# Electrical Engineering 3BB3: Cellular Bioelectricity

Day Class — Instructor: Dr. I. C. BRUCE
Duration of Examination: 1.5 hours
McMaster University Midterm Quiz #2 — March, 2007

This examination paper includes fourteen (14) pages and twelve (12) questions. You are responsible for ensuring that your copy of the paper is complete. Bring any discrepancy to the attention of your invigilator.

Special Instructions: Use of Casio *fx*-991 calculator only is allowed.
Some equations that may assist you are provided on pages 4–14.
Questions 1–8 are multiple-choice questions, each worth 5 pts. Only one answer, *a*, *b*, *c* or *d*, is correct for each question.
Questions 9–12 are short answer and/or mathematical questions, each worth 15 pts.

1. The minimum stimulus amplitude required to just reach threshold as the duration of a stimulating pulse tends towards infinity is referred to as the:
   a. cronkite,
   b. rheobase,
   c. chronaxie, or
   d. robitussin. **(5 pts)**

2. The larger the diameter of a *spherical excitable cell*, then:
   a. the smaller the membrane capacitance,
   b. the smaller the membrane time constant,
   c. the smaller the membrane resistance, or
   d. the smaller the membrane potential. **(5 pts)**

3. The larger the diameter of a *cylindrical axon*, then:
   a. the larger the space constant,
   b. the smaller the space constant,
   c. the larger the axoplasmic longitudinal resistance, or
   d. the smaller the membrane capacitance. **(5 pts)**

4. The termination impedance of a finite-length cable has a big effect if:
   a. the cable is less than one space constant in length,
   b. the cable is more than three space constants in length,
   c. the cable is more than ten space constants in length, or
   d. all of the above. **(5 pts)**

Continued on page 2

5. Field potentials measured on the surface of the body produced by excitable cells within the body depend on:
   a. the locations of the cells relative to the electrode(s),
   b. the orientation of the current sources and sinks produced by the cells,
   c. the relative timing of the action potentials fired by the different cells, or
   d. all of the above. **(5 pts)**

6. Consider the *temporal* response of the membrane potential for an *infinite-length cylindrical fiber* to a *current step* injected from an intracellular micro-pipette electrode. The membrane potential *at the point of current injection* grows to its steady-state value:
   a. *faster* than exponentially over time,
   b. *slower* than exponentially over time,
   c. *exactly* exponentially over time, or
   d. *instantaneously*. **(5 pts)**

7. *Alpha waves* are observed in EEG recordings mainly when the subject is:
   a. in REM sleep,
   b. awake and engaged in cognitive tasks,
   c. awake and resting with eyes closed, or
   d. in Stage 2 non-REM sleep. **(5 pts)**

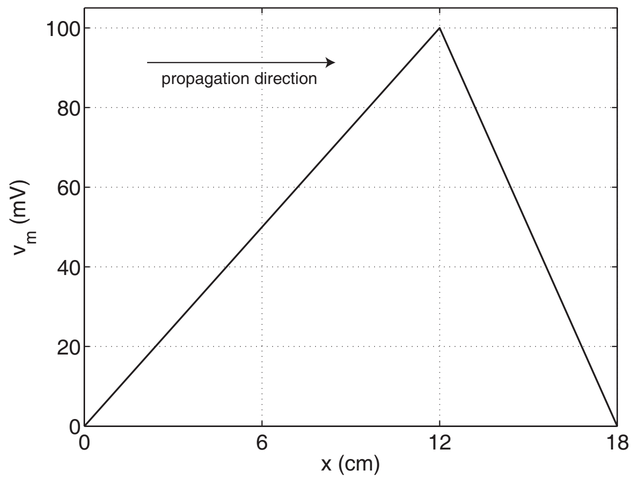
8. The membrane of inner hair cells in the cochlea:
   a. fires action potentials,
   b. acts as a high-pass filter,
   c. has excitatory synapses onto auditory nerve fibers, or
   d. all of the above. **(5 pts)**

9. Explain the theory and the application of the *activating function* for extracellular electrical stimulation of excitable cells. **(15 pts)**

10. Discuss the functional importance of the *space constant* for synaptic input on a dendrite. **(15 pts)**

Continued on page 3

11. An action potential with an approximately triangular spatial waveform is propagating (without dissipation) along an unmyelinated axon at $11\ \mathrm{m \cdot s^{-1}}$ in the $+\mathrm{ve}\ x$ direction, as shown below.




