1 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, θ_i, from realistic conductance-based equations. We consider a network of many neurons, each of which obeys a set of conductance-based, Hodgkin-Huxley-like 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.

$$\frac{dr(t)}{dt} << \frac{\bar{r}}{T} \tag{1.1}$$

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.

1.1 Kirchhoff's law for the postsynaptic neuron

We start with a conductance-based model for a single cell, for convenience written in terms of currents, i.e.,

$$C_m \, \frac{dV(t)}{dt} + g_L^o \left[V(t) \; - V_{leak}^{Nernst} \right] \; = \; I^{active}(V,t) \; + \; I^{applied}(t) \tag{1.2}$$

where C_m is the membrane capacitance, g_L^o is the leak conductance of the membrane, i.e., the resting conductance,V_L^{Nernst} is the reversal potential of the leak current, I^{active} (V, t) encompasses all voltage- and time-dependent active currents, and $I^{applied}$ (t) encompasses all time-dependent applied currents. At rest with no input, $V(t) = V_{leak}^{Nernst}$. Let

$$r(t) = f \left[I^{app}(t) \; - \; I_\theta \right] \tag{1.3}$$

where $f[\cdots]$ is the nonlinear gain function and I_θ is a threshold current. Typical choices are

$$f[x] \; = \; \frac{1}{1 \; + \; e^{-\beta x}}. \tag{1.4}$$

and

$$f[x] \; = \; [\beta x]_{+} \tag{1.5}$$

where β is the conversion gain.

A critical insight is that a change in the conductance of a cell, such as through the opening of any postsynaptic channel, will increase the leak conductance. Thus we incorporate the leak conductance into the rate through

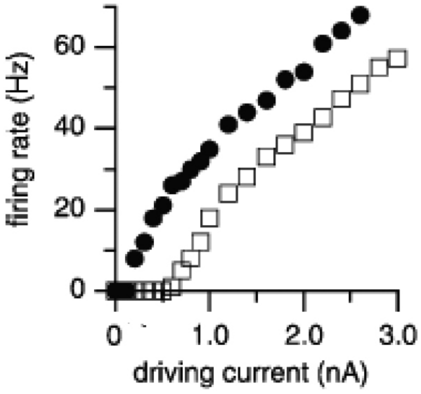
$$I_\theta = I_\theta^o \; + v_\theta \; g_L^{\text{total}} \tag{1.6}$$

where the constant v_θ scales the dependence of the firing threshold on the total leak conductance, g_L^{total}. We will derive an expression for g_L^{total}, which includes the membrane conductances g_L^o plus contributions from the opening of synaptic conductances. This, in fact, will allow us to incorporate network interactions into the firing rate of a single cell. All told,

$$r(t) = f[I^{app}(t) - I_\theta^o \; - v_\theta \; g_L^{\text{total}}\}. \tag{1.7}$$

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 (Figure 1), although it fails if adaptation (which we ignore here) is too strong (Figure 2). Nonetheless, we can deal with adaptation by introducing another averaged variable.

Figure 1: Effect of shunting on response gain. Dark squares are normal and open squares with 32 nS of additional conductance. From Chance, Abbott and Reyes, 2002.

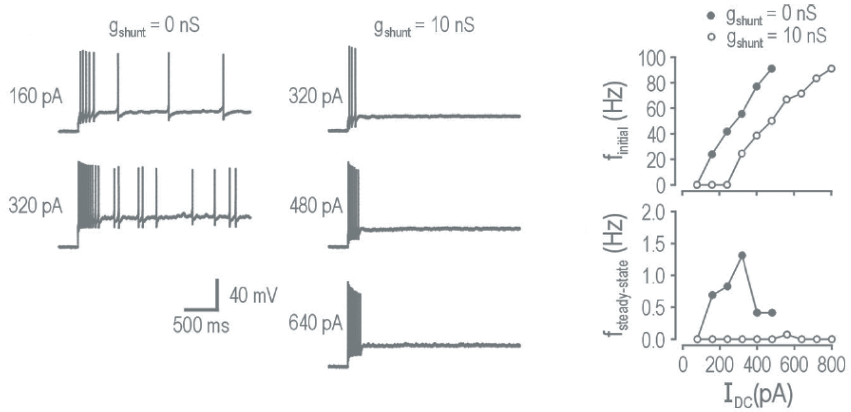


We now consider a network of neurons in which the applied currents $I^{app}(t)$ have two contributions. One contribution is from external stimuli and is formalized as $I^{ext}(t)$ and the other contribution is from other cells in the network and is formalized through $I^{net}(t)$, so that

$$C_m \frac{dV_i(t)}{dt} = g_L^o \left[V_{leak}^{Nernst} - V_i(t) \right] + I_i^{act}(V,t) + I_i^{ext}(t) + I_i^{net}(t). \tag{1.8}$$

