Theoretical Foundations of Wave Generation

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1 RNN with constant conduction delay

1.1 Literature review - Senk_arxiv_2018

This paper provided mathematical proof of the existence of traveling wave in a recurrently connected neural network with **constant delay.** In addition, it also proved the equivalence of rate neural network and spiking neural network around equilibrium.

1.1.1 General setup

$$\tau \frac{du(x,t)}{dt} + u(x,t) = \int_{-\infty}^{\infty} P(x-y)\psi(u(y,t-d))dy \tag{1}$$

where u is the firing rate of neuron located at x at time equals to t; τ is the membrane constant; P is the connection strength; ψ is the non-linear activation function, here $\psi(x) = \tanh(x)$; d is a constant delay. The equilibrium state u_0 (stationary across time and space) is given by $u_0 = \kappa\psi(u_0)$ where $\kappa = \int_{-\infty}^{\infty} P(x-y)dy$. $u_0 = 0$ is certainly an equilibrium state under tanh function.
We could linearize around the equilibrium state u_0 and denote a new $u = u - u_0$. Then we could get a linear ODE with respect to the new u: Given tanh function and $u_0 = 0$, then $\psi'(u_0) = 1$.

$$\tau \frac{du(x,t)}{dt} + u(x,t) = \int_{-\infty}^{\infty} P(x-y)\psi'(u_0)u(y,t-d)dy \tag{2}$$

During the following derivations, there are some important assumptions which don't apply to the hippocampal anatomy:

- Isotropic and symmetric connectivity, i.e. connection strength is proportional to the difference of neuron's location $P(r) = wp(r)$ **where $p(r)$ is a probability density function**. and $P(r) = P(-r)$.
- **Neurons are aligned on a ring-like structure.**
- Conduction delay is constant.

1.1.2 Side Note: One-dimensional wave equation and solutions

One-dimensional wave dynamics $u(x,t)$ is given by a simple partial derivative equation. One way to solve it is to utilize the eigenmode in frequency $u_w(x,t) = e^{-iwt}f(x)$ and the full solution is the superposition of all eigenmodes.

$$\begin{aligned}
\frac{\partial^2 u}{\partial t^2} &= c^2 \frac{\partial^2 u}{\partial x^2} \\
\text{Plug in eigenmode: } \frac{d^2}{dx^2} f(x) &= -(\frac{w}{c})^2 f(x) \\
f(x) &= Ae^{\pm ikx}, \quad k = \frac{w}{c} \\
u_w(x,t) &= e^{-iwt}(Ae^{-ikx} + Be^{ikx})
\end{aligned} \tag{3}$$

After solving for the eigenmodes in frequency, the full wave equation could be expressed as follows. Therefore, the spatial frequency of wave, represented by wave number k is essentially determined by the wave equation coefficient c and temporal frequency w.

$$\begin{aligned}
u(x,t) &= \int s(w) u_w(x,t) dw \\
&= \int s_+(w) e^{-i(kx+wt)} dw + \int s_-(w) e^{i(kx-wt)} dw
\end{aligned} \tag{4}$$

Note that the wave equation doesn't give a unique solution, which is usually obtained by a given initial conditions and boundary conditions

1.1.3 One uniform population

According to the eigenmode of the full wave equation (refer to Turing instability analysis and wave equations for details), plug $u(x,t) = e^{ikx}e^{\lambda t}, \lambda = \lambda(k)$ into Equation 2. Then we could try to solve the following equation for λ, which determines the growth mode in time domain: Notice that $\hat{p}(0) = 1$ given that $p(r)$ is a probability density function.

$$\begin{aligned}
(\tau\lambda + 1)e^{\lambda d} &= \int_{-\infty}^{\infty} P(x-y) e^{-ik(x-y)} dy \\
&= \int_{-\infty}^{\infty} P(r) e^{-ikr} dr \quad \text{(isotropic and symmetric connection)} \\
&= \hat{P}(k) = w\hat{p}(k)
\end{aligned} \tag{5}$$

We could solve for λ using the properties of Lambert W function.

