Assignment 2
Theoretical Neuroscience

Peter Latham, Quentin Huys

16 October 2004

Linear cable theory

1. **Infinite cable response to arbitrary time-varying input**

   - First, we'll derive the Green function for the infinite cable. The Green function is the impulse response of a system. If the system is linear, the impulse response function can be used to predict the system's response to any input. In our case, the impulse response of the infinite cable corresponds to finding the solution to the cable equation driven by a delta function in time and space:

     $$\tau \frac{\partial v}{\partial t} - \lambda^2 \frac{\partial^2 v}{\partial x^2} + v = Q r_L \delta(t)\delta(x)$$

     where v is voltage relative to rest, Q is the total injected charge and r_L is the longitudinal resistivity.

     Question 1a: Show that the right hand side has the correct units.

     Question 1b: Solve this equation. Hint: Fourier transform with respect to x (but not with respect to t!). Solve the resulting differential equation in time, then Fourier transform back.

     Question 1c: Plot the time course of the voltage at position $x = 0, \lambda, 2\lambda$. Write down an expression for the maximum amplitude of the voltage (with respect to time) as a function of x.

   - Let $v_\delta(x,t)$ be the solution from Question 1b. This is the Green function for the infinite, linear cable, which means the following: the solution to the equation

     $$\tau \frac{\partial v}{\partial t} - \lambda^2 \frac{\partial^2 v}{\partial x^2} + v = I_{inj}(t)$$

     is

     $$v(x,t) = \int_0^T dt' v_\delta(x, t-t') I_{inj}(t').$$

     Question 1d: Prove this.

     Question 1e: Assume you inject a step current into the cable. How near is the voltage to its steady-state value after one time constant? Compare this to the case of injecting a step current into a membrane patch. Why might this be different?

2. **Steady-state solution for finite cable**

   Consider the steady-state cable equation,

$$\lambda^2 \frac{\partial^2 v}{\partial x^2} = v - r_L I_0 \delta(x).$$

   For infinite cables, the solution is

$$V(x) = r_L I_0 \lambda/2 \exp(-|x|/\lambda).$$

   Find the solution for a finite cable with ends at $-x_0$ and $+x_1$ (both x_0 and x_1 are positive). Assume no current flows through the ends.

3. **Noise in the amount of neurotransmitter per vesicle**

   Assume that a synapse has n release sites. When an action potential arrives at the synapse, each site releases an amount q of neurotransmitter probabilistically. The release probability, denoted p, is the same for all sites, and release at one site is independent of release at another. The amount of release is also probabilistic; we'll denote its probability distribution $p(q)$. This distribution has mean $\overline{q}$ and variance σ_q^2.

   Question 3a: What is the mean amount of neurotransmitter released in terms of n, p, $\overline{q}$ and σ_q^2?

   Question 3b: What is the variance of the amount of neurotransmitter released in terms of n, p, $\overline{q}$ and σ_q^2?

   Question 3c: Assume $p(q)$ is Gaussian. Plot $P(q)$, the probability distribution of total neurotransmitter released. Assume $n = 10$ and $p = 0.25$.

   Question 3d: Why is the Gaussian assumption unrealistic?

   A couple of hints. First,

$$P(q) = \sum_k P(q|k) p(k)$$

   where k is the number of sites that release neurotransmitter and $P(q|k)$ is the probability distribution of q given that k sites released neurotransmitter. (Recall from class that $p(k)$ is multinomial.)

   Second,

$$p(q|k) = \int dq_1 dq_2 ... dq_k \, \delta\left(q - \sum_{l=1}^{k} q_l\right) \prod_{i=1}^{k} p(q_i).$$

   Third, the moment generating function for the binomial is

$$\langle k^l \rangle = \left(p\frac{d}{dp}\right)^l \sum_{k=0}^{n} \frac{n!}{k!(n-k)!} p^k \rho^{n-k}$$

   where the derivatives are evaluated at $\rho = 1 - p$. You should verify this for yourself!!!