Due 2019-02-14 11:59pm PST

Teamwork is the ability to work together toward a common vision - Andrew Carnegie (10 points)

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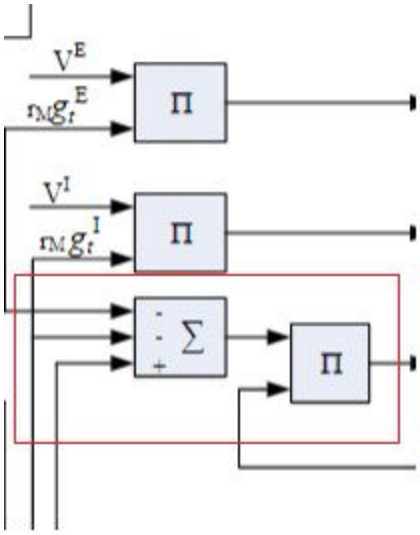
Spike Response Models (20 points)

Q: As you learned in your lectures, a simpler Spike Response Model was derived from discretized Hodgkin-Huxley model by removing certain "second-order" terms. To what extent is it actually second-order?

To get from the Hodgkin-Huxley model to the SRM0 model, we removed the second order terms:

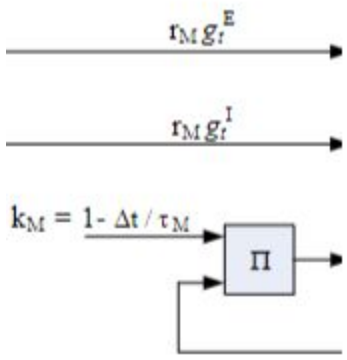
$$\mathrm{r_M}\, g_t^{\mathrm{E}} = \mathrm{r_M}\, g_{t-1}{}^{\mathrm{E}}\, \mathrm{k_E} + \sum \mathrm{r_M}\, \mathrm{g^E}\, s_{ti} w_{ij}$$
$$\mathrm{r_M}\, g_t^{\mathrm{I}} = \mathrm{r_M}\, g_{t-1}{}^{\mathrm{I}}\, \mathrm{k_I} + \sum \mathrm{r_M}\, \mathrm{g^I}\, s_{ti} w_{ij}$$

In essence, these second order terms characterize the dependency of the i-th output of membrane potential on all other inputs to the network:



As you can see in the above diagram from class, the red box corresponds to the second-order terms: it depends on all affine combinations of the input excitatory and inhibitory neurons as well as the previous potential Vt-1. Therefore, one small change in the inputs spikes does not change the new membrane potential linearly: if we take the derivative of output membrane potential with respect to input spiking values, we cannot express the change in output (dV) in linear combinations of the change in the inputs S (dS); instead, we will have to compute d(Vt)/d(Si) = d((Vt-1) * sum(S) * scalar)/d(Si) + constants. This will result in second order differential equations.

To understand this better, compare with the system diagram after the second term is removed:



Now, a change in the each input spikes will independently affect the output membrane potential. The only impact in output potential from previous output potential is characterized with a constant factor (Km). Now, the differential equation is first order and more easily solvable using methods like gradient descent or other approximation methods.

The original paper/book by Gerstner expressed similar ideas and explanations in Chapter 4.2.3 [2]. For example, it is mentioned that “In the nonlinear integrate-and-fire model, parameters are made ***voltage*** **dependent whereas in the SRM they depend on the time since the last output spike.** [….] While integrate-and-fire models are usually defined in terms of differential equations, the **SRM expresses the membrane potential at time *t* as an integral over the past**”. It is clear that the removal of the dependency on the second order terms allowed us to simplify the HH model to become the linear SRM model.

Q: Perform a literature search to find realistic constant values and compare the “second-order” terms with the “first-order” terms retained in the Spike Response Model.

This is a complicated question. The original Hodgkin-Huxley paper provided some of those constants and devoted most of part II of the paper to look at which constants should be used in the model (See “The ionic conductances” in PART II MATHEMATICAL DESCRIPTION OF MEMBRANE CURRENT DURING A VOLTAGE CLAMP in [1].)

Eventually after some experimentation with different depolarization of the axons, they asserted: “In the experiment illustrated by Fig. 3, gK. = 20 m.mho/cm2 at V = -100 mV. Gk was therefore chosen to be near 24 m.mho/cm2. ” and “The rate constants derived from these parameters were (in msec-1): alpha_n=0.21, beta_n-= 0.70 when V=0 and alpha_n= 0.90, beta_n = 0.43 when V= -25 mV. ” It seems that the actual choice of those parameters heavily depends on other conditions such as temperature and depolarization levels among others.

I then tried to research the constants used by the SRM0 model [2]:

x	E_x	g_x
Na	115 mV	120 $\mathrm{mS/cm^2}$
K	-12 mV	36 $\mathrm{mS/cm^2}$
L	10.6mV	0.3$\mathrm{mS/cm^2}$

x	$\alpha_x(u\,/\,\mathrm{mV})$	$\beta_x(u\,/\,\mathrm{mV})$
n	$(0.1-0.01\,u)\,/\,[\exp(1-0.1\,u)-1]$	$0.125\exp(-u\,/\,80)$
m	$(2.5-0.1\,u)\,/\,[\exp(2.5-0.1\,u)-1]$	$4\exp(-u\,/\,18)$
h	$0.07\exp(-u\,/\,20)$	$1\,/\,[\exp(3-0.1\,u)+1]$

Table 2.1: The parameters of the Hodgkin-Huxley equations. The membrane capacity is $C = 1\mu\mathrm{F/cm^2}$. The voltage scale is shifted so that the resting potential vanishes.

