Hodgkin-Huxley Equations

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Abstract

We will see the Hodgkin-Huxley equations, the experiments, assumptions and analysis.

0.1 Definitions

- Remember Cable Theory.
- The equation for the PASIVE cable are:

As we know the axon is not passive. It has active conductances. Let’s change the circuit:

Now, we have a cable with variable conductances. The problem is to find the new cable equation. This can be done, but we will only get to the variation of voltage with respect to time.

The total current in the capacitance of the cable is

\[ I = C_m \frac{dV}{dt} + I_i \]
where $I_i$ are the currents due to the variable conductances. If we apply a Voltage Clamp to the system $\frac{dV}{dt} = 0$, consequently,

$$I = I_i$$

this is what HH saw,

In order to study the dependence of this current with respect to sodium and potassium, HH bathe the axon in different concentrations of Na. They saw, that when there were no Na, the inward part of the current did not exists. They performed all their experiments with 30 experiments (sea water).

Using this, and the Nernst equation, they could corroborate the Na resting potential and be sure that the inward part of the current was due to it.

Let’s define the prime letters to be the variables of the 30 and the unprime to be the control.

Assumptions

- Assumption 1. The function $I_k(t)$ is independent of $[Na]_o$. This is $I_k(t) = I'_k(t)$.

- Assumption 2. If $I_{Na}(t)$ and $I'_{Na}(t)$ then
  
  $$\frac{I'_{Na}(t)}{I_{Na}(t)} = k$$

- Assumption 3. Let $[t_0, t_0 + T]$ denote the interval during which $I_{Na}(t)$ increases to its maximum value. We assume that if $t \in [t_0, t_0 + T/3]$ or $t_0 \leq t \leq t_0 + T/3$, then
  
  $$\frac{dI_K}{dt}(t) = 0$$
Now we also are under the assumption that

\[ I_i = I_{Na} + I_K \]

and

\[ I'_i = I'_{Na} + I'_K \]

easily we can get to

\[ I_{Na}(t) = \frac{I_i(t) - I'_i(t)}{1 - k} \]

and

\[ I'_K(t) = \frac{I'_i - kI_i}{1 - k} \]

### 0.2 The good stuff

Analyzing again the equation of ion currents:

\[ I_i = I_{Na} + I_K + I_l \]

where \( I_l \) is the leakage current. Using the concept of conductance and that the currents are separable we have that

\[ I_{Na} = gNa(E - E_{Na}) \]
\[ I_K = gK(E - E_K) \]

where \( gNa \) and \( gK \) are variables. And it turns to be that

\[ I_l = \tilde{g}l(E - E_{Na}) \]

with \( \tilde{g}l \) a constant (we will use this as the notation).

The whole current equation is

\[ I = C_m \frac{dV}{dt} + gNaV_{Na} + gkV_k + \tilde{g}lV_l \]

or, which is the same

\[ \frac{dV}{dt} = \frac{1}{C_m} [I - gNaV_{Na} - gkV_k - \tilde{g}lV_l] \]

this is the most famous form of the HH equation. Now, we have to determine the behavior of the conductances.

The procedure is standard. Let’s analyze the temporal behavior of each conductance and then try to fit a function.
• For potassium.

Conductance of Potassium in Voltage Clamp

and this is the touchstone of the theory, they propose a dimensionless variable \( n \).

\[
g_K = \tilde{g}_K[n(t)]^4
\]

that satisfy the differential equation

\[
\frac{dn}{dt} = \alpha_n(1 - n)\beta_n n
\]

with \( \alpha \) and \( \beta \) functions of \( V \). Experimentaly, we can determine the value of this variables using the next new variables,

\[
\tau_n = \frac{1}{\alpha_n + \beta_n}
\]

\[
n_\infty = \frac{\alpha_n}{\alpha_n + \beta_n}
\]

where \( n_\infty \) is the value of \( n \) after applying a nonzero voltage clamp, and can be determined by

\[
\tilde{g}_K n_\infty^4 = g_\infty
\]

determination of \( \tau_n \) is more complicated, but also can be obtained from experiments. With this two number we can get \( \alpha_n \) and \( \beta_n \) The final result is

\[
\alpha_n(V) = \frac{0.01(V + 10)}{exp[(V + 10)/10] - 1}
\]

\[
\beta_n(V) = 0.125exp(V/80)
\]
• For sodium. It is the same idea, but more complicated.

\[ g_{Na} = m^3 h g_{Na} \]
\[
\frac{dm}{dt} = \alpha_m (1 - m) - \beta_m m
\]
\[
\frac{dh}{dt} = \alpha_h (1 - h) - \beta_h h
\]
\[
\alpha_m = \frac{0.1(V + 25)}{\exp[(V + 25)/10] - 1}
\]
\[
\beta_m = 4\exp\left[\frac{V}{18}\right]
\]
\[
\alpha_h = 0.07\exp\left(\frac{V}{20}\right)
\]
\[
\beta_h = \frac{1}{\exp[(V + 30)/10] + 1}
\]

0.3 The analysis

• Good predictor of current clamp.

• Good predictor of anode break.

• When applying constant current (enough) the system will oscillate, and that is not what it happens.

• When applying a ramp of current the system will oscillate, and again, that is not true.