8 Derivation of Network Rate Equations from Single-Cell Conductance Equations

We consider a network of many neurons, each of which obeys a set of conductance-based, Hodgkin-Huxley 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 to connect single-cell equations, which are complicated, to simplified network equations, which are simple in that each cell is specified solely by its firing rate. Our goal is to understand the weights W_{ij} that define the synapses between pairs of cells in terms of cellular properties. We follow the derivations laid down by Sompolinsky and colleagues and by Ermentrout and colleagues, which holds for averaging. The critical issue is that the network dynamics and that the rate varies slowly over time, *i.e.*, slow on the time-scale of the time-constant of the neuron. in asynchronous.

8.1 Kirchhoff's law for one neuron

$$C \, \frac{dV(t)}{dt} + g_L \left[V(t) \ - E_L \right] \ = \ I^{active}(V, t) + I^{applied}(t) \tag{8.8}$$

where E_L = reversal potential of leak current, I^{active} (V, t) = all voltage- and time-dependent active currents, and $I^{applied}$ (t) = all time-dependent applied currents.

Let

$$r(t) = f\{I^{app}(t) \ - \ I_c\} \tag{8.9}$$

where r = firing rate, $f\{\cdots\}$ is the nonlinear gain function and I_c is a threshold current. A typical but not exclusive choice is

$$f\{\mu\} \ = \ f^{max} \, \frac{1 \ + \ tanh(\mu)}{2}. \tag{8.10}$$

We incorporate the leak conductance through

$$I_c = I_c^o \ + v_c \, g_L \tag{8.11}$$

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

$$r(t) = f\{I^{app}(t) - I_c^o \ - v_c \, g_L\}. \tag{8.12}$$

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.

FIGURE - Gain curve of Reyes

8.2 Network equations

We now consider a network of neurons in which the applied currents $I^{app}(t)$ have two contributions, ones from the "outside" come in through $I^{ext}(t)$ and inputs from other cells in the network come in through $I^{net}(t)$.

$$C\frac{dV_i(t)}{dt} = g_L\left[E_L - V_i(t)\right] + I_i^{act}(V,t) + I_i^{ext}(t) + I_i^{net}(t). \tag{8.13}$$

8.2.1 Averaging over external inputs

We consider the form of $I_i^{ext}(t)$, the external input to the i-th neuron, first, *i.e.*,

$$I_i^{ext}(t) = g_i^{in}(t)\left[E_{in} - V_i(t)\right] \tag{8.14}$$

where E_{in} in the reversal potential for external synaptic input. The conductance weights the external input and is described by a first order equation for $t \geq 0$, *i.e.*,

$$\tau_{in}\frac{dg_i^{in}(t)}{dt} + g_i^{in}(t) = G_{in}\,\tau_{in}\sum_{t_{in}}^{\text{all inputs}}\delta\left(t - t_{in}\right) \tag{8.15}$$

where the maximum conductance G_{in} and the time-constant τ_{in} is taken as the same for each synaptic input, a simplification that permits the summation to be taken as over all spikes from all external inputs to the i-th postsynaptic neuron.

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

$$g_i^{in}(t) = G_{in}\int_{-\infty}^{t}dt'e^{-(t-t')/\tau_{in}}\sum_{t_{in}}^{\text{all inputs}}\delta\left(t' - t_{in}\right). \tag{8.16}$$

The external input is taken to be an inhomogeneous Poisson process with a mean rate $r_i^{in}(t)$ that evolves on a time scale that is much longer than τ_{in}. Thus

$$
\begin{aligned}
\left\langle g_i^{in}(t)\right\rangle &= G_{in}\int_{-\infty}^{t}dt'e^{-(t-t')/\tau_{in}}\left\langle\sum_{t_{in}}^{\text{all inputs}}\delta\left(t' - t_{in}\right)\right\rangle \tag{8.17}\\
&= G_{in}\,r_i^{in}(t)\int_{-\infty}^{t}dt'e^{-(t-t')/\tau_{in}}\\
&= G_{in}\,r_i^{in}(t)\,\tau_{in}
\end{aligned}
$$

where the product $r_i^{in}(t)\tau_{in}$ 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 period of one time-constant of the post-synaptic cell.

