The biophysical basis of excitability

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For Karin, Claudia, Paula and Pedro

For Eliska, Jennifer, Joan, Dylan and Emily

For Freedom

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DEFINITIONS, ABBREVIATIONS AND CONVENTIONS

Symbol	
a	radius of a cell; chemical activity in solution; $=ZFV/RT\delta$; ratio between the numerical values of a concentration expressed in two different units (g/l and mol/l for example); $=4Dt$; mathematical coefficient
$a_{M^+(aq)}$	activity of metal ion M^+ in aqueous solution
a_n, b_n	real and imaginary amplitudes of the nth harmonic in a fourier series
A, A	ampere, unit of electric current; area; gain of an electronic amplifier; symbol for a channel-forming antibiotic in aqueous solution
A^-	anion
Ach	acetylcholine
A_m	channel-forming antibiotic dissolved in the membrane
b	$=\bar{J}/D$; mathematical coefficient
c	concentration; mathematical coefficient
c_m	capacitance of a small area element (in farads); complex amplitude of the mth harmonic in a complex fourier series; capacitance per unit length (farad·cm^{-1})
cm	symbol of centimetre, unit of length
$c_{m,1}$	concentration in membrane on side 1
c_{In}	concentration inside a cell or a compartment
c_{Na}	concentration of sodium
$c_{Na,In}$	concentration of sodium inside a cell or a compartment
$c_{Na,o}$	concentration of sodium outside a cell or a compartment
$c(x)$	concentration at point or a plane located at coordinate x
$c(x,t)$	concentration at point or a plane located at coordinate t
c_K^*	concentration of radioactive potassium

c_m^*	membrane capacitance per sector of axon, per unit length (farad·cm^{-1})
$c_{(1)}$	concentration in compartment (1)
[ch]	concentration of channels
C	symbol for a capacitor in an electrical circuit; coulomb, unit of charge
C_{m}	membrane capacitance (farads)
$\bar{C}_{\mathrm{m}}$	membrane capacitance per unit area (farad·cm^{-2})
$C(\tau)$	autocovariance function
$C_1(\tau)$	autocovariance function (of voltage, current or conductance) of channel 1
Cu	chemical symbol for copper
$Cu_{(s)}$	chemical symbol for metal copper: (s) means solid metal
Cu^{2+}	chemical symbol for ionic copper
$Cu^{2+}_{(aq)}$	chemical symbol for ionic copper in aqueous solution
dyn	symbol for dyne, unit of force in c.g.s. system
D	diffusion coefficient, as defined from 1st Law of Fick. Has the dimensions cm^2·s^{-1}
D_{i}	diffusion coefficient of ion i (example D_{Na}, for sodium ion)
D_{m}	diffusion coefficient of a given molecular species within the membrane
e, (e^-)	base of natural logarithms (2.71828); electronic charge (1.602×10^{-19} C)
E	energy (joules or calories); electromotive force; electrical potential difference ($V_{(2)} - V_{(1)}$)
$\vec{E}$	activation energy for the transition of a particle from the $\bar{n}$ state into the n state
$\bar{E}$	electrical field strength (in volts)
E_{eq}	equilibrium potential across an Ach-gated channel
E_{i}	equilibrium potential for ion i (for example, E_{Na} is the Nernst or equilibrium potential for sodium across a membrane)
E_{i}'	overall diffusion potential across a slab of solution of thickness l and unit cross-sectional area. It is given by the expression $E_i' = RT/ZF \ln(c_{\mathrm{i}}(l)/c_{\mathrm{i}}(0))$ where $c_{\mathrm{i}}(l)$ and $c_{\mathrm{i}}(0)$ are the concentrations at $x=1$ and $x=0$
EPP	end-plate potential (for muscle)
EPSP	excitatory postsynaptic potential (for nerve cells)
erf(x)	error function, defined as $\mathrm{erf}(x) = (2/\sqrt{\pi}) \int_0^x \mathrm{e}^{-n^2}\, dn$
E_{s}	electromotive force of a voltage source; reversal potential of an Ach channel