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

Figure 2: Effect of shunting on response gain. Note initial versus steady-state differences compared with Chance et al. From Prescott, Ratte, De Koninck and Sejnowski, 2006



1.1.1 Averaging over synaptic inputs

The current $I_i^{net}(t)$ for cell i that results from synaptic inputs is

$$I_i^{net}(t) \quad \equiv \quad \sum_{j=1}^{n} g_{syn;ij}(t) \left[V_{syn;i,j}^{Nernst} - V_i(t) \right] \tag{1.9}$$

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

$$\tau_{syn;ij} \; \frac{dg_{syn;ij}(t)}{dt} + \; g_{syn;ij}(t) = \tau_{syn;ij} \; G_{syn;ij} \sum_{t_j}^{\text{all events}} \delta\ (t - t_j) \tag{1.10}$$

and where the summation is over the spikes in pre-synaptic neuron ”j”. We now replace the spatial summation in synaptic input by the ensemble average. Noting that the inhomogeneous solution for $g_{syn;ij}(t)$ is

$$g_{syn;ij}(t) = G_{syn;ij} \; \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{syn\ ij}} \; \sum_{t_j}^{\text{all events}} \delta\ (t' - t_j) \tag{1.11}$$

the average over a large number of inputs is

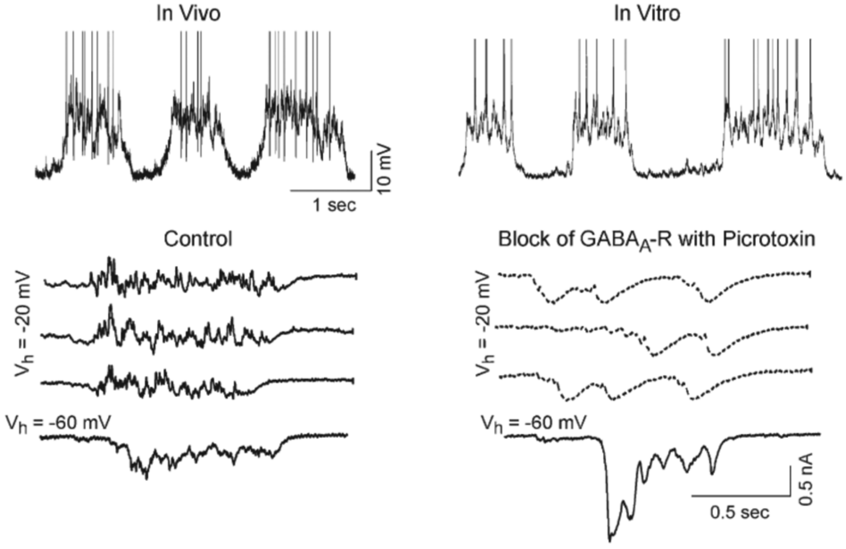
$$\langle g_{syn;ij}(t) \rangle = G_{syn;ij} \; \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{syn;ij}} \; \left\langle \sum_{t_j}^{\text{all events}} \delta\ (t - t_j) \right\rangle \tag{1.12}$$

as illustrated for ferret (Figure 3) and monkey (Figure 4)

We assume that the input is Poisson distributed and that we average over many separate presynaptic inputs or many post-synaptic potential from one input by a very slow synapse. That is, the presynaptic rates evolve on a time slow compared to $\tau_{syn;ij}$. Then

$$r_j(t) \; = \; \frac{1}{T} \int_{-T/2}^{T/2} dt' \sum_{t_j}^{\text{all events}} \delta\ (t' - t_j) \; \equiv \; \left\langle \sum_{t_j}^{\text{all events}} \delta\ (t' - t_j) \right\rangle . \tag{1.13}$$

Figure 3: Averaging of synaptic input in in ferret prefrontal cortex. From Hasenstaub, Shu, Haider, Kraushaar, Duque and McCormick, 2005.



