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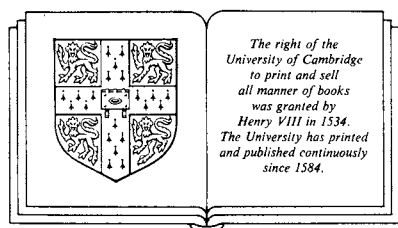
The biophysical basis of excitability

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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 n th 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 m th harmonic in a complex fourier series; capacitance per unit length (farad \cdot 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

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c_m^*	membrane capacitance per sector of axon, per unit length (farad \cdot 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}_m	membrane capacitance per unit area (farad \cdot 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
$Cu_{(aq)}^{2+}$	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 \cdot 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 $E'_i = RT/ZF \ln(c_i(l)/c_i(0))$ where $c_i(l)$ and $c_i(0)$ are the concentrations at $x = l$ and $x = 0$
EPP	end-plate potential (for muscle)
EPSP	excitatory postsynaptic potential (for nerve cells)
erf(x)	error function, defined as $\text{erf}(x) = (2/\sqrt{\pi}) \int_0^x e^{-n^2} dn$
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_{Cu}^0	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 \cdot cm $^{-1}$)
f'	driving force per mole (J \cdot mol $^{-1}$)
\bar{f}	average value of a function
f_q	frictional coefficient exerted on charge q (dyn \cdot cm $^{-1}$ \cdot s)
f'_q	frictional coefficient per unit charge (dyn \cdot cm $^{-1}$ \cdot C $^{-1}$)
F	symbol of farad, unit of capacitance; faraday (9.648456×10^4 C \cdot 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 \cdot 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 \cdot cm $^{-2}$)
\bar{G}_+	cation conductance per unit area of solution
G'_i	conductance per unit length (S \cdot cm $^{-1}$) of ion i in solution
\bar{G}_i	conductance per unit area (S \cdot 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)

xviii	<i>Definitions, abbreviations and conventions</i>
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{G}_K	potassium conductance per unit area of membrane at maximum potassium activation
\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 $\tilde{G}_{Na} = \bar{G}_{Na} m^a$ or $\tilde{G}_{Na} = \bar{G}_{Na} / h$
G_{Na}^*	sodium conductance of a membrane area element (S) (units S)
$\tilde{G}_{ch}(t)$	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 ($A \cdot cm^{-2}$)
$\bar{I}_{ch}(t)$	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 ($\text{mol} \cdot \text{s}^{-1}$)
\bar{J}	flux of a cation ($\text{mol} \cdot \text{s}^{-1}$)
\bar{J}	flux density ($\text{mol} \cdot \text{s}^{-1} \cdot \text{cm}^{-2}$)
\bar{J}	flux density from left to right ($\text{mol} \cdot \text{s}^{-1} \cdot \text{cm}^{-2}$)
\bar{J}_{DNa}	diffusional flux density of sodium
\bar{J}_{K}^*	flux density of radioactive potassium ($\text{mol} \cdot \text{s}^{-1} \cdot \text{cm}^{-2}$)
J_{K}^*	flux of radioactive potassium ($\text{mol} \cdot \text{s}^{-1}$)
\bar{J}_{Na}	Abbreviation for $P_{\text{Na}} U c_{\text{Na,o}} / (\exp(U) - 1)$ where $U = ZFV/RT$
J_{Na}	flux of sodium ($\text{mol} \cdot \text{s}^{-1}$)
$J(x)$	flux along x direction and at point x
J_{21}	flux from compartment 2 to compartment 1
k	Boltzmann constant ($1.380662 \times 10^{-23} \text{ J} \cdot \text{K}^{-1}$); decay constant (s^{-1}); conductivity ($\text{S} \cdot \text{cm}^{-1}$); 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 $\text{cm} \cdot \text{s}^{-1}$ or $\text{cm}^3 \cdot \text{s}^{-1}$ (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 $L_D = 1 / (8 c_{\text{NaCl}} \pi F (1/\epsilon) (F/RT))$
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 ($1 \text{ M} = 1 \text{ mol/l}$)