Assume that no currents are being injected into the intra- or extra-cellular space from external sources, and the intra- and extra-cellular resistances per unit length are $r_i = 1.0\ \mathrm{M\Omega/cm}$ and $r_e = 15\ \mathrm{k\Omega/cm}$, respectively.

Calculate the local circuit currents, i.e., the transmembrane current per unit length $i_m$ and the axial intra- and extra-cellular currents $I_i$ and $I_e$, respectively, *as a function of position* $x$.

**(15 pts)**

12. Consider a synapse onto the soma of a neuron with a resting potential $V_{\text{rest}} = -65\ \mathrm{mV}$, a membrane capacitance $C = 80\ \mathrm{pF}$, and a resting membrane resistance $R = 60\ \mathrm{M\Omega}$. The ion channel gated by the synaptic input has a reversal potential $E_{\text{syn}} = -80\ \mathrm{mV}$ and a maximum conductance $\bar{g}_{\text{syn}} = 15\ \mathrm{nS}$.

    a. Is this synapse excitatory or inhibitory?

    b. If the membrane is initially at rest and synaptic input is received, what is the *maximum* current $I_{\text{syn}}$ that could be produced by the channel?

    c. What is the *minimum* possible time constant of the soma when receiving synaptic input?

**(15 pts)**

## THE END

Continued on page 4

## Supplied Equations and Tables

*Table 3.3.* Numerical Values for Faraday's Constant $F$ and the Gas Constant R

| Constant | Value |
|---|---|
| $F$ | 96,487 coulombs/mole |
| $R$ | 8.314 joules/K mole |
| $RT/F$ | 8.314 × .300/96487 = 25.8 mV at 27 °C |

**Fick's law of diffusion:**

$$\bar{j}_d = -D\nabla C \tag{3.1}$$

**Ohm's law of drift:**

$$\bar{j}_e = -u_p \frac{Z_p}{|Z_p|} C_p \nabla\Phi \tag{3.2}$$

**Einstein's equation:**

$$D_p = \frac{u_p RT}{|Z_p|\, F} \tag{3.3}$$

**Nernst-Planck equation (ion flux):**

$$\bar{j}_p = -D_p \left( \nabla C_p + \frac{Z_p C_p F}{RT} \nabla\Phi \right) \tag{3.5}$$

**Nernst-Planck equation (electric current density):**

$$\bar{J}_p = -D_p F Z_p \left( \nabla C_p + \frac{Z_p C_p F}{RT} \nabla\Phi \right) \tag{3.6}$$

$$= -u_p \left( RT \frac{Z_p}{|Z_p|} \nabla C_p + |Z_p| C_p F \nabla\Phi \right) \tag{3.7}$$

Continued on page 5

**Equivalent conductance:**

$$\Lambda = \alpha F \left[\sum_i u_i\right] \times 1000 \qquad (3.12)$$

**Transference number:**

$$t_i = \frac{u_i}{\sum_i u_i}, \qquad \sum_i t_i = 1 \qquad (3.14)$$

**Nernst equation:**

$$V_m^{eq} = \Phi_i - \Phi_e = \frac{-RT}{Z_p F} \ln\left(\frac{[C_p]_i}{[C_p]_e}\right) \qquad (3.21)$$

**Boltzmann function for fraction of open channels:**

$$\frac{[\text{open}]}{[\text{open+closed}]} = \frac{1}{1+\exp\left(\frac{-Q_g V_m}{kT}\right)} \qquad (4.5)$$

**Macroscopic channel kinetics:**

$$N_c \underset{\beta}{\overset{\alpha}{\rightleftharpoons}} N_o \qquad (4.7)$$

$$\frac{\mathrm{d}N_c}{\mathrm{d}t} = \beta N_o - \alpha N_c \qquad (4.8)$$

$$\frac{\mathrm{d}N_o}{\mathrm{d}t} = \alpha N_c - \beta N_o \qquad (4.9)$$

Continued on page 6

**Single channel probabilities:**

$$p = \frac{\langle N_o \rangle}{N} \tag{4.15}$$

$$q = \frac{\langle N_c \rangle}{N} \tag{4.16}$$

**Mean number of open channels:**

$$\langle N_o \rangle = Np \tag{4.22}$$

**Variance in number of open channels:**

$$\sigma^2 = Np\,(1 - p) \tag{4.26}$$

**GHK transmembrane potential equation:**

$$V_m = \frac{RT}{F} \ln \left[ \frac{P_{\mathrm{K}}[\mathrm{K}]_e + P_{\mathrm{Na}}[\mathrm{Na}]_e + P_{\mathrm{Cl}}[\mathrm{Cl}]_i}{P_{\mathrm{K}}[\mathrm{K}]_i + P_{\mathrm{Na}}[\mathrm{Na}]_i + P_{\mathrm{Cl}}[\mathrm{Cl}]_e} \right] \tag{5.1}$$