where $r_j(t)$ is the slowly varying rate of spiking of neuron ”j” and

$$\begin{aligned} \langle g_{syn;ij}(t) \rangle &= G_{syn;ij}\ r_j(t) \int_{-\infty}^{t} dt' e^{-(t-t')\ \tau_{syn;ij}} \\ &= G_{syn;ij}\ r_j(t)\ \tau_{syn;ij}. \end{aligned} \tag{1.14}$$

the product $\tau_{syn;ij} r_j(t)$ corresponds to the mean number of spikes in a time period of $\tau_{syn;ij}$; we do not include synaptic depression and other time-dependent synaptic effects. The network contribution to the presynaptic current to cell ”i” becomes

$$I_i^{net}(t) \leftarrow \sum_{j=1}^{N}\ G_{syn;ij}\ \tau_{syn;ij}\ r_j(t) \left[V_{syn;ij}^{Nernst} - V_i(t) \right]. \tag{1.15}$$

1.1.2 Averaging over external inputs

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

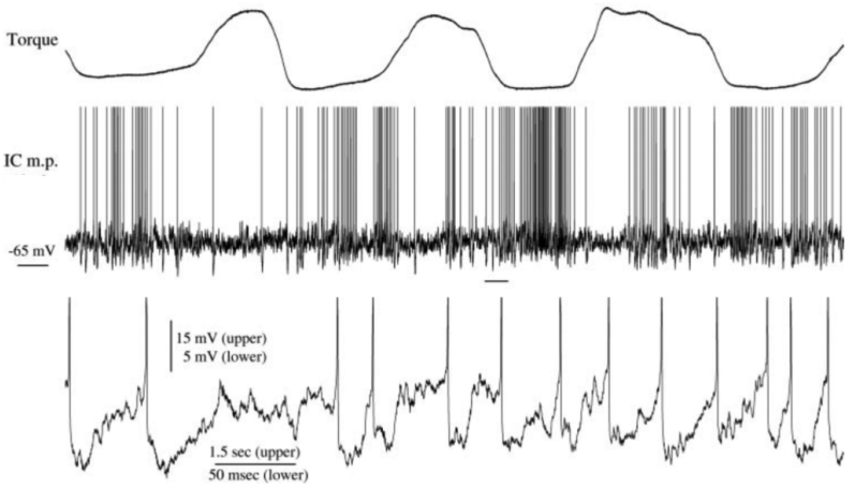
$$I_i^{ext}(t) = g_i^{ext}(t) \left[V_{ext}^{Nernst} - V_i(t) \right] \tag{1.16}$$

where V_{in} in 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.*,

$$\tau_{in}\ \frac{dg_i^{ext}(t)}{dt} + g_i^{ext}(t)\ =\ G_{ext}\ \tau_{ext} \sum_{t_{ext}}^{\text{all inputs}}\ \delta\ (t - t_{ext}) \tag{1.17}$$

where the maximum conductance G_{ext} and the time-constant τ_{ext} 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.

Figure 4: Averaging of synaptic input in monkey motor cortex. From Chen and Fetz, 2005.



Like the above case for network connections, the formal solution for the steady state of the inhomogeneous response is given by

$$g_i^{ext}(t) = G_{ext} \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{ext}} \sum_{t_{ext}}^{\text{all inputs}} \delta\ (t' - t_{ext}). \tag{1.18}$$

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

$$r_i^{ext}(t) \ = \ \frac{1}{T} \int_{-T/2}^{T/2} dt' \sum_{t_{ext}}^{\text{all inputs}} \delta\ (t' - t_{ext}) \ \equiv \ \left\langle \sum_{t_{ext}}^{\text{all inputs}} \delta\ (t' - t_{ext}) \right\rangle. \tag{1.19}$$

Thus

$$\begin{aligned} \left\langle g_i^{ext}(t) \right\rangle \ &= \ G_{ext} \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{ext}} \left\langle \sum_{t_{ext}}^{\text{all inputs}} \delta\ (t' - t_{ext}) \right\rangle \\ &= \ G_{ext}\ r_i^{ext}(t) \int_{-\infty}^{t} dt' e^{-(t-t')/\tau_{ext}} \\ &= \ G_{ext}\ r_i^{ext}(t)\ \tau_{ext} \end{aligned} \tag{1.20}$$

where the product $r_i^{ext}(t)\tau_{ext}$ is just the number of post-synaptic inputs, or equivalently pre-synaptic spikes from all external inputs, 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.,

$$I_i^{ext}(t) \leftarrow G_{ext}\ \tau_{ext}\ r_i^{ext}(t) \left[V_{ext}^{Nernst} - V_i(t) \right]. \tag{1.21}$$