We now have

$$I_i^{ext}(t) \rightarrow G_{in} \ \tau_{in} \ r_i^{in}(t) \left[E_{in} - V_i(t) \right]. \tag{8.18}$$

8.2.2 Averaging over synaptic inputs

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

$$I_i^{net}(t) \equiv \sum_{j=1}^{n} g_{ij}(t) \left[E_j - V_i(t) \right] \tag{8.19}$$

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

$$\tau_{ij} \frac{dg_{ij}(t)}{dt} + g_{ij}(t) = \tau_{ij} \ G_{ij} \sum_{t_j} \delta \ (t - t_j) \tag{8.20}$$

where the summation is over the spikes in pre-synaptic neuron "j". We replaced 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

$$g_{ij}(t) = G_{ij} \ \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{ij}} \sum_{t_j} \delta \ (t' - t_j) \tag{8.21}$$

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

$$\begin{aligned}
\langle g_{ij}(t) \rangle &= G_{ij} \ \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{ij}} \left\langle \sum_{t_j} \delta \ (t - t_j) \right\rangle \\
&= G_{ij} \ r_j(t) \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{ij}} \\
&= G_{ij} \ r_j(t) \ \tau_{ij}
\end{aligned} \tag{8.22}$$

where $r_j(t)$ is the slowly varying rate of spiking of neuron "j" and $\tau_{ij}r_j(t)$ corresponds to the mean number of spikes in a time period of τ_{ij}. The network contribution to the current to the cell become

$$I_i^{net}(t) \rightarrow \sum_{j=1}^{N} \ G_{ij} \ \tau_{ij} \ r_j(t) \left[E_j - V_i(t) \right]. \tag{8.23}$$

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8.2.3 Recapitulation of network equations

The sum of the external and network currents is thus

$$I_i^{ext}(t) \; + \; I_i^{net}(t) \;\; = \;\; G^{in} \; \tau^{in} \; r_i^{in}(t) \left[E_{in} - V_i(t)\right] \; + \; \sum_{j=1}^{N} \; G_{ij} \; \tau_{ij} \; r_j(t) \left[E_j - V_i(t)\right]$$
(8.24)

where N is the number of neurons in the network. This expression has constant terms and voltage dependent terms. Let's expand this expression and 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.

$$I_i^{ext}(t) + I_i^{net}(t) \;\; = \;\; G_{in}\tau_{in}r_i^{in}(t) \; (E_{in} - E_L) + \sum_{j=1}^{N} G_{ij} \; \tau_{ij} \; r_j(t) \; (E_j - E_L)$$
(8.25)

$$+ \left(G_{in} \; \tau_{in} \; r_i^{in}(t) + \sum_{j=1}^{N} \; G_{ij} \; \tau_{ij} \; r_j(t) \right) \left[E_L - V_i(t)\right].$$

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

$$I_i^{app}(t) \equiv G_{in}\tau_{in}r_i^{in}(t) \; (E_{in} - E_L) + \sum_{j=1}^{N} G_{ij} \; \tau_{ij} \; r_j(t) \; (E_j - E_L).$$
(8.26)

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, $g_i^{syn}(t)$ that adds to the leakage conductance g_L, *i.e.*,

$$g_i^{syn}(t) \equiv G_{in} \; \tau_{in} \; r_i^{in}(t) + \sum_{j=1}^{N} \; G_{ij} \; \tau_{ij} \; r_j(t).$$
(8.27)

The results of our efforts is that we can write Kirchhoff's law for one neuron, rather than the network, with effective parameters, In particular, $g_L + g_i^{syn}(t)$ is the effective leak current and

$$C \; \frac{dV_i(t)}{dt} = [g_L + g_i^{syn}(t)] \; [E_L - V_i(t)] - I_i^{act}(V, t) + I_i^{app}(t).$$
(8.28)

The modified firing rate is now

$$r_i(t) = f\{I_i^{app}(t) - I_c^o - v_c\, g_L - v_c\, g_i^{syn}(t)\} \tag{8.29}$$

$$= f\{G_{in}\tau_{in}r_i^{in}(t)(E^{in} - E_L) + \sum_{j=1}^{N} G_{ij}\tau_{ij}r_j(t)(E_j - E_L) - I_c^o - g_L v_c$$

$$-G_{in}\tau_{in}r_i^{in}(t)v_c - \sum_{j=1}^{N} G_{ij}\tau_{ij}\, r_j(t)v_c\}$$

$$= f\{\sum_{j=1}^{N} G_{ij}\, \tau_{ij}(E_j - E_L - v_c)\, r_j(t)\ +\ G^{in}\tau^{in}(E_{in} - E_L - v_c)r_i^{in}(t) - (I_c^o + g_L v_c)\}$$

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

Synapses

$$W_{ij} \equiv G_{ij}\tau_{ij}(E_j\ -\ E_L - v_c) \tag{8.30}$$

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

External Drive

$$W^{in} \equiv G_{in}\tau_{in}(E_{in} - E_L - v_c) \tag{8.31}$$

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

Threshold

$$\theta \equiv I_c^o + g_L v_c \tag{8.32}$$

is the threshold denoted θ. Thus the equation(s) for the firing rate become

Rate Equation

$$r_i(t) = f\{\sum_{j=1}^{N} W_{ij}r_j(t) + W^{in}r_i^{in}(t) - \theta\} \tag{8.33}$$

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 τ_{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 $E_L + v_c$.

