

## 9 Derivation of Rate Equations from Single-Cell Conductance (Hodgkin-Huxley-like) Equations

We consider a network of many neurons, each of which obeys a set of conductance-based equations for subthreshold and spike activity. Our goal is to derive an expression for the firing rate of the neuron in terms of the synaptic input to the cell. The equations are self-consistent in the sense that the output of each neuron contributes to the synaptic input of every other neuron.

We are motivated to this proof as a means of connecting single-cell equations, which are complicated, to simplified network equation, which are simple in that each cell is specified solely by its firing rate. Our goal is to understand the weights  $W_{ij}$  in terms of cellular properties. We follow the derivation laid down by Sompolinsky, which holds for averaging over Poisson inputs for a large networks. A similar derivation, which holds for averaging over a large number of spikes by a single synaptic input was given by Ermentrout. In each case the critical issue is that the network dynamics in asynchronous.

### Kirchoff's Law for One Neuron

$$C \frac{dV(t)}{dt} + g_L [V(t) - E_L] + I^{active}(t) = I^{applied}(t) \quad (9.1)$$

where  $E_L$  = reversal potential of leak,  $I^{active}(t)$  = all time-dependent active currents, and  $I^{applied}(t)$  = all time-dependent applied currents. Thus, simplifying the notation slightly

$$C \frac{dV(t)}{dt} = g_L [E_L - V(t)] - I^{act}(t) + I^{app}(t) \quad (9.2)$$

Let

$$f = \beta [I^{app} - I_c]_+ \quad (9.3)$$

where  $f$  = firing rate,  $\beta$  = gain, and we incorporate the leak conductance through

$$I_c = I_c^o + v_c g_L \quad (9.4)$$

where the constant  $v_c$  scales the dependence of firing threshold on the leak conductance. Thus

$$f = \beta [I^{app} - I_c^o - v_c g_L]_+ \quad (9.5)$$

where  $f$  is time-dependent through the time dependence of its arguments.

This formalism assumes that changes in conductance shifts the threshold level of the  $f - I$  curve, but does not effect the slope of the curve. This is approximately true, at least based on the experiments of Reyes.

**See gain curve reyes eps**

### Network Equations

$$C \frac{dV_i(t)}{dt} = g_L [E_L - V_i(t)] + I_i^{act}(t) + I^{ext}(t) + I^{net}(t) \quad (9.6)$$

where inputs from the "outside" come in through  $I^{ext}(t)$  and inputs from other cells in the network come in through  $I^{net}(t)$ . We consider the form of  $I_i^{ext}(t)$ , the input to the  $i$ -th neuron, first, i.e.,

$$I_i^{ext} = g_i^{in}(t) [E_{in} - V_i(t)] \quad (9.7)$$

The conductance weights the external input and is described by a first order equation

$$\tau_{in} \frac{dg_i^{in}}{dt} + g_i^{in} = G_{in} \tau_{in} R_{in}(t) \quad ; t \geq 0 \quad (9.8)$$

where the input  $R_{in}(t)$  is taken to be a Poisson process with mean rate  $f_i^{in}$ .

The formal solution for the state (steady state of inhomogeneous response) is given by

$$g_i^{in}(t) = G_{in} \int_{-\infty}^t dt' e^{-(t-t')/\tau_{in}} R_{in}(t) \quad (9.9)$$

so that the average over a large number of inputs (either separate presynaptic inputs or many post-synaptic potential from one input by a very slow synapse) is

$$\begin{aligned} \langle g_i^{in}(t) \rangle &= G_{in} \int_{-\infty}^t dt' e^{-(t-t')/\tau_{in}} \langle R_{in}(t) \rangle \\ &= G_{in} f_i^{in} \int_{-\infty}^t dt' e^{-(t-t')/\tau_{in}} \\ &= G_{in} f_i^{in} \tau_{in} \end{aligned} \quad (9.10)$$

where the product  $f_i^{in} \tau_{in}$  is just the number of post-synaptic inputs (or pre-synaptic spikes from all neighbors, since we do not include synaptic depression and other time-dependent synaptic effects) that occur in the time-constant of the post-synaptic cell.

Look at ratio of mean to standard deviation  $\frac{1}{\sqrt{\tau_{in} f_i^{in}}}$ . This goes down as the time-constant goes to infinity and as the frequency goes to infinity.

