SR/ER	Sarcoplasmic/endoplasmic reticulum
SRR	Serine-rich region
STARD	(StAR)-related lipid transfer domain protein
STIM	Stromal interaction molecule
STIMATE	STIM-activating enhancer
Synta66	*N*-(2′,5′-Dimethoxy[1,1′-biphenyl]-4-yl)-3-fluoro-4-pyridinecarboxamide
TAC	Transverse aortic constriction
TAD-C	C-terminal transcription activation domain
TAM	Tubular aggregate myopathy
TBHQ	2,5-Di-(tert-butyl)-1,4-benzohydroquinone
TCR	T-cell receptor
TG	Thapsigargin
TGN	Trans-Golgi network
Th_{eff}	T helper effector cells
TIRF	Total internal reflectance fluorescence
TM	Transmembrane
TMD	Transmembrane domain
TPC	Two-pore domain channel
TPEN	*N*,*N*,*N*′,*N*′-Tetrakis(2-pyridylmethyl)ethylenediamine
TRP	Transient receptor potential
TRPCs	Transient receptor potential canonical family of ion channels
TRPL	TRP-like
Trx	Thioredoxin
TTCC	T-type Ca^{2+} channel
t-tubules	Transverse tubules
UCP	Uncoupling protein
UPR	Unfolded protein response
UVRs	Ultraviolet-B receptors
VAP	Vesicle-associated membrane protein-associated protein
VAPA	Vesicle-associated membrane protein-associated protein A
VDAC	Voltage-dependent anion channel
VEC	Vascular endothelial cell
VEGF	Vascular endothelial growth factor
VEGFR	VEGF receptor
VGCCs	Voltage-gated Ca^{2+} channels

VM	Ventricular myocyte
VOCC	Voltage-operated Ca^{2+} channel
VSMC	Vascular smooth muscle cell
VT	Ventricular tachycardia
WT	Wild type
YFP	Yellow fluorescent protein
YPS	York platelet syndrome
ZAP-70	Z chain-associated protein kinase 70

Part I

SOCE: Fundamental Mechanistic Concepts

Introduction

1

James W. Putney

Abstract

This second edition volume will present an updated, state-of-the art description and analysis of the rapidly expanding field of store-operated Ca^{2+} entry (SOCE). And this first part will deal with the most fundamental mechanistic concepts underlying this process. In this brief introduction, I will try to summarize the historical development of the concept of store-operated Ca^{2+} entry and say a bit about some recent work that speaks to its general function in cell signaling. Much of the material below is taken from the Introduction to the first edition, updated for the second edition.

Keywords

Calcium channels • Orai • STIM1 • Oscillations • Store-operated channels • Mouse models

1.1 SOCE: Historical Development of the Concept

Many would attribute the origins of this concept to my 1986 hypothesis paper in *Cell Calcium* (Putney 1986), but in fact no idea is born in a vacuum, and much of the key elements for this concept developed from much earlier findings. One earlier and fundamental concept is that Ca^{2+} signals can arise in two very general ways: either by influx to the cytoplasm across the plasma membrane or by discharge to the cytoplasm from storage depots within the cell. Although it is now clear that this is a general property of Ca^{2+} signaling pathways, it was the smooth muscle physiologists who first appreciated it, based largely on the differential sensitivity

J.W. Putney (✉)
The Signal Transduction Laboratory, Department of Health and Human Services, National Institute of Environmental Health Sciences – NIH, Research Triangle Park, NC, USA
e-mail: putney@niehs.nih.gov

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