Nonlinear Dynamic project: Fast-Slow analysis on Neuronal Models

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1 Introduction

We have seen a system with two time scales in Van der Pol equation with relaxation oscillations when the control parameter is big, whereas the weakly nonlinear oscillators exist for a small parameter value. The same phenomena can be found in other places such as a robot manipulator powered by the electric can have slower mechanical dynamics and faster electrical dynamics. In neuronscience, many neuronal models contain a fast and a slow variables but not always proceed to a periodic spiking activity, so no oscillations exhibit. In this paper, I aim to show an example of such neuronal model, and use the separation of time scales technique to analyze the firing responses to the system.

2 Fast-slow analaysis

Consider the autonomous system of ODEs

$$\begin{aligned} \frac{du}{dt} &= F(u, x) \\ \epsilon \frac{dx}{dt} &= G(u, x) \end{aligned} \tag{1}$$

where u is the slow variable, and the x is the fast variable. One can perform separation of timescales to understand fixed points and their stabilities.

2.1 fast variable equation:

On the fast timescale, treat $u = u_0$ as a fixed constant since it becomes infinitely slow on this timescale, so $x(t)$ approximately obeys

$$\epsilon \frac{dx}{dt} = G(u_0, x) \tag{2}$$

On this timescale, the equation is accurate on time intervals $[t_0, t_0 + \delta]$ for δ sufficiently small. Assume that there is a unique stable fixed point, $x_0 = H(u_0)$, where $H(u_0)$ provides some expression with respect to u, for each value of u_0 in Eq.(1). Specifically, assume

$$G(u_0, H(u_0)) = 0$$

From stability, we need the Jacobian of Eq.(1) at $x_0 = H(u_0)$ has eigenvalues with negative real part. Also if assuming that this fixed point is globally attracting, the point $x = H(u)$ is called the quasi-steady state for x at u because it is the steady-state solution on the fast timescale, but not on the slow timescale since u changes on the slow timescale.

2.2 slow variable equation:

To solve this system, we first let $\epsilon \to 0$, then the second equation approaches its fixed point quickly. So, on the slow timescale, we have

$$\frac{du}{dt} = F(u(t), x(t)) \tag{3}$$

and

$$x(t) = H(u(t))$$

Specifically, these equations become accurate after a short transient while we wait for $x(t)$ to approach its quasi-steady state on the fast timescale.

Note that $x(t)$ is a dynamical system (i.e., its evolution in time only depends on its current value, i.e., $x(t + dt)$ only depends on $x(t)$ for any dt). Therefore it also satisfies an ODE, at least locally. This ODE can be written as

$$\frac{dx}{dt} = \frac{dx}{du}\frac{du}{dt} = \frac{dH(u)}{du}F(u, H(u))$$

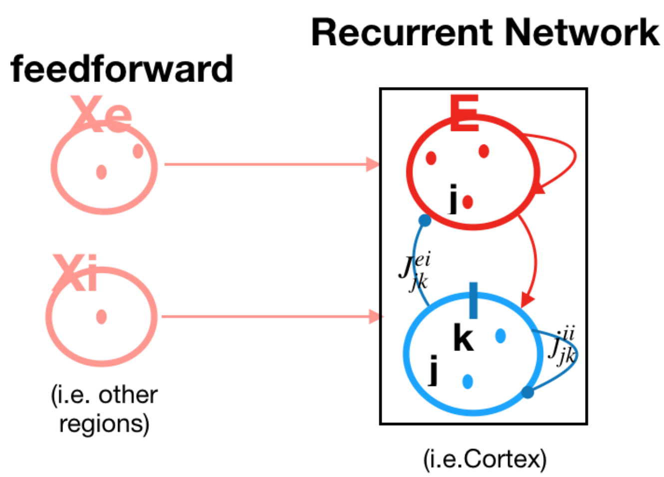
According to Wikipedia provided by a theorem from Tikhonov: as $\epsilon \to 0$, if we are given correct conditions to the system, the solution follows:

$$\begin{cases} \dot{u} = F(u, x) \\ G(u, x) = 0 \\ u(0) = u_0 \end{cases}$$

3 A recurrent neuronal model on Balanced Network

Now if we want to mimic the spiking behaviours of neurons in the cortical region that stimulated by other regions, we can consider a recurrent neuronal network of size N with constant feedforward input X. The network contains two sub-populations, one for excitatory and the other is inhibitory, where $a = e, i$ and $b = e, i, x$. Biologically, neurons communicate with each other through synapse. Hence we can model a neuron j in postsynaptic population a with connectivity strength J_{jk}^{ab} from its neighbouring neourn k from presynaptic population b. Notice that k can come from three sources, namely $b = e, i$ and x. The connectivity matrix J follows a blockwise Erdos-Renyi network

$$J_{jk}^{ab} = \frac{1}{\sqrt{N}} \begin{cases} j_{ab}. & \text{with prob. } p_{ab} \\ 0 \end{cases}$$



Experiment has shown that "neurons fire together wire together"(Bi &Pool, 1998), meaning that the synapse connection is not static, it changes along with the fast changing firing activities within a region, and it tries to adapt/learn the new environment. We call this synaptic plasticity, and biologically, the changes are very slow.