1.1.4 Two population (excitatory and inhibitory neurons)

Denote $\mathbf{u} = [u_E, u_I]^T = \mathbf{v}e^{ikx}e^{\lambda t}$ and plug into Equation 2. Note that $\tilde{P}(k)$ is a block matrix, which is separated by inhibitory connections and excitatory connections while $\hat{P}(k)$ is a scalar. We could treat $\hat{P}(k)$ as effective connection profile because $\hat{P}(k) = (\tau\lambda + 1)e^{\lambda d}$.

$$\begin{aligned}
\mathbf{v}(\tau\lambda + 1)e^{\lambda d} &= (\int_{-\infty}^{\infty} P(x-y) e^{-ik(x-y)} dy)\mathbf{v} \\
\hat{P}(k)\mathbf{v} &= \tilde{P}(k)\mathbf{v}
\end{aligned} \tag{6}$$

Next we will derive the effective connection profile in this case. To get a non-trivial solution of $\mathbf{v}$, we want $\det(\tilde{P}(k) - \hat{P}(k)) = 0$. Solving this equation for $\hat{P}(k)$, we could express it in terms of the elements of $\tilde{P}(k)$. If we reduce the connectivity matrix such that the connection strength only depends on the pre-synaptic neural type and neural distance. Then we could get the following matrix:

$$P(r) = \begin{bmatrix} w_E p_E(r) & w_I p_I(r) \\ w_E p_E(r) & w_I p_I(r) \end{bmatrix} \tag{7}$$

Then the expression of $\hat{P}(k)$ also reduced to $\hat{P}(k) = w_E \hat{p_E}(k) + w_I \hat{p_I}(k)$.

1.1.5 Linear stability analysis

The stability of the linearized system could be determined by solving λ from $(\tau\lambda + 1)e^{\lambda d} = \hat{P}(k)$. The equation could be solved using Lambert W function (the inverse function to $f(x) = xe^x$). To be more specific, multiply both sides by $\frac{d}{\tau}e^{\frac{d}{\tau}}$ and we get the following equation:

$$
\begin{aligned}
\frac{d}{\tau}(1+\tau\lambda)e^{\frac{d}{\tau}(1+\tau\lambda)} &= \hat{P}(k)e^{\frac{d}{\tau}}\frac{d}{\tau} \\
\lambda_b(k) &= -\frac{1}{\tau} + \frac{1}{d}W_b(\hat{P}(k)\frac{d}{\tau}e^{\frac{d}{\tau}}) \\
\mathrm{Re}[W_b(\hat{P}(k)\frac{d}{\tau}e^{\frac{d}{\tau}})] &< \frac{d}{\tau}, \quad \text{if locally stable}
\end{aligned} \tag{8}
$$

where W_b is a branch of Lambert W function and it has infinite number of branches. Thus, λ has infinite number of solutions.

The steady state of the system is locally stable if all λ (i.e. λ calculated from all branches of Lambert W function) has a negative real part. Side note: Lambert W function has its largest real part on principle branch if it is defined on $(-\infty, \infty)$. Typically, the principle branch of Lambert W function refers to the real branch defined on the interval $[-e^{-1}, \infty)$. Here we extend the definition to the whole real line by the complex branch with maximal real part and positive imaginary part on $(-\infty, -e^{-1}]$. Under this definition, we could only consider the λs (denoted as λ_0) on the principle branch of Lambert W function.

Then, we want to find out when $\mathrm{Re}(\lambda)$ becomes positive and the corresponding k^* during the transition. Let's denote the maximum value of $\hat{P}(k)$ as $\hat{P}_{max}$ and achieved at $k = k_{max}$, similarly, the minimum value of $\hat{P}(k)$ as $\hat{P}_{min}$ and achieved at $k = k_{min}$. We could list the situations as follows:

- For the principle branch defined on $[-e^{-1}, \infty)$, λ_0 always has real solution. The transition point happens when $\hat{P}_{max} = 1$, then by definition, we could have $\lambda_0 = 0$ and the system becomes destabilized from current steady state. If the transition happens at $k^* = 0$, the population activity is collectively destabilized and if $k^* > 0$, the activity shows spatial oscillations that grow exponentially in time.

- For the negative argument of the principle branch defined on $(-\infty, -e^{-1}]$, λ_0 comes with complex conjugate pairs. The transition (i.e. Hopf bifurcation) $\mathrm{Re}[W_b(\hat{P}(k)\frac{d}{\tau}e^{\frac{d}{\tau}})] = \frac{d}{\tau}$ could be achieved if $\hat{P}_{min} < -1$. The analytical expression of the transition point is:

$$
\frac{d^{crit}}{\tau} = \frac{\pi - \arctan(\sqrt{\hat{P}_{min}^{crit^2} - 1})}{\sqrt{\hat{P}_{min}^{crit^2} - 1}} \tag{9}
$$

  If the transition occurs at $k^* = 0$, temporal oscillations arise and if the transition occurs at $k^* > 0$, periodic traveling waves arise.