Continued on page 7

**Hodgkin-Huxley potassium channel model:**

$$g_{\mathsf{K}}(t, v_m) = \bar{g}_{\mathsf{K}} n^4(t, v_m) \quad (5.13)$$

$$\frac{\mathrm{d}n(t, v_m)}{\mathrm{d}t} = \alpha_n(v_m)\,(1-n) - \beta_n(v_m)\,n \quad (5.14)$$

or

$$\frac{\mathrm{d}n(t, v_m)}{\mathrm{d}t} = \frac{n_\infty - n}{\tau_n} \quad (5.17)$$

$$\alpha_n(v_m) = \frac{0.01\,(10 - v_m)}{\exp\left(\frac{10 - v_m}{10}\right) - 1} \quad (5.19)$$

$$\beta_n(v_m) = 0.125\,\exp\left(\frac{-v_m}{80}\right) \quad (5.20)$$

Continued on page 8

**Hodgkin-Huxley sodium channel model:**

$$g_{\mathrm{Na}}(t, v_m) = \bar{g}_{\mathrm{Na}} m^3(t, v_m)\, h(t, v_m) \qquad (5.21)$$

$$\frac{\mathrm{d}m(t, v_m)}{\mathrm{d}t} = \alpha_m(v_m)\,(1-m) - \beta_m(v_m)\, m \qquad (5.22)$$

$$\frac{\mathrm{d}h(t, v_m)}{\mathrm{d}t} = \alpha_h(v_m)\,(1-h) - \beta_h(v_m)\, h \qquad (5.23)$$

$$\alpha_m(v_m) = \frac{0.1\,(25 - v_m)}{\exp\left(\frac{25-v_m}{10}\right) - 1};$$

$$\beta_m(v_m) = 4\exp\left(\frac{-v_m}{18}\right) \qquad (5.31)$$

$$\alpha_h(v_m) = 0.07\exp\left(\frac{-v_m}{20}\right);$$

$$\beta_h(v_m) = \left\{\exp\left(\frac{30 - v_m}{10}\right) + 1\right\}^{-1} \qquad (5.32)$$

**Sodium pump efflux:**

$$-\frac{\mathrm{d}\left[{}^{24}\mathrm{Na}^{+}\right]_i}{\mathrm{d}t} = k\left[{}^{24}\mathrm{Na}^{+}\right]_i \qquad (5.45)$$

$$\Rightarrow \left[{}^{24}\mathrm{Na}^{+}\right]_i = A\exp(-kt) \qquad (5.46)$$

Continued on page 9

**Sodium pump stoichiometry:**

$$\begin{aligned}\mathsf{ATP} + x\,[\mathsf{Na}]_i + y\,[\mathsf{K}]_o &\longrightarrow \\ \mathsf{ADP} + \mathsf{P}_i + x\,[\mathsf{Na}]_o + y\,[\mathsf{K}]_i \end{aligned} \qquad (5.47)$$

**Frankenhaeuser-Huxley potassium channel model:**

$$I_{\mathsf{K}} = P_{\mathsf{K}} \frac{V_m^2 F^2}{RT} \left( \frac{[\mathsf{K}]_o - [\mathsf{K}]_i \, \mathsf{e}^{V_m F/RT}}{1 - \mathsf{e}^{V_m F/RT}} \right) \qquad (5.58)$$

$$P_{\mathsf{K}} = \bar{P}_{\mathsf{K}} n^2 \qquad (5.59)$$

$$\alpha_n = 0.02\,(v_m - 35) \left( 1 - \mathsf{e}^{\frac{35 - v_m}{10}} \right)^{-1} \qquad (5.60)$$

$$\beta_n = 0.05\,(10 - v_m) \left( 1 - \mathsf{e}^{\frac{v_m - 10}{10}} \right)^{-1} \qquad (5.61)$$