$E[x_i]$	expected value or average ($\bar{x}$) of a discrete random value (x_i)
E^0	standard electrode potential
E_{Cu}	electrical potential difference between a copper electrode (wire) and a copper solution in which it is dipped (half cell)
E^0_{Cu}	standard electrode potential of copper
$E_{H_2^+}$	electrode potential of a hydrogen half cell
E_j	junction potential
E_M	electrode potential of a half cell of metal M
f	symbol for frequency (in Hz); driving force (volt·cm^{-1})
f'	driving force per mole (J·mol^{-1})
$\bar{f}$	average value of a function
f_q	frictional coefficient exerted on charge q (dyn·cm^{-1}·s)
f'_q	frictional coefficient per unit charge (dyn·cm^{-1}·C^{-1})
F	symbol of farad, unit of capacitance; faraday (9.648456×10^4C·mol^{-1})
F_e	electrical force, or force executed by an electrical field on a charge q
F_f	frictional force
$F(\omega)$	Fourier integral of time function $f(t)$
g, g	symbol for gram; slope conductance, defined as dI/dV
gr-eq	quantity of a substance whose mass in grams is equal to its equivalent weight. The equivalent weight is the atomic weight divided by the charge number or valence. A gram-equivalent of calcium corresponds to 20 grams of calcium
g_i	internal conductance (cytoplasmic conductance) per unit length (S·cm)
$g_i^*(P)$	internal conductance of a sector (P) of cytoplasm per unit length (e.g. 8.35)
g^*_{Na}	membrane sodium conductance per unit length of a sector of squid axon
G	symbol for a conductance in an electrical circuit (siemens, S)
G_A	conductance of a conductor of cross-sectional area A
$\bar{G}$	conductance per unit area (S·cm^{-2})
$\bar{G}_+$	cation conductance per unit area of solution
G'_i	conductance per unit length (S·cm^{-1}) of ion i in solution
$\bar{G}_i$	conductance per unit area (S·cm^{-2}) of an ion i
G_{Na}	membrane sodium conductance (S)
G_t	total membrane conductance
G'_t	total membrane conductance per unit length
$\bar{G}_b$	backward conductance per unit area (in Goldman rectification)
$\bar{G}_f$	forward conductance per unit area (in Goldman rectification)
$\bar{G}_m$	membrane conductance (S)

G_p	conductance of a pore (S)
G_g	conductance of a Gramicydin-induced channel (S)
ΔG_{Na}	free energy change due to the movement of m moles of sodium from compartment (1) to compartment (2) (joules)
ΔG_t	total change in free energy in a given process (J)
$\bar{G}_m$	membrane conductance per unit area ($S \cdot cm^{-2}$)
G_{Kch}	conductance of a potassium channel (S)
$\bar{\bar{G}}_K$	potassium conductance per unit area of membrane at maximum potassium activation
$\bar{\bar{G}}_{Na}$	sodium conductance per unit area of membrane at maximum sodium activation
$\tilde{G}_{Na}$	sodium conductance per unit area of membrane when inactivation is removed ($h=1$). Given by $\tilde{G}_{Na} = \bar{\bar{G}}_{Na} m^a$ or $\tilde{G}_{Na} = \bar{G}_{Na}/h$
G^*_{Na}	sodium conductance of a membrane area element (S) (units S)
$\dot{G}_{ch}(t)$	mean conductance of population of channels at time t (S)
G_s	conductance of an Ach channel (S)
G_{sK}	potassium conductance of an Ach channel
G_{sNa}	sodium conductance of an Ach channel
$h, \bar{h}, h(t)$	sodium inactivation parameters of H. H model of squid axon
H_2	symbol for molecular hydrogen
$H^+_{(aq)}$	protons (or hydrogen ions) in aqueous solution
H	enthalpy
H_σ	enthalpy of a system
Hz	unit of frequency (s^{-1})
i_m	membrane current per unit length
$i_m(j)$	membrane current per unit length at port j in a multiport axon
$i_t^*(p)$	total membrane current per unit length and for sector p of axon
I	symbol for electric current (measured in amperes, A)
$\bar{I}$	current density ($A \cdot cm^{-2}$)
I_+	current due to the flow of a cation (A)
$\bar{I}_+$	current density due to the flow of a cation ($A \cdot cm^{-2}$)
$\bar{I}_c$	capacitative current density ($A \cdot cm^{-2}$)
$\dot{I}_{ch}(t)$	average current of a population of channels at time t (A)
$\bar{I}_i$	ionic current density ($A \cdot cm^{-2}$)
$\bar{I}_{Na,0}$	sodium current density at time zero ($A \cdot cm^{-2}$)
$\bar{I}_{Na,t}$	sodium current density at time t

