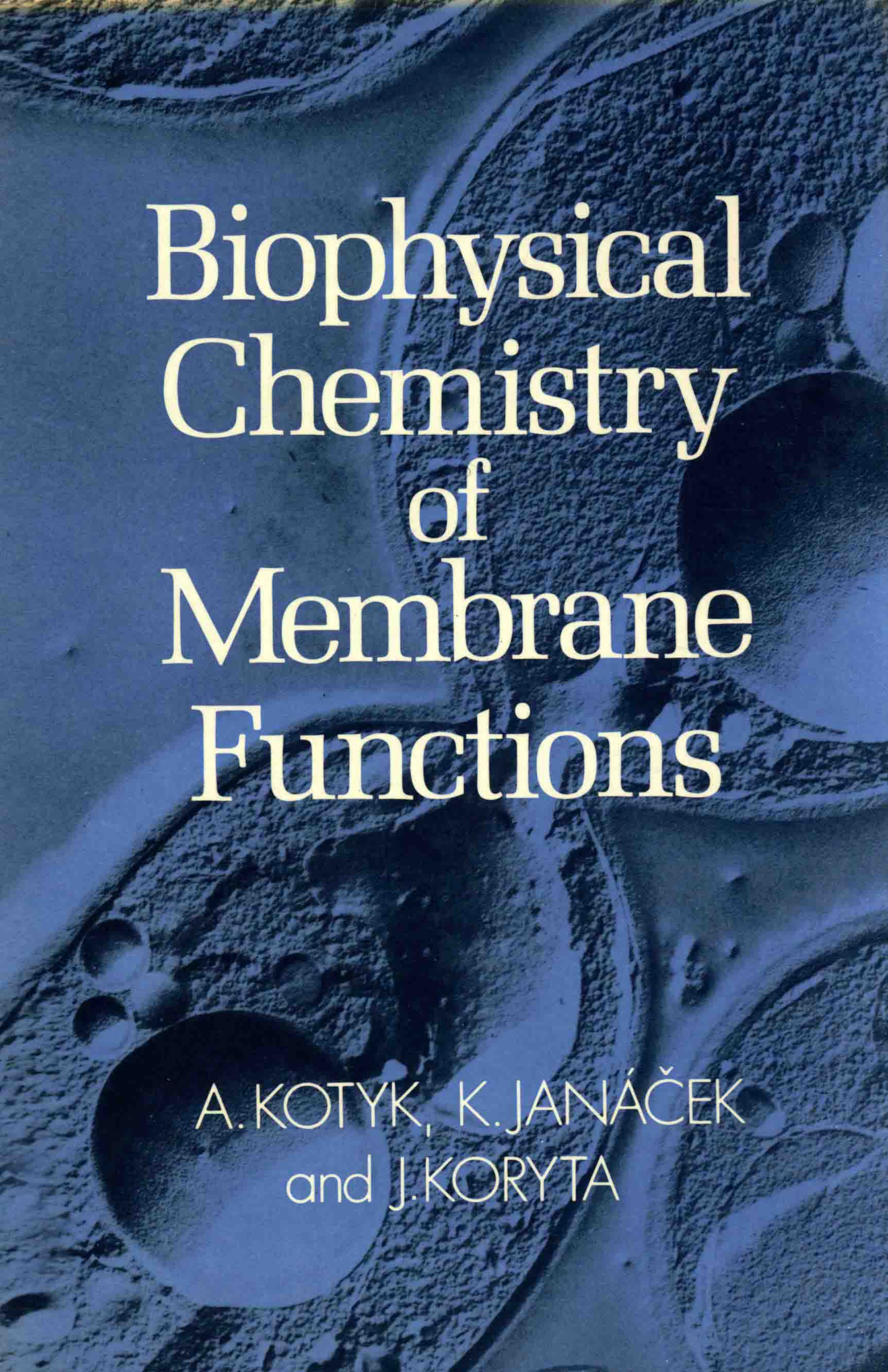

Biophysical Chemistry of Membrane Functions

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Biophysical Chemistry of Membrane Functions