As you can see, small simplifications are made in the SRM paper and they also seem to have ignored different experimental conditions.

Now we compare the terms in the SRM0 model with the original non-linear model. In the SRM0 after second order terms are removed, the SRM paper writes:

The simplified model SRM_0 defined in (4.42) with the η kernel defined in (4.43) can be reinterpreted as a model with a dynamic threshold,

$$\vartheta(t-\hat{t}) = \vartheta - \eta_0(t-\hat{t})\,, \tag{4.44}$$

that is increased after each spike. Firing occurs if

$$h_i(t) = \vartheta(t-\hat{t})\,, \tag{4.45}$$

where h_i is the input potential,

$$h_i(t) = \sum_j w_{ij} \sum_{t_j^{(f)}} \epsilon_0(t-t_j^{(f)}) + \int_0^\infty \kappa_0(s)\, I^{\mathrm{ext}}(t-s)\,\mathrm{d}s\,. \tag{4.46}$$

We emphasize that h_i depends on the input only. In particular, there is no dependence upon $\hat{t}_i$. The next spike occurs if the input potential $h_i(t)$ reaches the dynamic threshold $\vartheta(t-\hat{t})$; cf. Fig. 4.10.

To compare with the original equations for the non-linear model:

$$\begin{aligned} u_i(t) &= \eta(t-\hat{t}_i) + \sum_j w_{ij} \sum_f \epsilon_{ij}(t-\hat{t}_i, t-t_j^{(f)}) \\ &\quad + \int_0^\infty \kappa(t-\hat{t}_i, s)\, I^{\mathrm{ext}}(t-s)\,\mathrm{d}s \end{aligned} \tag{4.24}$$

As you can see, the time-dependent terms are taken out from the non-linear model to form the SRM0 model. However, I am not entirely sure how this model fits with the original HH model, since the author of the SRM paper simplified the HH model to begin with and ignored many factors such as temperature and also set resting voltage to 0. With that said, I suspect the non-linear model and the original HH model refer to the same curve. Therefore, one can probably fit the SRM0 model with the HH model after removing `eta` and setting the e and k to independent of time.

Citations:

[1] https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1392413/pdf/jphysiol01442-0106.pdf
[2] http://icwww.epfl.ch/~gerstner/SPNM/node27.html

Getting Into Inhibition! (25 points)

3.1 In lab2.pdf please explain the functional difference between FeedForward Inhibition (FFI) and Lateral Inhibition (LI).

- Feed Forward Inhibition (FFI):
    - Takes in spike volley as input and will potentially inhibit excitatory neurons downstream within the same excitatory column. FFI will either block or allow all spikes within a volley to pass to neurons downstream depending on the number of spikes and the timeframe in which the spikes were received. In TNNs FFI is modeled as a function of the volley (TL), the number of spikes (TF), and a timeframe with respect to the first spike. If more than the number of spikes are received within the timeframe, the FFI block will inhibit the neurons and nullify the input spikes, otherwise they pass through as normal.
- Lateral Inhibition (LI):
    - Takes in spike volley as input and will potentially inhibit neurons within another excitatory column. LI allows only the early set of spikes within a volley to propagate to downstream neurons, later spikes are nullified. Can be modeled as a winner-take-all function based on the number of spikes allowed to pass through and potentially a time window where spikes are allowed to pass. In this model, up to ‘k’ spikes are allowed to pass that arrive within time window TL.

3.4 In lab2.pdf list any parameters that you had to pick, the values that you picked for them, and why you picked those values.

For feedforward inhibition, the parameter for inhibit_k was set to 3. This meets that within a given timestep, there can only be 3 spikes coming out of the first layer at the same time. Any more would result in cancelling out the spike volley. Generally, there were between 2-4 spikes per timestep, so the inhibit_k was set to 3 eliminated the case where there was a fourth spike.

Extra Excited about Excitatory Columns! (45 points)

4.3 In lab2.pdf report what response function you used.

We used simple threshold response function. The outputs of each neuron will spike if the affine combination exceeds pre-determined threshold value. When a neuron spike, we always use output value 0 to represent the firing of the neuron. Since the decay is linear, this is a piecewise linear response function.

4.4 In lab2.pdf report the spiking threshold you chose. Why did you choose this threshold?

As the weights are currently untrained, they range between 0 and 1 and are random. As a result, the threshold for a single neuron to fire is 2.5. This threshold was set high enough to limit the number of spikes coming out of the output layer and was set low enough so there would generally be at least one spike per image.

I set a parameter for the decay rate of the neuron sum with each time step to be 0.5. Since I limited the k value to 3, hitting the 2.5 threshold generally would require at least 2 consecutive timesteps. They needed to be consecutive otherwise the decay would lower the neuron_sums enough that they wouldn't reach the threshold.