IPSP	inhibitory postsynaptic potential
I_s	synaptic current
$\bar{I}_t$	total current density at time t
j, j	$\sqrt{-1}$; activity coefficient
j'	$RT \ln(j)$
J	symbol for joule, unit of energy; flux ($mol \cdot s^{-1}$)
J	flux of a cation ($mol \cdot s^{-1}$)
$\bar{J}$	flux density ($mol \cdot s^{-1} \cdot cm^{-2}$)
$\vec{J}$	flux density from left to right ($mol \cdot s^{-1} \cdot cm^{-2}$)
$\bar{J}_{DNa}$	diffusional flux density of sodium
$\bar{J}^*_K$	flux density of radioactive potassium ($mol \cdot s^{-1} \cdot cm^{-2}$)
J^*_K	flux of radioactive potassium ($mol \cdot s^{-1}$)
$\mathcal{J}_{Na}$	Abbreviation for $P_{Na} U c_{Na,o}/(\exp(U)-1)$ where $U = ZFV/RT$
J_{Na}	flux of sodium ($mol \cdot s^{-1}$)
$J(x)$	flux along x direction and at point x
J_{21}	flux from compartment 2 to compartment 1
k	Boltzmann constant ($1.380662 \times 10^{-23}\ J \cdot K^{-1}$); decay constant ($s^{-1}$); conductivity ($S \cdot cm^{-1}$); dielectric constant
k_f, k_b	rate constants in the forward and backward directions; dimensions depend on molarity of reaction
k_D	rate constant of diffusion of transmitter away from synapse. Defined by $J_D = k_D[T]$
k_E	rate constant of enzymatic breakdown of Ach
$k_{m,s}$, $k_{s,m}$	rate constants of release and uptake of a substance by membrane $cm \cdot s^{-1}$ or $cm^3 \cdot s^{-1}$ (according to method of expressing flux)
k_1, k_{-1}	rate constants of a reaction in the forward and backward directions
k_+	conductivity of an electrolyte solution due to the cation
K	degree Kelvin
K	equilibrium constant
l	distance (cm); symbol for litre, unit of volume
L_D	Debye length, given by $L_D = 1/(8 c_{NaCl} \pi F (1/\varepsilon)(F/RT))$
m	symbol for metre
m, $\bar{m}$, $m(t)$	sodium activation parameters of H.H model of squid axon
mol	abbreviation for mole
M	molar concentration (1 M = 1 mol/l)

M	symbol for a metal in solid form
$M^{2+}_{(aq)}$	divalent ionic metal in aqueous solution
$M_{(S)}$	metal in solid form
MEPP	miniature end-plate potential
n	number of moles
$n, \bar{n}, n(t)$	potassium activation parameters of H.H model of squid axon
n_0, n_∞	value of n at t=zero and $t \to \infty$ respectively
N	abbreviation for newton, unit of force
$\bar{N}, N$	potassium activation parameters of H.H model of squid axon related to n and $\bar{n}$ by the expressions $n = N/(N+\bar{N})$ and $\bar{n} = \bar{N}/(N+N)$
N_A	Avogadro's number (6.022045×10^{23} mol^{-1})
N_{ch}	number of open channels per unit area of membrane
N_{ch_T}	total number of channels per unit area of membrane
N_T	maximum number of particles per unit membrane
p	correction factor in equation (8.92); see Laplace variable
$p(x)$	probability density of occurrence of value x where x is a random variable
P	permeability (cm·s^{-1}); pressure
$P(A1/A2)$	probability of occurrence of event A1 once event A2 has taken place (in a conceptual random experiment)
$P(A1, A2)$	probability of the simultaneous occurrence of events A1 and A2 (in a conceptual random experiment)
$P(A)$	probability of occurrence of event A (in a conceptual random experiment)
$\bar{P}_c(t)$	probability of not closing one channel during time t
$P_c(t)$	probability of closing one channel during time t
$P_o(t)$	probability that a channel is open at time t
P_K^E	permeability to potassium due to an exchange process (measured with radioisotopes)
P_K^D	diffusional permeability to potassium
$P_n(t)$	probability of releasing n quanta during time t
$P_n(x)$	probability of obtaining outcome x in a conceptual random experiment performed n times
P_{Na}	sodium permeability (cm·s^{-1})
$\bar{P}_o(t)$	probability of not opening a channel during time t
$P_o(t)$	probability of opening a channel during time t
$P_o(0/t)$	probability of finding a channel open at time t when it was open at time zero