1.1.3 Recapitulation of network equations

The sum of the network and external currents is

$$I_i^{ext}(t) \ + \ I_i^{net}(t) \ \ = \ \ G^{ext}\ \tau^{ext}\ r_i^{in}(t) \left[V_{ext}^{Nernst} - V_i(t) \right] \tag{1.22}$$

$$+ \quad \sum_{j=1}^{N} G_{syn;i,j}\ \tau_{syn;i,j}\ r_j(t) \left[V_{syn;i,j}^{Nernst} - V_i(t)\right]$$

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 the terms

$$G_{ext}\tau_{ext} r_i^{ext}(t)\ V_{leak}^{Nernst} \ + \ \sum_{j=1}^{N} G_{syn;i,j}\ \tau_{syn;ij}\ r_j(t)\ V_{leak}^{Nernst}$$

so that all of the voltage terms are with respect to V_{leak}^{Nernst}. Thus the input gains a term that appears similar in form to that of g_L, i.e.,

$$\begin{aligned} I_i^{ext}(t) \ + \ I_i^{net}(t) &= G_{ext}\tau_{ext} r_i^{ext}(t)\ \left[V_{ext}^{Nernst} - V_{leak}^{Nernst}\right] \\ &+ \ \sum_{j=1}^{N} G_{syn;i,j}\ \tau_{syn;i,j}\ r_j(t)\ \left[V_{syn;i,j}^{Nernst} - V_{leak}^{Nernst}\right] \\ &+ \ \left(G_{ext}\ \tau_{ext} r_i^{ext}(t) + \sum_{j=1}^{N} G_{syn;i,j}\tau_{syn;i,j}\ r_j(t)\right) \left[V_{leak}^{Nernst} - V_i(t)\right]. \end{aligned} \tag{1.23}$$

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.,

$$\begin{aligned} I_i^{app}(t) \ &\equiv \ G_{in}\tau_{ext} r_i^{ext}(t)\ (V_{ext}^{Nernst} - V_{leak}^{Nernst}) \\ &+ \ \sum_{j=1}^{N} G_{syn;i,j}\ \tau_{syn;i,j}\ r_j(t)\ (V_{syn;i,j}^{Nernst} - V_{leak}^{Nernst}). \end{aligned} \tag{1.24}$$

The important thing is that the external and network contributions have a voltage dependence that is proportional to the difference between the synaptic reversal potential and the leakage reversal potential. The third term in $I_i^{ext}(t) \ + \ I_i^{net}(t)$ appears as a leakage current; 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.*,

$$g_i^{syn}(t) \equiv G_{ext}\ \tau_{ext}\ r_i^{ext}(t) + \sum_{j=1}^{N}\ G_{syn;i,j}\ \tau_{syn;i,j}\ r_j(t). \tag{1.25}$$

and write Kirchhoff's law for a single neuron with effective parameters that depend on the network interactions, as opposed to N separate equations for all neurons in the network. The equation for the single cell is

$$C_m\ \frac{dV_i(t)}{dt} = [g_L^o + g_i^{syn}(t)] \left[V_{leak}^{Nernst} - V_i(t)\right] + I_i^{act}(V,t) + I_i^{app}(t). \tag{1.26}$$

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

$$\begin{aligned} r_i(t) &= f\left[I_i^{app}(t) - I_\theta^o - v_\theta\ g_L^{total}(t)\right] \qquad (1.27)\\ &= f\left[I_i^{app}(t) - I_\theta^o - v_\theta\ g_L^o - v_\theta\ g_i^{syn}(t)\right]\\ &= f[G_{ext}\tau_{ext}r_i^{ext}(t)(V_{ext}^{Nernst} - V_{leak}^{Nernst})\\ &\quad + \sum_{j=1}^{N} G_{syn;ij}\tau_{syn;ij}r_j(t)(V_{syn;i,j}^{Nernst} - V_{leak}^{Nernst})\\ &\quad - I_\theta^o - v_\theta g_L^o - G_{ext}\tau_{ext}r_i^{ext}(t)v_\theta - \sum_{j=1}^{N} G_{syn;ij}\tau_{syn;ij}\ r_j(t)v_\theta]\\ &= f[\sum_{j=1}^{N} G_{syn;ij}\ \tau_{syn;ij}(V_{syn;i,j}^{Nernst} - v_\theta - V_{leak}^{Nernst})\ r_j(t)\\ &\quad + G_{ext}\tau_{ext}(V_{ext}^{Nernst} - v_\theta - V_{leak}^{Nernst})r_i^{in}(t) - (I_\theta^o + v_\theta g_L^o)]. \end{aligned}$$

