Assignment 3
Theoretical Neuroscience

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1. **Stability of equilibria**

   Consider Wilson-Cowan equations of the form

$$\tau \dot{\nu}_E = \phi_E(\nu_E, \nu_I) - \nu_E \tag{1a}$$
$$\tau \dot{\nu}_I = \phi_I(\nu_I, \nu_E) - \nu_I \tag{1b}$$

   where the gain functions, ϕ_E and ϕ_I, are increasing functions of ν_E and decreasing functions of ν_I (e.g, $\phi_E(\nu_E, \nu_I) \sim 1 + \tanh(W_{EE}\nu_E - W_{EI}\nu_I + \theta_E)$).

   Nullclines for Eq. (1) are sketched in the figure below. Show that equilibria A and C are stable, B is unstable, and D may or may not be stable. Give conditions for the stability of equilibrium D in terms of the derivatives of the gain functions evaluated at the equilibrium.

   Hint: This problem is relatively hard, in the sense that it requires a somewhat deep understanding of nullclines and their construction, and also strong familiarity with linear stability analysis in two dimensions. On the other hand, the answer doesn't require a huge amount of algebra – only a few lines. The main insight you need is that you can compute the slopes of the nullclines in terms of derivatives of the gain functions. Once you do that, the rest should be easy (ish).

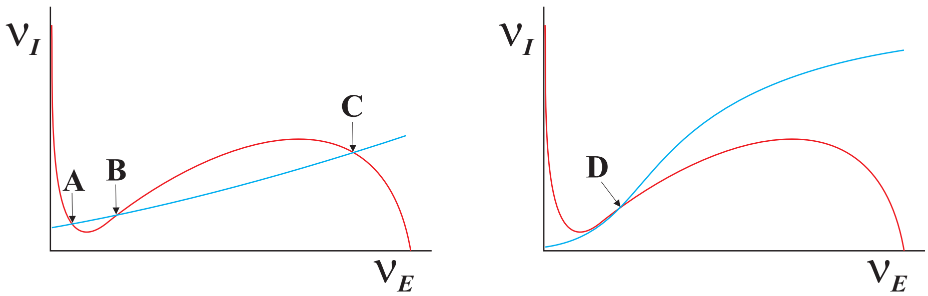

Figure 1: Two possible sets of nullclines. In both figures, the red curve is the excitatory nullcline and the blue curve is the inhibitory one.

2. **Adaptation**

Consider a network of N analog neurons that obey the time-evolution equations

$$\tau \frac{dx_i}{dt} = \phi\left(\sum_{j=1}^{N} W_j x_j - \theta_i\right) - x_i\,. \tag{2}$$

(a) Assume that $\theta_i = \theta\ \forall i$. Show that Eq. (2) can be effectively reduced to a one-variable model,

$$\tau \frac{dz}{dt} = \phi\left(Jz - \theta\right) - z\,. \tag{3}$$

Write down expressions for z in terms of the W_i and x_i and J in terms of the W_i.

(b) Let's go back to Eq. (2), where θ_i depends on i. Show that Eq. (2) can still be reduced to a one-variable model,

$$\tau \frac{dz}{dt} = \tilde{\phi}\left(Jz\right) - z \tag{4}$$

where J is the same as in part (a). Write down an expressions for $\tilde{\phi}(\cdot)$ in terms of $\phi(\cdot)$ and W_i and θ_i.

(c) Assume that both W_i and θ_i are correlated random variables with joint distribution $p(W, \theta)$. Assuming $N \to \infty$, write down an expression for $\tilde{\phi}(Jz)$ as an integral over this joint distribution.

(d) Let's go back to the case in which $\theta_i = \theta$, so that z evolves according to Eq. (3). Let $\phi(y) = \tanh(y)$ (which isn't realistic because it allows negative firing rates, but it makes the analysis easier). To model spike frequency adaptation, let θ evolve according to

$$\tau_0 \dot{\theta} = -(\theta - \theta_0 z)\,, \tag{5}$$

with $\tau_0 \gg \tau$. Assume that $\theta_0 > J - 1 > 0$. Sketch the nullclines.