- **Questions remained:** in the real simulation, what determines the wave number k in the simulation. Does oscillation only appear at Hopf bifurcation (it seems that as long as $d > d^{crit}$, we could have oscillations/waves in this paper, Fig 3E/F). Possible answer: the wave number k depends on the dynamics of the system (Check Wikipedia on 'wave equation' for details). Initial conditions and boundry effects only affect amplitude and phases. Oscillation only appears at Hopf bifurcation, but since $\hat{P^{crit}}$ depends on k, the parameter plot for traveling wave is a region instead of a single line.

1.1.6 Conditions for traveling wave

In general, we want the Hopf bifurcation ($\mathrm{Re}(\lambda) = 0$, $\mathrm{Im}(\lambda) \neq 0$) occurs at $k \neq 0$. (Wave equations have a family of solutions with continuous speed, i.e. continuous k)

If we denote the maximum value of $\hat{P}(k)$ as $\hat{P}_{max}$ and achieved at $k = k_{max}$, similarly, the minimum value of $\hat{P}(k)$ as $\hat{P}_{min}$ and achieved at $k = k_{min}$. Then the specific condition for traveling wave in this scenario is that:

$$\begin{aligned} \hat{P}_{max} &< 1 \\ \hat{P}_{min} &= \hat{P}_{min}^{crit} \\ d &= d^{crit} \\ k_{min} &> 0 \end{aligned} \tag{10}$$

The critical solutions are solved under $\mathrm{Re}(\lambda) = 0$ and the negative argument of Lambert W function ($\hat{P}_{min} < -1$). The analytical solution is: Note that the critical solution is closely related to τ.

$$\frac{d^{crit}}{\tau} = \frac{\pi - \arctan(\sqrt{\hat{P}_{min}^{crit^2} - 1})}{\sqrt{\hat{P}_{min}^{crit^2} - 1}} \tag{11}$$

1.1.7 Example: Two population with Boxcar connection

The connection probability density for both excitatory and inhibitory could be expressed as: where r is the physical distance between two neurons.

$$\begin{aligned} p_E(r) &= \frac{1}{2R_E}\Theta(R_E - r) \\ p_I(r) &= \frac{1}{2R_I}\Theta(R_I - r) \end{aligned} \tag{12}$$

Then the effective connectivity profile is:

$$\begin{aligned} \hat{P}(k) &= w_E \frac{\sin(R_E k)}{R_E k} + w_I \frac{\sin(R_I k)}{R_I k} \\ \hat{B}(k) &= \frac{\sin(\kappa)}{\kappa} - \eta \frac{\sin(\rho\kappa)}{\rho\kappa} \quad (\rho = \frac{R_I}{R_E}, \eta = -\frac{w_I}{w_E}, \kappa = R_E k) \end{aligned} \tag{13}$$

1.1.8 Discretization and Simulation

A network of $N_E = 4000$ and $N_I = 1000$ rate neurons was simulated. The model neurons within each population are equally spaced on a ring of perimeter $L = 1mm$. The connection matrix was given by Equation 7 and 12. The discretized version of neural dynamics was given by:

$$\begin{aligned} \tau \frac{du_i}{dt} &= -u_i + \sum_j w_{ij}\psi(u_j(t-d)), \quad \psi(x) = \tanh(x) \\ w_{ij} &= \begin{bmatrix} w'_E p_E(r) & w'_I p_I(r) \\ w'_E p_E(r) & w'_I p_I(r) \end{bmatrix} \end{aligned} \tag{14}$$

During the simulation, we assume each neuron has a fixed in-degree (fixed number of incoming connections) K_E and K_I per source population. This is similar to balance the synaptic input from each source population. So the coefficients of weights are normalized by the in-degree: $w' = w/K$. There are three steady states associated with equation: $u_0 = \sum_j w_j \psi(u_0)$. I think the instability happens near $u_0 = 0$ since $\psi'(0) = 1$. Then the key of simulation is to keep the dynamics locally and away from the other two steady states.