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

Our goal is to derive the form of the abstract quantities in rate equations, such as the synaptic weights, $W_{ij}$, and thresholds, $\theta_i$, from realistic conductance-based equations. We consider a network of many neurons, each of which obeys a set of conductance-based, Hodgkin-Huxley equations for the membrane voltage and channel activation. We derive an expression for the firing rate of each neuron in terms of the synaptic and external inputs 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 perform this derivation as a means to connect single-cell equations, which are complicated, to simplified network equations, in which the output of each cell is specified solely by its firing rate. We follow the path laid down by Sompolinsky and colleagues, which holds for averaging across many inputs, and is similar to one by Ermentrout and colleagues, which holds for averaging over time. Two critical assumptions are that the rate varies slowly on the time-scale of the time-constant of the neuron, i.e.

$$\frac{dr(t)}{dt} << \bar{r} \frac{1}{T} \quad (8.8)$$

where $r =$ firing rate, $\bar{r}$ is the average rate of the experiment, $T$ is a behaviorally- or physiologically-relevant time scale, and spiking is asynchronous.

8.1 Kirchhoff’s law for the postsynaptic neuron

We start with the standard form of a conductance-based model for a single cell, i.e.,

$$C \frac{dV(t)}{dt} + g_L^0 [V(t) - E_L] = I^{\text{active}}(V, t) + I^{\text{applied}}(t) \quad (8.9)$$

where $g_L^0$ is the leak conductance of the membrane, $E_L$ is the reversal potential of the leak current, $I^{\text{active}}(V, t)$ encompasses all voltage- and time-dependent active currents, and $I^{\text{applied}}(t)$ encompasses all time-dependent applied currents. Let

$$r(t) = f\{I^{\text{app}}(t) - I_c\} \quad (8.10)$$

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

$$f\{\mu\} = f^{\text{max}} \frac{1 + \tanh(\mu)}{2}. \quad (8.11)$$
A critical assumption is to incorporate the leak conductance into the rate through

$$I_c = I_c^o + v_c g_{L}^{\text{total}}$$  \hspace{1cm} (8.12)

where the constant $v_c$ scales the dependence of the firing threshold on the leak conductance, $g_{L}^{\text{total}}$. Further, $g_{L}^{\text{total}}$ includes the membrane conductances $g_{L}^o$ plus contributions from the opening of synaptic conductances; this is allow us to incorporate network interactions into the firing rate of a single cell. All told,

$$r(t) = f \{ I^{\text{app}}(t) - I_c^o - v_c g_{L}^{\text{total}} \}.$$  \hspace{1cm} (8.13)

Our formalism assumes that changes in conductance shift the threshold level of the $f - I$ curve, but does not effect the slope of the curve. This is approximately true, as illustrated by the experiments of Reyes, shown below.

We now consider a network of neurons in which the applied currents $I^{\text{app}}(t)$ have two contributions. One contribution is from external stimuli and is formalized as $I^{\text{ext}}(t)$ and the other contribution is from other cells in the network and is formalized through $I^{\text{net}}(t)$, so that

$$CdV_i(t)\over dt = g_i^o [E_L - V_i(t)] + I^{\text{ext}}_i(V,t) + I^{\text{net}}_i(t).$$  \hspace{1cm} (8.14)

We proceed by averaging the internal inputs over presynaptic spikes, which depend on the rate of spiking of presynaptic neurons.

### 8.1.1 Averaging over external inputs

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

$$I_i^{\text{ext}}(t) = g_i^{\text{in}}(t) [E_{in} - V_i(t)]$$  \hspace{1cm} (8.15)

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

$$\tau_i \frac{dg_i^{\text{in}}(t)}{dt} + g_i^{\text{in}}(t) = G_{in} \sum_{t_{in}}^{\text{all inputs}} \delta(t - t_{in})$$  \hspace{1cm} (8.16)
where the maximum conductance \( G_{in} \) and the time-constant \( \tau_{in} \) is assumed to be 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 steady state of the inhomogeneous response is given by

\[
g_{in}^i(t) = G_{in} \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{in}} \sum_{t_{in}} \delta(t' - t_{in}). \tag{8.17}
\]