(e) Show that the system exhibits bursting, and sketch $z(t)$ and $\theta(t)$ versus time. Here "bursting" just means a limit cycle in θ-z space. We call it bursting because $\tau_0 \gg \tau$, so z spends most of its time changing slowly, with only brief periods during which it changes very rapidly from positive to negative or back.

3. **Why we can ignore temporal correlations**

We're going to consider a randomly connected network of excitatory and inhibitory neurons with current-based synapses and linear integrate-and-fire (aka LIF) neurons,

$$\tau \frac{dV_{E,i}}{dt} = -(V_{E,i} - V_{\text{rest}}) + \frac{1}{\sqrt{n}} \sum_{j=1}^{n} W_{EE,ij}\, g_{E,j}(t) - \frac{1}{\sqrt{n}} \sum_{j=1}^{n} W_{EI,ij}\, g_{I,j}(t) + \sqrt{n} h_E \tag{6a}$$

$$\tau \frac{dV_{I,i}}{dt} = -(V_{I,i} - V_{\text{rest}}) + \frac{1}{\sqrt{n}} \sum_{j=1}^{n} W_{IE,ij}\, g_{E,j}(t) - \frac{1}{\sqrt{n}} \sum_{j=1}^{n} W_{II,ij}\, g_{I,j}(t) + \sqrt{n} h_I\,. \tag{6b}$$

If a neuron exceeds threshold, it spikes and is reset to V_{rest}. This is a bit unrealistic: connectivity is all-all, and the number of excitatory and inhibitory neurons are the same. But making it more realistic would only complicate the analysis without adding any insight.

As usual, $g_{E,j}(t)$ and $g_{I,j}(t)$ are the conductance changes due to presynaptic spikes,

$$g_{E,j}(t) = \sum_k g(t - t_{E,j}^k) \tag{7a}$$

$$g_{I,j}(t) = \sum_k g(t - t_{I,j}^k) \tag{7b}$$

where $t_{E,j}^k$ is the time of the k^{th} spike on excitatory neuron j, and similarly for $t_{I,j}^k$. We'll choose $g(t)$ so that it integrates to 1,

$$\int_0^\infty dt\, g(t) = 1 \tag{8}$$

with $g(t)$ non-negative. And, of course, $g(t < 0) = 0$.

We can perform the usual manipulations,

$$\begin{aligned} \frac{1}{\sqrt{n}} \sum_{j=1}^n W_{EE,ij} g_{E,j}(t) &= \sqrt{n}\, W_{EE} \nu_E + \frac{1}{\sqrt{n}} \sum_j \delta W_{EE,ij} \nu_{E,j} \\ &\quad + \sqrt{n}\, W_{EE} G_E(t) + \frac{1}{\sqrt{n}} \sum_j \delta W_{EE,ij} \delta g_{E,j}(t) \end{aligned} \tag{9}$$

where most quantities have obvious definitions,

$$W_{EE} = \frac{1}{n^2} \sum_{ij} W_{EE,ij} \tag{10a}$$

$$\delta W_{EE,ij} = W_{EE,ij} - W_{EE} \tag{10b}$$

$$\nu_{E,j} = \langle g_{E,j}(t) \rangle_t \tag{10c}$$

$$\nu_E = \frac{1}{n} \sum_j \nu_{E,j} \tag{10d}$$

$$\delta g_{E,j}(t) = g_{E,j}(t) - \nu_{E,j} \tag{10e}$$

$$G_E(t) = \frac{1}{n} \sum_j \delta g_{E,j}(t)\,, \tag{10f}$$

and similarly for the inhibitory neurons. Inserting this into Eq. (6a) gives us

$$\begin{aligned} \tau \frac{dV_{E,i}}{dt} &= -(V_{E,i} - V_{\text{rest}}) + \sqrt{n} \left[W_{EE} \nu_E - W_{EI} \nu_I + h_E \right] \\ &\quad + \sqrt{n} \left[W_{EE} G_E(t) - W_{EI} G_I(t) \right] \\ &\quad + \frac{1}{\sqrt{n}} \sum_{j=1}^n \delta W_{EE,ij} \nu_{E,j}(t) - \frac{1}{\sqrt{n}} \sum_{j=1}^n \delta W_{EI,ij} \nu_{I,j}(t) \\ &\quad + \frac{1}{\sqrt{n}} \sum_{j=1}^n \delta W_{EE,ij} \delta g_{E,j}(t) - \frac{1}{\sqrt{n}} \sum_{j=1}^n \delta W_{EI,ij} \delta g_{I,j}(t)\,. \end{aligned} \tag{11}$$