List of Abbreviations

Ab	antibody
Ag	antigen
ADP	adenosine diphosphate
AMP	adenosine monophosphate
ATP	adenosine triphosphate
BChl	bacteriochlorophyll
BPh	bacteriopheophytin
bR	bacteriorhodopsin
cAMP	cyclic adenosine 3′, 5′-monophosphate
cGMP	cyclic guanosine 3′, 5′-monophosphate
Ch	cholesterol
Chl	chlorophyll
CL	cardiolipin
CoA	coenzyme A
CTP	cytidine triphosphate
cyt	cytochrome
DAP	dihydroxyacetone phosphate
dATP	deoxyadenosine triphosphate
DCCD	dicyclohexylcarbodiimide
DES	diethylstilbestrol
DIDS	4, 4′-diisothiocyano-2, 2′-stilbene disulphonate
DPG	diphosphatidylglycerol
DNP	2, 4-dinitrophenol
FA	fatty acid
FAD	flavin adenine dinucleotide
FCCP	carbonylcyanide fluorophenylhydrazone
Fd	ferredoxin
FMN	flavin mononucleotide (riboflavin 5′-phosphate)

Fuc	fucose
Gal	galactose
GalNAc	N-acetyl-D-galactosamine
Glc	glucose
GlcNAc	N-acetyl-D-glucosamine
GTP	guanosine triphosphate
hR	halorhodopsin
Ig	immunoglobulin
ITIES	interface of two immiscible electrolyte solutions
ITP	inosine triphosphate
LPC	lysophosphatidylcholine
Man	mannose
NAD	nicotinamide adenine dinucleotide
NADP	nicotinamide adenine dinucleotide phosphate
NEM	N-ethylmaleimide
PC	phosphatidylcholine; plastocyanin
PCMB	*p*-chloromercuribenzoate
PA	phosphatidic acid
PE	phosphatidylethanolamine
PG	phosphatidylglycerol
Ph	pheophytin
PI	phosphatidylinositol
PQ	plastoquinone
PS	phosphatidylserine; photosystem
Q	quinone
SA	sialic (neuraminic) acid
SITS	4-acetamido-4′-isothiocyano-2, 2′-stilbenedisulphonic acid
SP	sphingomyelin
sR	sensory rhodopsin
TG	triglyceride
TPAs	tetraphenylarsonium
TPB	tetraphenylborate
TPT	triphenyltin
UQ	ubiquinone
UTP	uridine triphosphate
TMT	trimethyltin

List of Symbols

$^\circ$(such as μ°, G°, E°)	standard quantities relevant when activities rather than concentrations are used
$^\ominus$(such as $\mu^\ominus$, $E^\ominus$)	formal quantities relevant when concentrations rather than activities are used and the pH is defined
$^\neq$(such as $K^\neq$, $G^\neq$, $S^\neq$, $H^\neq$)	quantities related to the activated state of reaction
A	Helmholtz free energy
A	surface area
$\mathscr{A}$, A_r	affinity of a chemical reaction
a_i	activity of substance i
C	capacity
$\bar{c}$	mean or equilibrium concentration
c_i	molar concentration of substance i (in mol $dm^{-3} \equiv M$)
c_m	membrane capacity (per unit length)
D	diffusion coefficient
d	distance
E	elastic energy
E	redox potential
E_a	activation energy
E_i	Nernst–Donnan potential of substance i
e	elementary charge ($1.602 \cdot 10^{-19}$ C)
F	Faraday constant (96.49 kC mol^{-1})
G	Gibbs free energy
G_i	membrane conductivity for substance i
H	enthalpy (heat content)
$\mathscr{H}$	Hamiltonian
h	Planck constant ($6.626 \cdot 10^{-34}$ J s)
I	ionic strength
i	electric current

J	flux
$\vec{J}, \overleftarrow{J}$	unidirectional fluxes
J_{max}	maximum rate of transport
j_i	electric current carried by ion i
K	equilibrium constant
K	splay bending elasticity
$\bar{K}$	saddle-splay bending elasticity
K_m, K_T	Michaelis or half-saturation constant of an enzyme and transport reaction, respectively
k	rate constant
k_B	Boltzmann constant ($1.38 \cdot 10^{-23}$ J K^{-1})
L_D	Debye length
L_{ij}	phenomenological coefficients
l	membrane thickness
M	molar mass
M_r	relative molar mass (molecular weight)
m	molecular mass
N_A	Avogadro number ($6.023 \cdot 10^{23}$ mol^{-1})
P	permeability coefficient (constant)
p	momentum
p	pressure
q	generalized coordinate
q	heat
R	gas constant (8.314 J mol^{-1} K^{-1})
R_{ij}	phenomenological coefficients of resistance nature
r	resistance
S	entropy
S	order parameter
T	absolute temperature
T_i	transference number for substance i
t	time
U	difference of electric potential
U	internal energy
U_i	electrolytic mobility of substance i
u_i	mobility of substance i
V	volume
$\bar{V}_i$	partial molal volume of substance i