The external input is assumed to be an inhomogeneous Poisson process with a rate \( r_{in}^i(t) \) that evolves on a time scale that is much longer than \( \tau_{in} \), i.e.,

\[
r_{in}^i(t) = \frac{1}{T} \int_{-T/2}^{T/2} dt' \sum_{t_{in}} \delta(t' - t_{in}) \equiv \left\langle \sum_{t_{in}} \delta(t' - t_{in}) \right\rangle. \tag{8.18}
\]

Thus

\[
\left\langle g_{in}^i(t) \right\rangle = G_{in} \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{in}} \left\langle \sum_{t_{in}} \delta(t' - t_{in}) \right\rangle \tag{8.19}
\]

\[
= G_{in} r_{in}^i(t) \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{in}}
\]

\[
= G_{in} r_{in}^i(t) \tau_{in}
\]

where the product \( r_{in}^i(t) \tau_{in} \) 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 an expression for the slowly evolving external input, i.e.,

\[
I_{ext}^i(t) \leftarrow G_{in} \tau_{in} r_{in}^i(t) [E_{in} - V_i(t)]. \tag{8.20}
\]

### 8.1.2 Averaging over synaptic inputs

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

\[
I_{net}^i(t) \equiv \sum_{j=1}^{n} g_{ij}(t) [E_j - V_i(t)] \tag{8.21}
\]

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

\[
\tau_{ij} \frac{dg_{ij}(t)}{dt} + g_{ij}(t) = \tau_{ij} G_{ij} \sum_{t_j} \delta(t - t_j) \tag{8.22}
\]

and 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

\[
g_{ij}(t) = G_{ij} \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{ij}} \sum_{t_j} \delta(t' - t_j) \tag{8.23}
\]
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

\[
\langle g_{ij}(t) \rangle = G_{ij} \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{ij}} \left( \sum_{t_j} \delta(t - t_j) \right) \tag{8.24}
\]

\[
= G_{ij} r_j(t) \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{ij}} \tag{8.25}
\]

\[
= G_{ij} r_j(t) \tau_{ij}
\]

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 \( \tau_{ij} \). The network contribution to the presynaptic current to cell "i" becomes

\[
I_{\text{net}}^i(t) \leftarrow \sum_{j=1}^{N} G_{ij} \tau_{ij} r_j(t) [E_j - V_i(t)]. \tag{8.26}
\]

8.1.3 Recapitulation of network equations

The sum of the external and network currents is thus

\[
I_{\text{ext}}^i(t) + I_{\text{net}}^i(t) = G_{\text{in}} \tau_{\text{in}} r_{\text{in}}^i(t) [E_{\text{in}} - V_i(t)] + \sum_{j=1}^{N} G_{ij} \tau_{ij} r_j(t) [E_j - V_i(t)] \tag{8.27}
\]

where \( N \) is the number of neurons in the network. This expression has constant terms and voltage dependent terms. Let’s expand this expression by adding and subtracting equal terms so that all of the voltage terms are with respect to \( E_L \). Thus the input gains a term that appears in form similar to that of \( g_L \), i.e.,

\[
I_{\text{ext}}^i(t) + I_{\text{net}}^i(t) = G_{\text{in}} \tau_{\text{in}} r_{\text{in}}^i(t) (E_{\text{in}} - E_L) + \sum_{j=1}^{N} G_{ij} \tau_{ij} r_j(t) (E_j - E_L) \tag{8.28}
\]

The first two terms to the right of the equality are independent of \( V(t) \). We consider these as an effective applied current, i.e.,

\[
I_{\text{app}}^i(t) \equiv G_{\text{in}} \tau_{\text{in}} r_{\text{in}}^i(t) (E_{\text{in}} - E_L) + \sum_{j=1}^{N} G_{ij} \tau_{ij} r_j(t) (E_j - E_L). \tag{8.28}
\]