Assume, as usual, that $n \gg 1$. Then, the first term on the right hand side of Eq. (11) fixes the mean firing rates, to within $\mathcal{O}(1/\sqrt{n})$. The second term ensures that the average temporal fluctuations are $\mathcal{O}(1/\sqrt{n})$. It's this term that reduces correlations among neurons – or at least correlations among the whole population. There can, of course, be instabilities that lead to oscillations, in which case neurons do become highly correlated. But there are also regimes where oscillations are small.

(a) Finally, the actual homework problem. Define

$$\delta G_{E,i}(t) \equiv \frac{1}{\sqrt{n}} \sum_{j=1}^{n} \delta W_{EE,ij} \delta g_{E,j}(t)\,, \tag{12}$$

and similarly for $\delta G_{E,i}(t)$. Assume the weights are random – the elements are draws *iid* from some distribution. Show that, in the large n limit,

$$\langle \delta G_{E,i}(t) \delta G_{E,i'}(t-\tau) \rangle_t = \delta_{ii'} C(\tau) \text{Var}[W_{EE,ij}] \tag{13a}$$

$$\langle \delta G_{E,i}(t) \delta G_{I,i'}(t-\tau) \rangle_t = 0 \tag{13b}$$

where

$$C_E(\tau) \equiv \frac{1}{n} \sum_j \langle \delta g_{E,j}(t) g_{E,j}(t-\tau) \rangle_t\,. \tag{14}$$

Thus, in the large n limit, we get to ignore temporal correlations among neurons! What's even better is that all excitatory neurons have the same temporal correlational structure, as do all inhibitory neurons. Of course, that correlational structure has to be found self-consistently, which is nontrivial. But it's nice to know that it exists.

4. **Adding a little rigor to tacky math**

Consider an all-inhibitory network of N neurons for which the firing rate of neuron i, denoted ν_i, is given by

$$\nu_i = \phi\left(\sqrt{N} h_0 - \frac{1}{\sqrt{N}} \sum_j w_{ij} \nu_j\right)\,. \tag{15}$$

The gain function, ϕ, is sigmoidal, the external input, h_0, is positive, and the weights are non-negative, independent and identically distributed, and their mean and variance is give by $\overline{w}$ and σ_w^2, respectively. As usual, we write $w_{ij} = \overline{w} + \delta w_{ij}$, so that

$$\frac{1}{\sqrt{N}} \sum_j w_{ij} \nu_j = \sqrt{N}\, \overline{w}\, \overline{\nu} + \frac{1}{\sqrt{N}} \sum_j \delta w_{ij} \nu_j \tag{16}$$

where

$$\overline{\nu} \equiv \frac{1}{N} \sum_j \nu_j\,. \tag{17}$$

(a) Show that in the large N limit

$$\sigma^2 \equiv \sum_i \frac{1}{N} \left(\frac{1}{\sqrt{N}} \sum_j \delta w_{ij} \nu_j\right)^2 = \overline{\nu^2} \sigma_w^2 \tag{18}$$

where

$$\overline{\nu^2} \equiv \frac{1}{N} \sum_j \nu_j^2 \tag{19}$$

and corrections are $\mathcal{O}(1/\sqrt{N})$.

(b) We can now write the following equation for ν_i,

$$\nu_i = \phi\left(\sqrt{N}(h_0 - \overline{w}\,\overline{\nu}) + \sigma\xi_i\right) \tag{20}$$

where

$$\xi_i \equiv \frac{1}{\sqrt{\sigma N}} \sum_j \delta w_{ij} \nu_j \,. \tag{21}$$

