Lecture 3: 
Neuroexcitability I

*Electrical Equivalent Circuit Model of the Membrane:*
*Resting Potential and Passive Membrane Properties*
*Use of the Voltage Clamp to Analyze the Action Potential*

I. The electrical signals carried by a neuron can be understood by representing the neuron by an electrical equivalent circuit model, consisting of:
   A. Capacitors
   B. Conductances
   C. Batteries

II. The lipid bilayer acts as a capacitor-
   A. It consists of a lipid insulator that separates two conductors (ECF and cytoplasm).
   B. It can store excess + and - charge (Q), although bulk electroneutrality is maintained (except for the region immediately adjacent to the membrane).
   C. Separation of + and – charges on either side of the membrane gives rise to an electrical potential difference, the membrane potential ($V_m = Q/C$).
   D. C is directly proportional to membrane area (because the lipid membrane is uniform in composition and thickness).
   E. In order for membrane potential to change, Q must change, so capacitance acts to slow the rate of change of $V_m$ in response to current flow across the membrane.

III. Ion channels endow the membrane with two additional electrical properties:
   A. Conductance ($g$)
      1. Virtually all current flow across the membrane is through ion channels
      2. $g = 1/R$
   B. Electromotive force (EMF) (acts as a battery)
      1. Because of:
         a. Selective conductance
         b. Unequal ion distributions
      2. Battery value is determined by Nernst equilibrium potential

IV. The resting membrane consists of channels that are permeable to $K^+$, $Na^+$, and $Cl^-$, in parallel with the membrane capacitance and ion pumps and carriers:
   A. $V_m = (g_K E_K + g_{Cl} E_{Cl} + g_{Na} E_{Na})/(g_K + g_{Cl} + g_{Na})$
B. $g_K$ (and therefore $E_K$) predominate at rest
C. Active pumping of $Na^+$ and $K^+$ keeps the ionic batteries from running down

V. The membrane **time constant**:
   A. Membrane capacitance slows the rate of change of membrane potential
   B. Time constant ($\tau$) = $R_m \times C_m$
   C. Affects the time course of synaptic potentials

VI. The membrane **length constant**
   A. The combination of membrane leakage channels and axial resistance causes membrane potential changes to decrement with distance
   B. Length constant ($\lambda$) = $\sqrt{r_m / r_a}$
   C. Affects the decay with distance of synaptic potentials

VII. Generation and conduction of the action potential-
   A. is needed for long distance communication via a digital pulse code
   B. has a threshold
   C. is all-or-none in height
   D. is conducted without decrement
   E. results form a positive feedback cycle involving $g_{Na}$

VIII. Use of the **voltage clamp** to analyze the action potential:
   A. The voltage clamp is a current generator with two functions:
      1. It steps $V_m$ away from $V_{rest}$
      2. It clamps $V_m$ at this value, in spite of the opening of voltage-gated ion channels
   B. When Na$^+$ channels open, the voltage clamp interrupts the feedback cycle by breaking the link between $I_{Na}$ and depolarization
   C. Clamp I = membrane I ($I_m$)