8.3 Main result

A final point is that we need a differential equation for the rates r_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 $\mu_i(t)$ as the input to the cell, we have

$$\tau_i \frac{du_i(t)}{dt} + u_i(t) = \sum_{j=1}^{N} W_{ij} r_j(t) + W^{in} r_i(t)^{in} - \theta \tag{8.34}$$
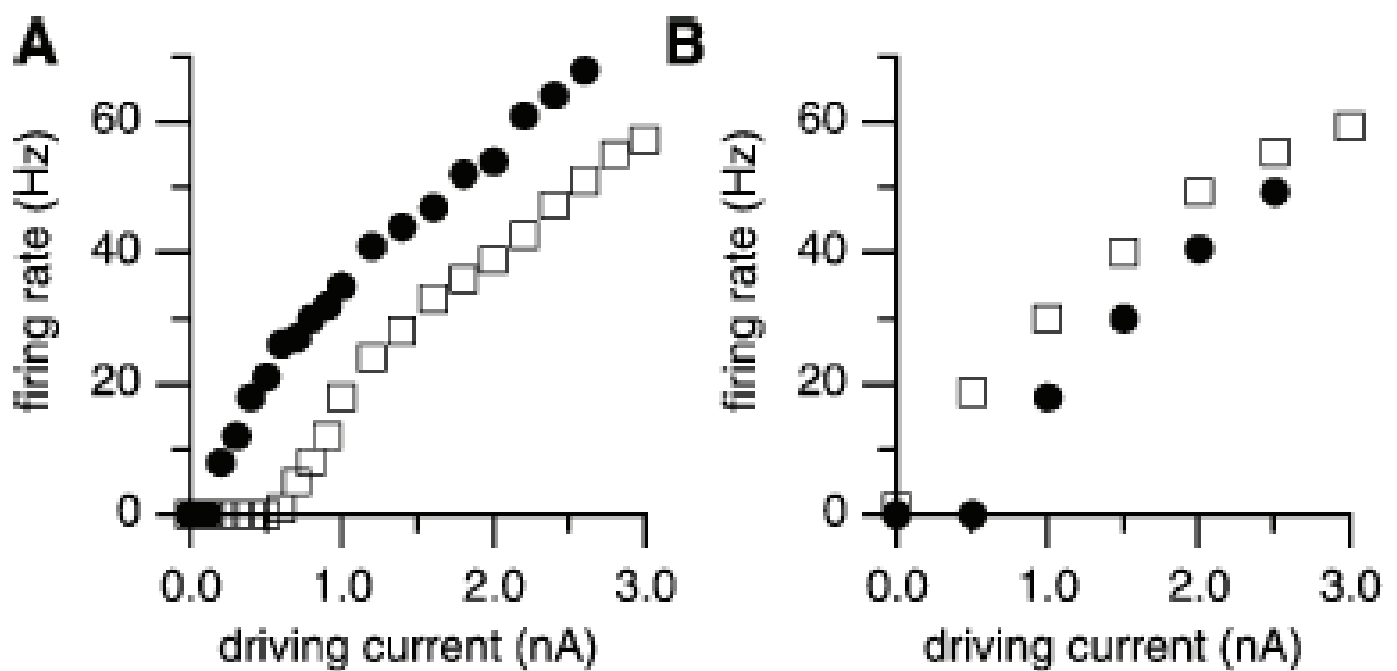
and

$$r_i(t) = f\{\mu_i(t)\} \tag{8.35}$$

While for the discrete case, we have simply

$$r_i i(t+1) \leftarrow f\{\sum_{j=1}^{N} W_{ij} r_j(t) + W^{in} r_i^{in}(t) - \theta\} \tag{8.36}$$

where, in terms of the previous symmetric and normalized notation, we have $S_i(t)$ $= (2r_i(t) - r^{max})/2r^{max}$, which ranges between -1 and +1. For the special case of binary neurons, i.e., $S_i = \pm 1$, which corresponds to $\beta \to \infty$ with a saturating firing rate, f^{max}, we have

$$S_i(t+1) \leftarrow sgn\left[\sum_{j=1}^{N} W_{ij} S_j(t) + W^{in} S_i^{in}(t) - \theta\right]. \tag{8.37}$$

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.