In the large N limit, $\sum_i \xi_i^2/N = 1$, but that tells us nothing about its distribution. What we want to argue is that ξ_i is a Gaussian random variable. For that we need δw_{ij} and ν_j to be weakly correlated. To check if that's true, compute the empirical covariance (squared), denoted ρ_i^2,

$$\rho_i^2 = \frac{\left(\sum_j \delta w_{ij} \nu_j\right)^2}{\left(\sum_j w_{ij}^2\right)\left(\sum_j \nu_j^2\right)} \,. \tag{22}$$

Show that on average

$$\frac{1}{N} \sum_i \rho_i^2 \sim \mathcal{O}\left(\frac{1}{\sqrt{N}}\right) \,. \tag{23}$$

If we were mathematicians, this wouldn't mean much. But as physicists, we'll declare this to be sufficiently weakly correlated that we can treat ξ_i as a zero mean, unit variance Gaussian random variable.

We now need to show that ν_i and ξ_i are weakly correlated. You can do that using a minor extension of the above analysis.

5. **Low rank networks with time-varying dynamics**

Consider a network of N neurons that evolves according to

$$\frac{dx_i}{dt} = \phi\left(\sum_j W_{ij} x_j + \sum_\mu J_{i\mu} z_\mu + \sum_\mu C_{i\mu} u_\mu(t)\right) - x_i \tag{24}$$

where $u_\mu(t)$ is a control signal, ϕ is the gain function (as usual, it's more or less sigmoidal), and $\mathbf{z}$ is related to $\mathbf{x}$ via

$$z_\mu = \sum_j A_{\mu j} x_j . \tag{25}$$

In this setting the dimensionality of both $\mathbf{z}$ and $\mathbf{u}$ is typically much less than N (which is why this section is titled "Low rank networks"), but that's not necessary for the questions.

(a) Show that z_μ evolves according to

$$\frac{dz_\mu}{dt} = \sum_i A_{\mu i}\phi\left(\sum_j W_{ij}x_j + \sum_\nu J_{i\nu}z_\nu + \sum_\nu C_{i\nu}u_\nu(t)\right) - z_\mu \tag{26}$$

Thus, if $W_{ij} = 0$,

$$\frac{dz_\mu}{dt} = f_\mu\big(\mathbf{z}, \mathbf{u}(t)\big) \tag{27}$$

where the function f_μ is given by a neural network with one hidden layer.

(b) Assume the goal of the network is to produce as output the function $z_\mu^*(t)$. Show that under the learning rule

$$\Delta A_{\mu i} = \eta\big(z_\mu^*(t) - z_\mu(t)\big)x_i(t), \tag{28}$$

the instantaneous error, $\big(z_\mu^*(t) - z_\mu(t)\big)^2$, decreases. Assume that η, the learning rate, is small. Is there any guarantee that the total error, which is the time average of $\big(z_\mu^*(t) - z_\mu(t)\big)^2$, will decrease?

6. **Coupled line attractor**

Consider a coupled network of N neurons whose units evolve according to

$$\frac{dr_i}{dt} = \phi\Big(\sum_j W_{i-j}r_j + h_i\Big) - r_i \tag{29a}$$

$$\tau\frac{dh_i}{dt} = g(t)\sum_j A_{i-j}r_j - h_i. \tag{29b}$$

We'll take W to be symmetric: $W_{i-j} = W_{j-i}$. Assume that when $h_i = 0$, Eq. (29a) has a stable equilibrium given by $f(\theta_i - \theta)$,

$$f(\theta_i - \theta) = \phi\Big(\sum_j W_{i-j}f(\theta_j - \theta)\Big) \tag{30}$$

where the θ_i are equally spaced. Assume that this equation is satisfied for all θ, making it a true line attractor.

(a) In the limit that $g(t)$ is infinitesimally small, show that the position on the line attractor, θ, evolves according to

$$\tau\frac{d^2\theta}{dt^2} + \frac{d\theta}{dt} = g(t)\sum_{ij} v_{0i}^\dagger(\theta)\phi_i' A_{i-j}f(\theta_j - \theta) \tag{31}$$

where

$$\phi_i' \equiv \phi'\Big(\sum_j W_{i-j}f(\theta_j - \theta)\Big), \tag{32}$$

$\mathbf{v}_0^\dagger(\theta)$ is the adjoint eigenvalue of the linearized dynamics whose eigenvalue is 0,