**Calcium channel model:**

$$I_{\mathsf{Ca}} = 4 \frac{P_{\mathsf{Ca}} V_m^2 F^2}{RT} \left( \frac{[\mathsf{Ca}]_o - [\mathsf{Ca}]_i \, \mathsf{e}^{2V_m F/RT}}{1 - \mathsf{e}^{2V_m F/RT}} \right) \qquad (5.64)$$

**Cable equation intracellular axial resistance per unit length:**

$$r_i = \frac{R_i}{\pi a^2} \quad \Omega/\mathsf{cm} \qquad (6.1)$$

**Cable equation membrane resistance times unit length:**

$$r_m = \frac{R_m}{2\pi a} \quad \Omega\ \mathsf{cm} \qquad (6.2)$$

Continued on page 10

**Cable equation membrane capacitance per unit length:**

$$c_m = C_m 2\pi a \quad \mu\text{F/cm} \tag{6.3}$$

**Cable equation extra- and intra-cellular axial electric potential gradients:**

$$\frac{\partial \Phi_e}{\partial x} = -I_e r_e \tag{6.4}$$

$$\frac{\partial \Phi_i}{\partial x} = -I_i r_i \tag{6.5}$$

**Cable equation intra- and extra-cellular axial current gradients:**

$$\frac{\partial I_i}{\partial x} = -i_m \tag{6.6}$$

$$\frac{\partial I_e}{\partial x} = i_m + i_p \tag{6.7}$$

**Cable equation total axial current:**

$$I = I_i + I_e \tag{6.8}$$

**Cable equation membrane potential vs. transmembrane and applied currents:**

$$\frac{\partial^2 V_m}{\partial x^2} = (r_i + r_e)\, i_m + r_e i_p \tag{6.24}$$

**Cable equation intracellular potential vs. transmembrane current:**

$$i_m = \frac{1}{r_i} \frac{\partial^2 \phi_i}{\partial x^2} \tag{6.25}$$

Continued on page 11

**Hodgkin-Huxley cable equation:**

$$\frac{\partial V_m}{\partial t} = \frac{1}{C_m}\left(\frac{a}{2R_i}\frac{\partial^2 V_m}{\partial x^2}\right) - \frac{\sum I_{\mathrm{ion}}}{C_m} \tag{6.31}$$

$$\begin{aligned}\sum I_{\mathrm{ion}} = {} & \bar{g}_{\mathrm{K}} n^4 (V_m - E_{\mathrm{K}}) + \bar{g}_{\mathrm{Na}} m^3 h (V_m - E_{\mathrm{Na}}) \\ & + g_L (V_m - E_L) + I_0 \end{aligned} \tag{6.32}$$

**Hodgkin-Huxley propagating action potential equation:**

$$\begin{aligned}\frac{a}{2R_i\theta^2}\frac{\mathrm{d}^2 V_m}{\mathrm{d}t^2} = {} & C_m \frac{\mathrm{d}V_m}{\mathrm{d}t} + g_{\mathrm{K}}(V_m - E_{\mathrm{K}}) \\ & + g_{\mathrm{Na}}(V_m - E_{\mathrm{Na}}) \\ & + g_L(V_m - E_L) \end{aligned} \tag{6.41}$$

**Isopotential membrane patch response to an intracellular current step:**

$$v_m = I_0 R \left(1 - \mathrm{e}^{-t/\tau}\right) \tag{7.3}$$

$$= V_0 \left(1 - \mathrm{e}^{-t/\tau}\right) \tag{7.4}$$

**Strength-duration relationship:**

$$V_0 = V_T / \left(1 - \mathrm{e}^{-T/\tau}\right) \tag{7.5}$$

**Chronaxie:**

$$T_c = \tau \ln 2 = 0.693\tau \tag{7.8}$$

Continued on page 12

**Linear cable equation for extracellular current injection:**

$$\lambda^2 \frac{\partial^2 v_m}{\partial x^2} - \tau \frac{\partial v_m}{\partial t} - v_m = r_e \lambda^2 i_p \tag{7.11}$$

**Space constant and time constant:**

$$\lambda = \sqrt{\frac{r_m}{r_i + r_e}} \quad \text{and} \quad \tau = r_m c_m \tag{7.12}$$