$P_o(c/t)$	probability of finding a channel open at time t when it was closed at time zero
q	quantity of electricity (C)
Q	quantity of electricity or charge in the plates of a capacitor; amount of a solute in moles
Q_{cy}	total amount of charge in the cytoplasm of a cell due to its anions (or its cations) (C)
Q_t	total charge stored in a capacitor with plates of surface areas (C)
Q_0	amount of charge injected across a membrane at time zero
Q_{10}	change in the rate of a reaction (expressed as a ratio) when the temperature is increased by 10 °C
r	stoichiometry of the sodium pump
r_i	resistance of cytoplasm (internal resistance) per unit length ($\Omega \cdot cm^{-1}$)
r_i^*	internal resistance of sector of axon per unit length ($\Omega \cdot cm^{-1}$)
R_m	membrane resistance per unit length
R	resistance (Ω); symbol for a resistor; gas constant (8.31441 $J \cdot K^{-1} \cdot mol^{-1}$)
[IR]	concentration of transmitter–receptor
$\bar{R}_i$	resistance · unit area ($\Omega \cdot cm^2$) of a solution due to ion i
R_i	resistance of a solution, due to ion i (Ω)
R_i^*	longitudinal resistance of a volume element (see (8.15))
R_{In}	input resistance (see (8.74))
$\bar{R}_m$	membrane resistance · unit area ($\Omega \cdot cm^2$)
R_s	source resistance (Ω)
[R_t]	total concentration of transmitter receptor
[RT]	concentration of transmitter–receptor complex
s, s	symbol for second; Laplace variable
s^2	variance of a random variable
S, S	entropy ($J \cdot K^{-1} \cdot mol^{-1}$); surface area of a cell membrane; symbol for Siemens, unit of conductance
S(t)	time-varying signal
t_y	decay constant of function $y(t)$ (see e.g. (7.45)), s^{-1}
t_+, t_-	transport numbers
T, T	absolute temperature (in K); period of a function $= 1/f$ (units, s); normalized time given by $T = t/\tau_m$
[T]	concentration of transmitter
T_i	transmitter in inactive form
TTX	tetrodotoxin
u_+	mobility of cation ($cm^2 \cdot s^{-1} \cdot V^{-1}$)

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More information

u'_{Na}	mobility of sodium defined as $u'_{Na} = u_{Na}/ZF$ (cm · s^{-1} · N^{-1} · mol)
U	a quantity defined as ZFV/RT; or as $(X^2 + 4(T-\Delta T)^2)/4(T-\Delta T)$
v	velocity (cm · s^{-1})
$\bar{v}$	average velocity (of a particle in a random walk)
v_b, v_f	velocity of a reaction (mol · s^{-1}) in the backward (b) and forward (f) reactions
v_+	velocity of a cation (cm · s^{-1})
v_1, v_{-1}	similar to v_b, v_f
V, V	symbol of volt, unit of electrical potential; symbol of voltmeter in electrical circuit; voltage
$\bar{V}$	average value of a time-varying voltage
$V_{(aq),1}$	voltage at aqueous compartment (1)
$V_{(aq)}$	voltage in aqueous phase
$\bar{V}_{EPP}$	average value of end-plate potential
$\bar{V}_h$, $\bar{V}_n$, $\bar{V}_m$	parameters of functions which give the voltage dependence of the rate constants α_h, β_h, α_n, β_n and α_m, β_m in H.H model of squid axon
V_m	voltage in the cytoplasm
$\bar{V}_{MEPP}$	average voltage of miniature end-plate potentials
V_j	$V(j)$ voltage at station (j)
V_m	voltage inside the membrane
$V_{m,1}$	voltage inside the membrane at the interphase with compartment (1)
V_0	voltage at $t = 0$ or at $x = 0$ according to definition in text
V_{oc}	open-circuit voltage (when I_t = zero)
$V_{(\delta)}$	voltage at point δ
V_s	source voltage
$V_{(x)}$	voltage at x
$V(x, t)$	voltage at x and t
$V_{(1)}$	voltage in compartment (1)
$V(\infty)$ or V_∞	voltage at $t \to \infty$ or at $x \to \infty$ according to definitions in text
V'	$= -V$
v	volume (cm^3); velocity
W_1	energy, work (J); also expressed as J · mol^{-1} · K^{-1} (Boltzmann's formula)
x	distance (cm)
x_i	discrete random variable
$\bar{x}$	average value of a discrete random variable