$$\sum_j v_{0j}^\dagger(\theta)\phi_j' W_{j-i} = v_{0i}^\dagger(\theta) \tag{33}$$

and it's normalized so that

$$\sum_i v^\dagger_{0i}(\theta) f'(\theta_i - \theta) = 1. \tag{34}$$

(b) Recall that the adjoint eigenvector is related to $f(\theta_i - \theta)$ via

$$v^\dagger_{0i}(\theta) = \frac{f'(\theta_i - \theta)/\phi'_i(\theta)}{Z} \tag{35}$$

where

$$Z \equiv \sum_i \frac{f'(\theta_i - \theta)^2}{\phi'_i(\theta)} \,. \tag{36}$$

Consequently, θ evolves according to

$$\tau \frac{d^2\theta}{dt^2} + \frac{d\theta}{dt} = \frac{g(t)}{Z} \sum_{ij} f'(\theta_i - \theta) A_{i-j} f(\theta_j - \theta). \tag{37}$$

Show that in the large N limit, Z is independent of θ.

(c) Show that in the large N limit, the right hand side of Eq. (37) becomes independent of θ. Show also that if A_{i-j} is even ($A_{i-j} = A_{j-i}$), the right hand side is zero.

7. **Sparse connectivity**

Consider a network whose equilibrium is given by

$$\nu_i = \phi(h_i) \tag{38a}$$

$$h_i = \frac{1}{\sqrt{k}} \sum_{j=1}^{n} w_{ij} \nu_j \tag{38b}$$

where the weights are given by

$$w_{ij} = \begin{cases} \overline{w} + \xi_{ij} & \text{probability } k/n \\ 0 & \text{probability } 1 - k/n \,, \end{cases} \tag{39}$$

and the ξ_{ij} are independent zero-mean random variables with variance σ^2. The parameter k is the average number of connections/neurons. As usual, we're interested in the empirical mean and variance of h_i with respect to the index i.

Show that, in the large k limit,

$$h_i = \sqrt{k}\,\overline{w} \langle \nu \rangle + \eta_i \tag{40}$$

where η_i is a zero mean random variable with variance (with respect to index i) given by

$$\text{Var}[\eta_i] = \left[\sigma^2 + \overline{w}^2 (1 - k/n)\right] \langle \nu^2 \rangle \,. \tag{41}$$

As usual,

$$\langle \nu^p \rangle = \frac{1}{n} \sum_i \nu_i^p \,. \tag{42}$$

8. **More fun with averages**

Assume w_{ij} are a set independent, zero-mean, random variables with variance σ^2, with both indices running from 1 to n. Assume $n \gg 1$. Define

$$z_i \equiv \frac{1}{\sqrt{n}} \sum_{j=1}^{n} w_{ij} \nu_j \tag{43}$$

where the ν_j are a fixed set of firing rates. Define

$$z \equiv \frac{1}{n} \sum_i z_i \,. \tag{44}$$

We want to compute the variance of z with respect to the index, i (the mean is obviously zero). The variance, denoted σ_z^2, is given by

$$\sigma_z^2 = \frac{1}{n} \left(\frac{1}{\sqrt{n}} \sum_{j=1}^{n} w_{ij} \nu_j \right)^2 \,. \tag{45}$$

As usual, we write this

$$\begin{aligned} \sigma_z^2 &= \frac{1}{n} \sum_{jk} \nu_j \nu_k \frac{1}{n} \sum_i w_{ij} w_{ik} \qquad (46) \\ &= \frac{1}{n} \sum_j \nu_j^2 \frac{1}{n} \sum_i w_{ij}^2 + \frac{1}{n} \sum_{j \neq k} \nu_j \nu_k \frac{1}{n} \sum_i w_{ij} w_{ik} \,. \end{aligned}$$

The first term is easy – in the large n limit it's $\langle \nu^2 \rangle \sigma^2$. In class we claimed that the second term was small. Your job is to verify that. Show that

$$\text{Var} \left[\frac{1}{n} \sum_{j \neq k} \nu_j \nu_k \frac{1}{n} \sum_i w_{ij} w_{ik} \right] \approx \frac{2 \langle \nu^2 \rangle^2 \sigma^4}{n} \,. \tag{47}$$