If we are interested in how the slow changing synapses from inhibitory sub-population to other sub-populations involved with the rapid changing firing rate, we can apply the separation of time-scale analysis as before:

$$\frac{dW^{ai}}{dt} = F(r, W) = -\eta_a (r^a - \rho_a)(r^i)^T \odot W^{ai}$$
$$\epsilon \frac{dr^a}{dt} = G(r, W) = -r^a + f(I)$$

where $0 < \epsilon \ll 1$, η_a is the learning rate/timesclae for the synaptic weights to adapt an environment of the network, $r = [r^e, r^i]^T$, and I is the input synaptic current such that $I = Wr + X$. f is a non-decreasing function such as $f = 0$ if $I < 0$ and increases might or might not reach to a threshold like a sigmoid function or a hyperbolic tanh for $I > 0$. Notice that f captures the relationship between input current and firing rates, and it depends on the different type of the states(i.e. balanced or semi-balanced). The analysis is performed in the $\epsilon \to 0$ limit. Empirically, we know that this will work because rates get close to their fixed point within around 100ms, but weights take more like 10s to reach their fixed point. Individual elements of r are $\mathcal{O}(1)$, whereas the individual elements of J scale like $\mathcal{O}(1/\sqrt{N})$, here we see a drastic time scale difference in the system. In the end, we reach the conclusion that, at the slow timescale, weights evolve according to

$$\frac{dW}{dt} = F(r_0(W), W)$$

where $r_0(W)$ is a function of W that satisfies $F(r_0(W), W) = 0$. In addition, we would conclude that $r(t) \approx r_0(W)$ for all t after a short transient to overcome initial conditions.

In balanced network, currents from excitatory and inhibitory almost cancel each other and give arise to a total input staying at $\mathcal{O}(1)$. $I = \sqrt{N}[Wr + X]$, where $W^{ab}_{jk} = j_{ab} p_{ab} \frac{N_b}{N}$. Hence, for the network to "balanced" after taking $N \to \infty$, we have $r \approx -W^{-1}X$ from cancellation. Here demonstrate a 2D system with a 2×2 connectivity matrix W and its entry $W^{ab}_{jk} = w_{ab}$. Then the firing rates follow:

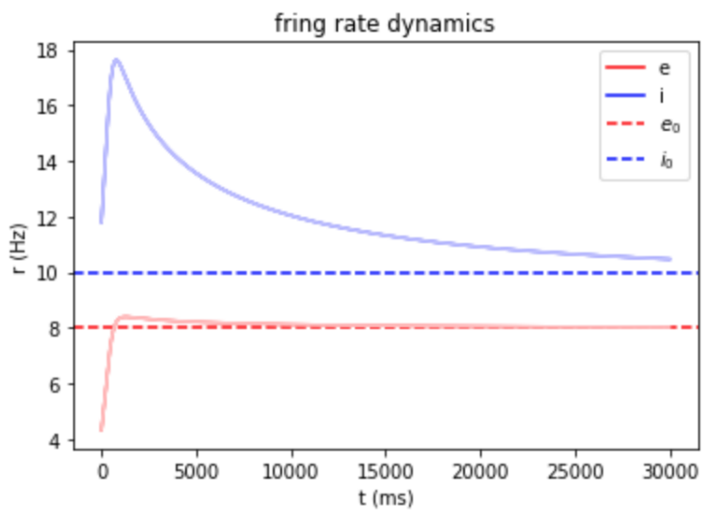
$$r = \frac{1}{\Delta(W)} \begin{bmatrix} w_{ii}X_e - w_{ei}X_i \\ -w_{ie}X_e + w_{ee}X_i \end{bmatrix}$$

Note that the firing rate for realistic reasons must be positive, so we have $r^e_0 = \frac{w_{ii}X_e - w_{ei}X_i}{-\Delta(W)} > 0$ and $r^i_0 = \frac{-w_{ie}X_e + w_{ee}X_i}{-\Delta(W)} > 0$. As the external inputs typically are excitatory neurons, so $X_a > 0$. Furthermore, by letting the network size grows very large, the stability analysis on the fast rate equations would have the Jacobian scaled like $\mathcal{O}(\sqrt{N}) - \mathcal{O}(1)$, which implies

$w_{ee}w_{ii} - w_{ie}w_{ei} > 0$. Hence, putting all together for realistic stable firing rate equations, we impose a condition $\frac{X_e}{X_i} > \frac{w_{ei}}{w_{ii}} > \frac{w_{ee}}{w_{ie}}$.