X normalized distance defined as

$X = x/\lambda$

in which λ is a space constant as defined below; term defined as

$X = P_{Na}c_{Na,1} + P_K c_{K,1} + P_{Cl}c_{Cl,2}$

Y term defined as

$Y = P_{Na}c_{Na,2} + P_K c_{K,2} + P_{Cl}c_{Cl,1}$

Z, Z_i valence or charge number (gr-eq · mol^{-1}); length of the arc expressed in radians

α, β rates of closing and opening the transmitter–receptor complex

$\alpha_n, \alpha_m, \alpha_h, \bar{\alpha}_n, \bar{\alpha}_m, \bar{\alpha}_h, \beta_n, \beta_m, \beta_h, \bar{\beta}_n, \bar{\beta}_m, \bar{\beta}_h$ rate constants in H.H model of squid axon

α_1 ratio P_K/P_{Na}

β partition coefficient given by

$\beta = c_{(0)}/c_{(1)} = c_{(\delta)}/c_{(2)}$

γ' activity coefficient

δ thickness of a membrane (cm)

$\delta(t), \delta(t-t_0)$ delta function

$\delta_\tau(t)$ periodic delta function (period τ)

ε permittivity of a dielectric; mean of Poisson and normal distributions

ε_0 permittivity of vacuum

θ probability of getting a favourable outcome in a conceptual random experiment with only two possible outcomes

λ space constant (cm) defined as

$\lambda = \sqrt{(r_m/r_i)}$

λ_i molar conductivity of ion i in solution (S · cm^2 · mol^{-1})

λ_0 limiting conductivity (S · cm^2 · mol^{-1})

μ electrochemical potential (J · mol^{-1})

μ^0 standard electrochemical potential (J · mol^{-1})

$\mu_{Na,m}$ electrochemical potential of sodium in membrane

$\mu^0_{1(aq)}$ standard electrochemical potential in aqueous compartment (1)

$\mu^0_{i(m)}$ standard electrochemical potential of component i in membrane

π 3.14159 . . .

ρ charge density (C · cm^{-3})

ρ_{In} resistivity of cytoplasm (Ω · cm)

$\rho(t)$ rate of production of transmitter (mol · s^{-1} · cm^{-3})

σ standard deviation

τ_m membrane time constant

τ_h, τ_m, τ_n time constants of, respectively, sodium inactivation, sodium activation and potassium activation

ϕ	angle in degrees
Ψ	electrical potential (V)
$\Psi_{tt}(\tau)$	autocorrelation function
Ω	symbol for ohm, unit of resistance
ω	angular velocity (radians $\cdot$ s^{-1})

Please note that

$$(\mathrm{d}/\mathrm{d}t)(x) \equiv \mathrm{d}x/\mathrm{d}t \equiv \frac{\mathrm{d}x}{\mathrm{d}t}$$

and

$$(\mathrm{d}/\mathrm{d}t)^2(x) \equiv \mathrm{d}^2x/\mathrm{d}t^2 \equiv \frac{\mathrm{d}^2x}{\mathrm{d}t^2}$$

Other symbols are defined as they are introduced.