**Steady-state solution to homogeneous infinite linear cable equation:**

$$v_m = A\mathrm{e}^{-x/\lambda} + B\mathrm{e}^{x/\lambda} \tag{7.15}$$

**Steady-state solution to infinite linear cable equation with extracellular current injection at the spatial origin:**

$$v_m = -\frac{r_e \lambda I_0}{2} \mathrm{e}^{-|x|/\lambda} \tag{7.31}$$

**General time-varying solution to infinite linear cable equation with intracellular current step at the spatial origin:**

$$\begin{aligned} v_m(X,T) = \frac{r_i \lambda I_0}{4} \Bigg\{ & \mathrm{e}^{-X} \left[ 1 - \mathrm{erf}\left( \frac{X}{2\sqrt{T}} - \sqrt{T} \right) \right] \\ & - \mathrm{e}^{X} \left[ 1 - \mathrm{erf}\left( \frac{X}{2\sqrt{T}} + \sqrt{T} \right) \right] \Bigg\} \end{aligned} \tag{7.45}$$

**Input impedance for semi-infinite cable:**

$$Z_0 = \frac{v_m(x=0)}{I_i(x=0)} \tag{7.52}$$

$$= \sqrt{r_m r_i} \tag{7.58}$$

Continued on page 13

**Extracellular field potential for applied monopole point current source:**

$$\phi_a = \frac{I_0}{4\pi\sigma_e r} \qquad (7.70)$$

**Initial transmembrane response to an applied extracellular field:**

$$r_i \frac{\partial v_m}{\partial t} = \frac{1}{c_m}\frac{\partial^2 \phi_e}{\partial z^2}$$

**Extracellular field produced by a fiber:**

$$\Phi_e\left(x', y', z'\right) = \frac{1}{4\pi\sigma_e}\int \frac{i_m(x)\,\mathrm{d}x}{\sqrt{\left(x - x'\right)^2 + \left(y'\right)^2 + \left(z'\right)^2}} \qquad (8.4)$$

**Approximate extracellular field produced by a cylindrical fiber:**

$$\phi_e = \frac{a^2\sigma_i}{4\sigma_e}\int \frac{\partial^2 v_m / \partial x^2}{r}\,\mathrm{d}x \qquad (8.10)$$

**Monopole source density for a cylindrical fiber:**

$$I_l = \pi a^2 \sigma_i \frac{\partial^2 v_m}{\partial x^2} \qquad (8.12)$$

$$\phi_e = \frac{1}{4\pi\sigma_e}\int \frac{I_l}{r}\,\mathrm{d}x$$

Continued on page 14

**Dipole source density for a cylindrical fiber:**

$$\bar{\tau}_l = -\pi a^2 \sigma_i \frac{\partial v_m}{\partial x} \bar{a}_x \qquad (8.18)$$

$$\phi_e = \frac{1}{4\pi\sigma_e} \int \bar{\tau}_l \cdot \nabla\left(\tfrac{1}{r}\right) \mathrm{d}x$$

**Quadrupole source density for a cylindrical fiber:**

$$q(x) = \pi a^2 \sigma_i v_m(x) \qquad (8.23)$$

**Lumped dipole strength for a cylindrical fiber:**

$$\begin{aligned} D &= -\pi a^2 \sigma_i \int_{x_1}^{x_2} \frac{\partial v_m}{\partial x} \mathrm{d}x \\ &= \pi a^2 \sigma_i \left[ v_m(x_1) - v_m(x_2) \right] \end{aligned} \qquad (8.24)$$

**Lumped monopole strength for a cylindrical fiber:**

$$\begin{aligned} M &= \pi a^2 \sigma_i \int_{x_a}^{x_b} \frac{\partial^2 v_m}{\partial x^2} \mathrm{d}x \\ &= \pi a^2 \sigma_i \left( \left.\frac{\partial v_m}{\partial x}\right|_{x=x_b} - \left.\frac{\partial v_m}{\partial x}\right|_{x=x_a} \right) \end{aligned} \qquad (8.27)$$

**Postsynaptic current equation:**

$$I_{\mathsf{syn}} = g_{\mathsf{syn}}(t) \left[ V_m(t) - E_{\mathsf{syn}} \right] \qquad \text{(Koch 1.18)}$$

**Postsynaptic conductance alpha equation:**

$$g_{\mathsf{syn}}(t) = \mathsf{const} \cdot t\, \mathrm{e}^{-t/t_{\mathsf{peak}}} \qquad \text{(Koch 1.21)}$$

**END OF SUPPLIED EQUATIONS AND TABLES**