xx	<i>Definitions, abbreviations and conventions</i>
M	symbol for a metal in solid form
$M_{\text{(aq)}}^{2+}$	divalent ionic metal in aqueous solution
$M_{\text{(s)}}$	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 $t = \text{zero}$ and $t \rightarrow \infty$ 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 $n = N/(N + \bar{N}) \quad \text{and} \quad \bar{n} = \bar{N}/(N + \bar{N})$
N_A	Avogadro's number ($6.022045 \times 10^{23} \text{ mol}^{-1}$)
N_{ch}	number of open channels per unit area of membrane
N_{chT}	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 ($\text{cm} \cdot \text{s}^{-1}$); 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 ($\text{cm} \cdot \text{s}^{-1}$)
$\bar{P}_o(t)$	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_o	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 ($\Omega \cdot \text{cm}^{-1}$)
r_i^*	internal resistance of sector of axon per unit length ($\Omega \cdot \text{cm}^{-1}$)
R_m	membrane resistance per unit length
R	resistance (Ω); symbol for a resistor; gas constant ($8.31441 \text{ J} \cdot \text{K}^{-1} \cdot \text{mol}^{-1}$)
$[\text{IR}]$	concentration of transmitter–receptor
\bar{R}_i	resistance \cdot unit area ($\Omega \cdot \text{cm}^2$) 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 \cdot unit area ($\Omega \cdot \text{cm}^2$)
R_s	source resistance (Ω)
$[\text{R}_i]$	total concentration of transmitter receptor
$[\text{RT}]$	concentration of transmitter–receptor complex
s, s	symbol for second; Laplace variable
s^2	variance of a random variable
S, S	entropy ($\text{J} \cdot \text{K}^{-1} \cdot \text{mol}^{-1}$); 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 $T = t/\tau_m$
$[\text{T}]$	concentration of transmitter
T_i	transmitter in inactive form
TTX	tetrodotoxin
u_+	mobility of cation ($\text{cm}^2 \cdot \text{s}^{-1} \cdot \text{V}^{-1}$)

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u'_{Na}	mobility of sodium defined as $u'_{\text{Na}} = u_{\text{Na}} / ZF \text{ (cm} \cdot \text{s}^{-1} \cdot \text{N}^{-1} \cdot \text{mol)}$
U	a quantity defined as ZFV/RT ; or as $(X^2 + 4(T - \Delta T)^2) / 4(T - \Delta T)$
v	velocity ($\text{cm} \cdot \text{s}^{-1}$)
\bar{v}	average velocity (of a particle in a random walk)
v_b, v_f	velocity of a reaction ($\text{mol} \cdot \text{s}^{-1}$) in the backward (b) and forward (f) reactions
v_+	velocity of a cation ($\text{cm} \cdot \text{s}^{-1}$)
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
$V_{(\text{aq}),1}$	voltage at aqueous compartment (1)
$V_{(\text{aq})}$	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 $\alpha_h, \beta_h, \alpha_n, \beta_n$ 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 $I_t = \text{zero}$)
$V_{(\delta)}$	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 $t \rightarrow \infty$ or at $x \rightarrow \infty$ according to definitions in text
V'	$= -V$
v	volume (cm^3); velocity
W_1	energy, work (J); also expressed as $\text{J} \cdot \text{mol}^{-1} \cdot \text{K}^{-1}$ (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 $X = P_{Na}c_{Na,1} + P_Kc_{K,1} + P_{Cl}c_{Cl,2}$
Y	term defined as $Y = P_{Na}c_{Na,2} + P_Kc_{K,2} + P_{Cl}c_{Cl,1}$
Z, Z_i	valence or charge number ($\text{gr}\cdot\text{eq}\cdot\text{mol}^{-1}$); 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
$\delta_i(t)$	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 ($\text{S}\cdot\text{cm}^2\cdot\text{mol}^{-1}$)
λ_0	limiting conductivity ($\text{S}\cdot\text{cm}^2\cdot\text{mol}^{-1}$)
μ	electrochemical potential ($\text{J}\cdot\text{mol}^{-1}$)
μ^0	standard electrochemical potential ($\text{J}\cdot\text{mol}^{-1}$)
$\mu_{Na,m}$	electrochemical potential of sodium in membrane
$\mu_{i(aq)}^0$	standard electrochemical potential in aqueous compartment (1)
$\mu_{i(m)}^0$	standard electrochemical potential of component i in membrane
π	3.14159 . . .
ρ	charge density ($\text{C}\cdot\text{cm}^{-3}$)
ρ_{In}	resistivity of cytoplasm ($\Omega\cdot\text{cm}$)
$\rho(t)$	rate of production of transmitter ($\text{mol}\cdot\text{s}^{-1}\cdot\text{cm}^{-3}$)
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

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

Please note that

$$(d/dt)(x) \equiv dx/dt \equiv \frac{dx}{dt}$$

and

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

Other symbols are defined as they are introduced.