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

Rate equations:

$$r_i(t) = f\left[\sum_{j=1}^{N} W_{ij}r_j(t) + W^{ext}r_i^{ext}(t) - \theta\right]. \qquad (1.28)$$

is in the form of rates and abstract weights.

Synaptic inputs:

$$W_{ij} \equiv G_{syn;ij}\tau_{syn;ij}\left[V_{syn\ i,j}^{Nernst}\ -\ v_\theta\ -\ V_{leak}^{Nernst}\right] \qquad (1.29)$$

is the synaptic efficiency, or connection strength, between neurons in the network. It is not surprising that the synaptic coupling W_{ij} proportional to $G_{syn;ij}$ and has units of charge, i.e., conductance × time × voltage. Further, the form of the voltage dependence suggests

$$\langle V_j(t)\ -\ V_{leak}^{Nernst}\rangle_{\text{time}} \simeq \left[V_{syn\ i,j}^{Nernst}\ -\ v_\theta\ -\ V_{leak}^{Nernst}\right].$$

Lastly, the issue of the scaling of weights by the size of the network has been suppressed; we simply took $W_{ij} \propto O(\frac{1}{N})$.

External input:

$$W^{ext} \equiv G_{ext}\tau_{ext}\left[V_{ext}^{Nernst} - V_{leak}^{Nernst} - v_\theta\right] \qquad (1.30)$$

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

Threshold:

$$\theta \equiv I_\theta^o + g_L^o v_\theta \qquad (1.31)$$

is the fixed threshold denoted θ.

We 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 $\tau_{syn;ij}$).

1.2 Self-consistency

A final point is that we need a differential equation for the rates r_i, so that they may evolve over time. This is equivalent to letting the input to the neuron evolve with the time-constant of the neuron. Using our previous notation $\mu_i(t)$ as the input to the cell, we have

$$\tau_i \frac{d\mu_i(t)}{dt} + \mu_i(t) = \sum_{j=1}^{N} W_{ij} r_j(t) + W^{ext} r_i(t)^{ext} - \theta \tag{1.32}$$

and

$$r_i(t) = f\left[\mu_i(t)\right]. \tag{1.33}$$

Uniform feedback Let's look at the special case of the steady-state of the rates, i.e., $r_i(t + \Delta t) = r_i(t)$, and do so in an "easy" limit. Without loss of generality, we take take $r_i^{ext}(t) = 0$. We further take $W_{ij} = W_o$ and $f[\mu] = [\mu]_+$, so that

$$r_i = \beta \left[W_o \sum_{j=1}^{N} r_j - \theta \right]_+ . \tag{1.34}$$

With the mean activity defined as r_o, i.e.,

$$r_o \equiv \frac{1}{N} \sum_{i=1}^{N} r_i \ , \tag{1.35}$$

we have

$$r_o = \left[\beta N W_o r_o - \beta\theta\right]_+ \tag{1.36}$$

This has the solution

$$r_o = \begin{cases} 0 & \text{if } N\beta W_o < 1 \\ \frac{\theta}{NW_o - 1/\beta} & \text{if } N\beta W_o > 1 \end{cases} \tag{1.37}$$

which states that networks of only excitatory neurons will be active for sufficiently strong synapses or large network size.

1.2.1 Binary neurons

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

$$\begin{aligned} S_i(t+1) \ &\leftarrow sgn \ \left[\sum_{j=1}^{N} W_{ij} \ \frac{S_j(t)+1}{2} + W^{ext} \ \frac{S_i^{ext}(t)+1}{2} - \theta \right] \\ &\leftarrow sgn \ \left[\sum_{j=1}^{N} W_{ij} \ S_j(t) \ + \ W^{ext} S_i^{ext}(t) \ - \ \theta_i' \right] \end{aligned} \tag{1.38}$$

where

$$\theta'_i = 2\theta - \sum_{j=1}^{N} W_{ij} - W^{ext}. \tag{1.39}$$

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, $\theta'_i \approx 0$.