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 third term in \( I_{\text{ext}}^i(t) + I_{\text{net}}^i(t) \) appears as a leakage current, in which the synaptic input adds to this leakage consistent with the increase in conductance from both excitatory and
inhibitory conductances. We define an effective synaptic conductance, \( g_i^{syn}(t) \), that encompasses the leakage conductance \( g_L \), i.e.,

\[
g_i^{syn}(t) \equiv G_{in} \tau_{in} r_i^{in}(t) + \sum_{j=1}^{N} G_{ij} \tau_{ij} r_j(t). \tag{8.29}
\]

The result of our efforts is that we can write Kirchhoff’s law for a single neuron with effective parameters that depend on the network interactions, rather than \( N \) separate equations for all neurons in the network. The equation for the single cell is

\[
C \frac{dV_i(t)}{dt} = \left[ g_L^o + g_i^{syn}(t) \right] [E_L - V_i(t)] + I_i^{act}(V, t) + I_i^{app}(t). \tag{8.30}
\]

We identify \( g_L^{total} = g_L^o + g_i^{syn}(t) \) is the total leakage conductance. The modified firing rate is now

\[
r_i(t) = f \left\{ I_i^{app}(t) - I_c^o - v_c g_L^o - v_c g_i^{syn}(t) \right\} \tag{8.31}
\]

\[
= f \left\{ G_{in} \tau_{in} r_i^{in}(t)(E_{in} - E_L) + \sum_{j=1}^{N} G_{ij} \tau_{ij} r_j(t)(E_j - E_L) - I_c^o - v_c g_L^o \right.
\]

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

\[
= \left\{ \frac{N}{j=1} G_{ij} \tau_{ij}(E_j - E_L - v_c) r_j(t) + G_{in}^{in}(E_{in} - E_L - v_c) r_i^{in}(t) - (I_c^o + v_c g_L^o) \right\}. \tag{8.31}
\]

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

**Rate equations:**

\[
r_i(t) = f \left\{ \sum_{j=1}^{N} W_{ij} r_j(t) + W^{in} r_i^{in}(t) - \theta \right\}. \tag{8.32}
\]

is in the form of rates and abstract weights.

**Synaptic inputs:**

\[
W_{ij} \equiv G_{ij} \tau_{ij}(E_j - E_L - v_c) \tag{8.33}
\]

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

**External input:**

\[
W^{in} \equiv G_{in}^{in}(E_{in} - E_L - v_c) \tag{8.34}
\]

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

**Threshold:**

\[
\theta \equiv I_c^o + g_L^o v_c \tag{8.35}
\]

is the fixed threshold denoted \( \theta \).
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 $E_L + v_c$.

### 8.2 Self-consistency

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

$$\tau_i \frac{d\mu_i(t)}{dt} + \mu_i(t) = \sum_{j=1}^{N} W_{ij} r_j(t) + W_{in}^{in} r_i(t)^{in} - \theta$$

(8.36)

and

$$r_i(t) = f\{\mu_i(t)\}.$$  

(8.37)

A further assumption is the discrete case, where time is clocked. We have simply

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

(8.38)

For the special case of binary neurons, i.e., $S_i = \pm 1$, we have

$$S_i(t + 1) \leftarrow \text{sgn} \left[ \sum_{j=1}^{N} W_{ij} S_j(t) + \frac{1}{2} W_{in}^{in} S_i^{in}(t) + 1 - \theta \right]$$

(8.39)

where

$$\theta'_{i} = 2\theta - \sum_{j=1}^{N} W_{ij} - W_{in}^{in}.$$  

(8.40)

This last form illustrates why cells with predominantly inhibitory input, so that $\theta' < 0$, will have a large positive bias, and vice versa. Simply, cells with predominantly inhibitory input must be biased positive if they are to fire at all. Many neurons in the brainstem follow this rule. Conversely, cells with predominantly excitatory input must be biased negative if they are to substantially increase their rate with synaptic input. For balanced networks, $\theta'_{i} \approx 0.$