Now wee solve the ODE of $\frac{dr}{dt}$ and see how it involves with synaptic weight dynamics:

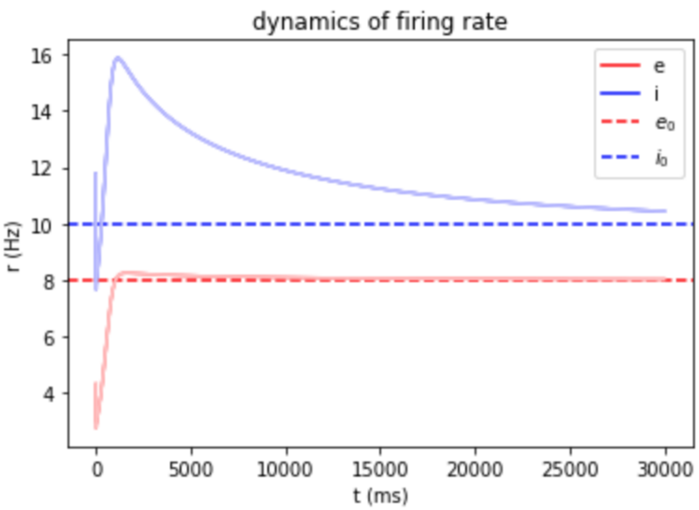
$$
\begin{aligned}
\frac{dr_e}{dt} &= \frac{dr_e}{dw_{ei}}\frac{dw_{ei}}{dt} + \frac{dr_e}{dw_{ii}}\frac{dw_{ii}}{dt} \\
&= \frac{r_i^2}{w_{ee}X_i - w_{ie}X_e}\Big((r_e w_{ie} + X_i)\eta_e(r_e - \rho_e^0) - (r_e w_{ee} + X_e)\eta_i(r_i - \rho_i^0)\Big) \\
\frac{dr_i}{dt} &= \frac{dr_i}{dw_{ei}}\frac{dw_{ei}}{dt} + \frac{dr_i}{dw_{ii}}\frac{dw_{ii}}{dt} \\
&= \frac{r_i^3}{w_{ee}X_i - w_{ie}X_e}\Big(w_{ie}\eta_e(r_e - \rho_e^0) - w_{ee}\eta_i(r_i - \rho_i^0)\Big)
\end{aligned}
$$



The numerical simulation on the recurrent neuronal network of size $N = 5000$ contains an $80 - 20\%$ splits for the excitatory and inhibitory subpopulations. The firing rate above takes the learning rate $\eta_e = 10 \times N_e$, and $\eta_i = 5 \times N_i$. To generate the initial connectivity matrix W_0, we used probability $p_{ab} = 0.05$, and connectivity strength $w_{ee} = 50, w_{ei} = -350, w_{ei} = 225$, and $w_{ii} = -500$. The constant feedforward input is $X_e = .4 * \sqrt{N}$, and $X_i = .3 * \sqrt{N}$. These parameters are chosen to satisfied the stability as we described above $\frac{X_e}{X_i} > \frac{w_{ei}}{w_{ii}} > \frac{w_{ee}}{w_{ie}}$. Target rates are $\rho_e = 0.008$ and $\rho_i = 0.01$ as the fact that neurons in cortical areas fire around $10Hz$, but the inhibitory neurons fire more frequently than the excitatory neurons.

4 Results and Discussion

We see that both excitatory and inhibitory firing rates approach to their target rates within $10 \sim 30 sec$. At the early iterations, both excitatory and inhibitory neurons appear at a high frequency, then gradually cool down to the target rates and stabilized there as the inhibitory synaptic weight learned to adapt the new environment. To check the result, we can compared it with the original firing rate dynamics $\frac{dr}{dt} = -r + f(I)$, using a rectified linear $f = g_a[I]^+$, where $g_a = 0.002$ from a spiking network simulation.



The plot also showed a similar result with the fast-slow analysis that the firing rates approach to their targets along with the updates of inhibitory synaptic weights. Since the scale of W^{ai} depends on N_a, the effective timescale of the dynamics will hence depend on N_a. One direction that can go beyond is through coarsening, we can subdivide each excitatory and inhibitory into M_a groups of size m_a, and investigate on the firing rate results, I would expect to have a similar firing rate dynamics.

5 Reference

1. Eugene M. Izhikevich.Dynamical Systems in Neuroscience.The MIT Press. (2010).
2. Single Pertubation, `https://en.wikipedia.org/wiki/Singular_perturbation`, note = Accessed: 2020-04-30