We now have

$$I_i^{ext} \rightarrow G_{in} \tau_{in} f_i^{in} [E_{in} - V_i(t)] \quad (9.11)$$

We turn to the current that results from synaptic inputs, i.e.,

$$I_i^{net} \equiv \sum_{j=1}^n g_{ij}(t) [E_j - V_i(t)] \quad (9.12)$$

where  $g_{ij}(t)$  is the post-synaptic conductance triggered by pre-synaptic spike

$$\tau_{ij} \frac{dg_{ij}}{dt} + g_{ij} = \tau_{ij} G_{ij} \sum_{t_j} \delta(t - t_j) ; t \geq 0 \quad (9.13)$$

where the summation is over the spikes in pre-synaptic neuron “j”.

We replace the spatial summation in synaptic input by the ensemble average, as in the case of the external input. This holds for Poisson firing rates among the neurons in the network. Thus

$$g_{ij}(t) = G_{ij} \int_{-\infty}^t dt' e^{-(t-t')/\tau_{ij}} \sum_{t_j} \delta(t - t_j) \quad (9.14)$$

so that the average over a large number of inputs (either separate presynaptic inputs or many post-synaptic potential from one input by a very slow synapse) is

$$\begin{aligned} \langle g_{ij}(t) \rangle &= G_{ij} \int_{-\infty}^t dt' e^{-(t-t')/\tau_{ij}} \left\langle \sum_{t_j} \delta(t - t_j) \right\rangle \\ &= G_{ij} f_j \int_{-\infty}^t dt' e^{-(t-t')/\tau_{ij}} \\ &= G_{ij} f_j \tau_{ij} \end{aligned} \quad (9.15)$$

]] where the integral is just  $\tau_{ij} f_j =$  mean number of spikes. The network controbution to the current to the cell become

$$I_i^{net} \rightarrow \sum_{j=1}^N G_{ij} \tau_{ij} f_j [E_j - V_i(t)] \quad (9.16)$$

The sum of the external and network currents is thus

$$I_i^{ext} + I_i^{net} = G_{in} \tau_{in} f_i^{in} [E_{in} - V_i(t)] + \sum_{j=1}^N G_{ij} \tau_{ij} f_j [E_j - V_i(t)] \quad (9.17)$$

where  $N$  is the number of neurons in the network. This expression has constant terms and voltage dependent terms. Let's put all the voltage terms with respect to  $E_L$ , so that the input gains a term that appears in form similar to that of  $g_L$ .

$$\begin{aligned}
I_i^{ext} + I_i^{net} &= G_{in} \tau_{in} f_i^{in} (E_{in} - E_L) + \sum_{j=1}^N G_{ij} \tau_{ij} f_j (E_j - E_L) \quad (9.18) \\
&+ \left( G_{in} \tau_{in} f_i^{in} + \sum_{j=1}^N G_{ij} \tau_{ij} f_j \right) [E_L - V_i(t)]
\end{aligned}$$

The first term to the right of the equality is a constant, i.e., independent of  $V(t)$ . We consider this as an effective applied current

$$I_i^{app} \equiv G_{in} \tau_{in} f_i^{in} (E_{in} - E_L) + \sum_{j=1}^N G_{ij} \tau_{ij} f_j (E_j - E_L) \quad (9.19)$$

The important thing is that the external and network terms have a voltage dependence that is proportional to the difference between the synaptic reversal potential and the leakage reversal potential, i.e., the resting potential.

The second term appears as a leakage current, in which the synaptic input adds to this leakage. We define an effective synaptic conductance,  $g_i^{syn}$  that adds to the leakage conductance  $g_L$ , i.e.,

$$g_i^{syn} \equiv G_{in} \tau_{in} f_i^{in} + \sum_{j=1}^N G_{ij} \tau_{ij} f_j \quad (9.20)$$

The results of our efforts is that we can write Kirchoff's law for one neuron, rather than the network, with effective parameters, In particular,  $(g_L + g_i^{syn})$  is the effective leak current.

$$C \frac{dV_i(t)}{dt} = -(g_L + g_i^{syn}) [E_L - V_i(t)] - I_i^{act}(t) + I_i^{app} \quad (9.21)$$