w	work
w'	useful work
W	probability
X_i (i = 1, 2. . . .)	generalized force in steady-state thermodynamics
X_i	mole fraction of substance *i*
Z	number of particle collisions
z	valency (charge number)
α	coefficient of thermal expansion
β	adsorption coefficient
β	coefficient of compressibility
β	partition coefficient
Γ_i	surface concentration of component *i*
γ	activity coefficient
γ	interfacial tension
δ, δ_N	thickness of the unstirred (Nernst) layer
δ_0	thickness of the Prandtl layer
ε	permittivity, dielectric constant
ζ	electrokinetic potential
η	viscosity
θ	surface free energy
κ	compressibility
κ	conductivity
λ	ionic conductivity
λ	lattice distance
μ_i	chemical potential of substance *i*
$\tilde{\mu}_i$	electrochemical potential of substance *i*
ν	frequency
ν	stoichiometric coefficient
ξ	pore edge energy
$d\xi$	extent of chemical reaction
π	osmotic pressure
ρ	density
σ	reflection coefficient
τ	lifetime
Φ	dissipation function
ϕ	electric potential
$\Delta\phi_m$	membrane potential
ψ, ψ_s	surface potential

Preface

Membranology is a highly interdisciplinary science and to write a book about it requires merging three major scientific areas, biology, chemistry and physics. This is to justify the tripartite title of the book. By sheer coincidence, the functions dealt with are also of three categories, flow of matter, flow of energy and flow of information. And, for better or worse, three authors cooperated in writing the volume, most parts having been written by a single author, but all of them discussed by all three.

We spent hours debating the scope, the level of sophistication and the extent of literature references to be cited. In the end, we decided to attempt to write a detailed textbook-like volume, with as much concrete information as possible without jeopardizing its readability, and of necessity to cut down the number of literature sources to a selected few.

We are indebted to several of our colleagues who read the parts that were farther off the area of our main interest, in particular to Dr I. Šetlík of the Institute of Microbiology, Czechoslovak Academy of Sciences, Třeboň. Our thanks are due to Dr Jiří Pečený who prepared about a half of the drawings appearing in the book.

Dr Tomáš Soukup of the Institute of Physiology, Dr Eva Streiblová of the Institute of Microbiology, both in Prague, and Professor Oldřich Nečas with his team at the Faculty of Medicine, J. E. Purkyně University, in Brno, provided us with some unique microphotographs and their assistance is gratefully acknowledged.

The first author is especially thankful to his friend Dr Jiří Luštinec who let him use for several weeks the facilities of his mountain retreat where, far from the irritating obligations of living and working in a large city but with a carload of books and reprints (and a grand piano for the moments or despair), he was able to complete the major part of the manuscript.

Prague, February 1987

ARNOŠT KOTYK
KAREL JANÁČEK
JIŘÍ KORYTA

Contents

Most of the sections of the book were written by the first author. The ones written by Karel Janáček are specified by KJ, the ones written by Jiří Koryta by JK.

1 The Membrane Principle of Cell Organization

1.1 BIOMEMBRANES PAST AND PRESENT

Periods of data accumulation alternate with periods of synthetic accomplishments. This holds perhaps more in biology than in other areas of science and membranology is no exception. After half a century of gathering information on membranes—and during the early years of seeking arguments to support their credibility—a new cell biology has emerged, one that has membranes in its emblem.

Membranes have not only been recognized as objective entities but they have been found to be endowed with an immense variety of capabilities indispensable for cell survival. Those who see farther ahead in the epistemology of biology and probe deeper into the abysses of subcellular life recently attempted to categorize the principles according to which life—represented materially by the cell—is constructed to function as it has for the nearly four billions of years.

One of the architectural principles put forth, and certainly the more ubiquitous of the two, is the membrane principle of cell organization, the companion principle being that of the cytoskeleton. This principle can be described by stating that living matter in its functional form is composed of self-contained compartments with different internal contents, some of the compartments being often enclosed within other, larger compartments. The boundaries of these compartments are of a uniform fundamental type and are called membranes, biomembranes or biological membranes. The principle is obviously independent of the material from which membranes are composed—it would be equally valid if membranes were made of pure protein, polysaccharide or, for that matter, polymethacrylate. However, although many types of membranes are easily constructed by polymer chemists, biomembranes are unique, being characterized as organized planar structures made of lipids, with an appreciable content of admixed proteins.

The origin of membranes is obscure and probably will remain so. The earliest indications of the existence of material that has some of the physicochemical properties of membranes take the origin back to the time when the solar system itself became differentiated: The interior of the Murchison carbonaceous chondrite (1–3 per cent organic carbon), a meteorite found immediately after