The modified firing rate is now

$$\begin{aligned}
f_i &= \beta [I_i^{app} - I_c^o - v_c g_L - v_c g_i^{syn}]_+ \quad (9.22) \\
&= \beta \left[ G_{in} \tau_{in} f_i^{in} (E_{in} - E_L) + \sum_{j=1}^N G_{ij} \tau_{ij} f_j (E_j - E_L) - I_c^o - g_L v_c - G_{in} \tau_{in} f_i^{in} v_c - \sum_{j=1}^N G_{ij} \tau_{ij} f_j v_c \right]_+ \\
&= \beta \left[ \sum_{j=1}^N G_{ij} \tau_{ij} (E_j - E_L - v_c) f_j + G_{in} \tau_{in} (E_{in} - E_L - v_c) f_i^{in} - (I_c^o + g_L v_c) \right]_+
\end{aligned}$$

We can now identify terms in the conductance equations that correspond to terms in our network equations. In particular,

### Synapses

$$W_{ij} \equiv G_{ij} \tau_{ij} (E_j - E_L - v_c) \quad (9.23)$$

is the synaptic efficiency, or connection strength, between neurons in the network.

### External Drive

$$W^{in} \equiv G_{in}\tau_{in}(E_{in} - E_L - v_c) \quad (9.24)$$

is the synaptic efficiency, or strength, for an external input to the neuron.

### Threshold

$$\theta \equiv I_c^o + g_L v_c \quad (9.25)$$

is the threshold denoted  $\theta$ . Thus the equation(s) for the firing rate become

### Rate Equation

$$f_i = \beta \left[ \sum_{j=1}^N W_{ij} f_j + W^{in} f_i^{in} - \theta \right]_+ \quad (9.26)$$

We now have derived the rate equations, under the assumption that the threshold of the  $f - I$  curve is shifted by the changes in synaptic conductance and that the cell receives multiple inputs (PSPs) during each integration period (nominally  $\tau_{ij}$ ).

It is not surprising that the synaptic efficiency depend on the conductances, i.e.,  $W_{ij} \propto G_{ij}$ . It is surprising that the synaptic efficiency depends on the combination  $E_j - E_L - v_c$ ; the synaptic reversal potential must be taken relative to  $E_L + v_c$ .

### Main Result

A final point is that we need a differential equation for the rates  $f_i$ , or for the discrete case a difference equation, so that the rates evolve over time. This is equivalent to letting the input to the neuron evolve with the time-constant of the neuron. Thus for the continuous case, using our previous notation  $\mu_i$  as the input to the cell, we have

$$\tau_i \frac{du_i(t)}{dt} + u_i = \sum_{j=1}^N W_{ij} f_j(t) + W^{in} f_i(t)^{in} - \theta \quad (9.27)$$

and

$$f_i = \beta [\mu_i]_+ \quad (9.28)$$

While for the discrete case, we have simply

$$f_i(t+1) \leftarrow \beta \left[ \sum_{j=1}^N W_{ij} f_j(t) + W^{in} f_i^{in}(t) - \theta \right]_+ \quad (9.29)$$

In terms of the previous symmetric and normalized notation, we have  $S_i = (2f_i - f^{max})/2f^{max}$ , which ranges between -1 and +1. For the special case of binary

neurons, i.e.,  $S_i = \pm 1$ , which corresponds to  $\beta \rightarrow \infty$  with a saturating firing rate,  $f^{max}$ , we have

$$S_i(t+1) \leftarrow \left[ \sum_{j=1}^N W_{ij} S_j(t) + W^{in} S_i^{in}(t) - \theta \right]_+ \quad (9.30)$$

### Response of Homogeneous Population of Neurons

We consider a homogeneous population, the simplest network, to gain insight into behavior of the network

$$W_{ij} \rightarrow W \text{ and } f_i^{in} \rightarrow f^{in}$$

therefore

$$f_i(t+1) = \beta \left[ W \sum_{j=1}^N f_j(t) + W^{in} f^{in} - \theta \right]_+ \quad (9.31)$$

and homogeneity across all neurons gives a steady-state ( $t \rightarrow \infty$ ) result of

$$f = \beta \left[ NWf + W^{in} f^{in} - \theta \right]_+ \quad (9.32)$$

where the rate is the same for all neurons ( $f_i \rightarrow f$ ). Thus

$$\text{if } NWf < W^{in} f^{in} - \theta, \quad f = 0$$

$$\text{if } NWf > W^{in} f^{in} - \theta, \quad f \neq 0$$

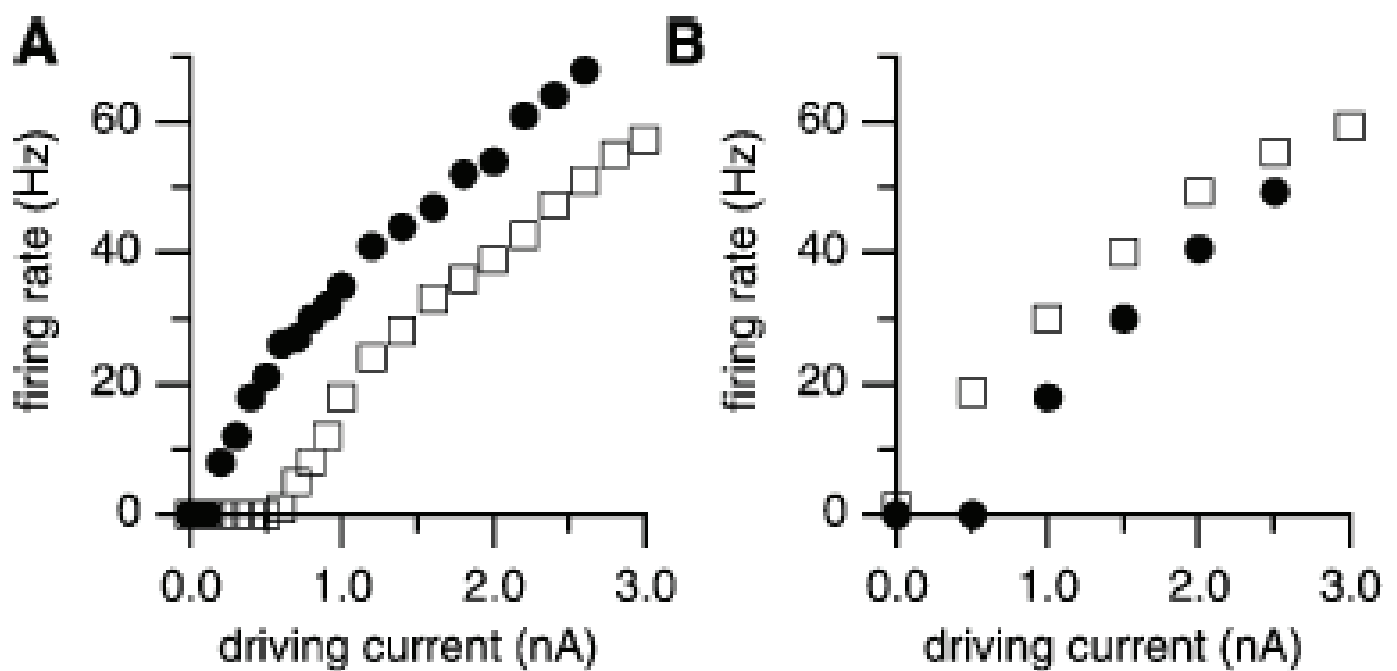
For the nonzero case:

$$f = \beta NWf + \beta(W^{in} f^{in} - \theta) \quad (9.33)$$

or

$$f = \frac{\beta}{1 - NW\beta} (W^{in} f^{in} - \theta) \quad (9.34)$$

We see that the firing rate,  $f$ , monotonically increases as the number of neurons,  $N$ , increases, until it reaches a singularity at  $N = 1/(T\beta)$ . In reality, saturation occurs first, which can be included by adding, for example, a term proportional to  $-[I - I_c]_+^2$  to the gain  $(f - I)$  function, which still allows us to get an analytical result.



**Figure 3. Separate Effects of Shunting and Noise on Response Gain and Variability**

(A) Firing rate versus constant driving current for a neuron without (closed circles), and with (open squares) 32 nS of additional constant conductance in the absence of any additional noise from background synaptic input. The result is a pure shift of the firing-rate curve.

(B) Firing rate versus constant driving current for a different neuron in the 1X condition (closed circles) and with the same level of conductance but input noise equivalent to the 3X condition (open squares). The effect is an increase in firing rate that is largest at low rates, resulting in a change in the slope of the firing-rate curve.