

# Assignment 9

## Theoretical Neuroscience

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### 1. Stability of equilibria

Consider Wilson-Cowan equations of the form

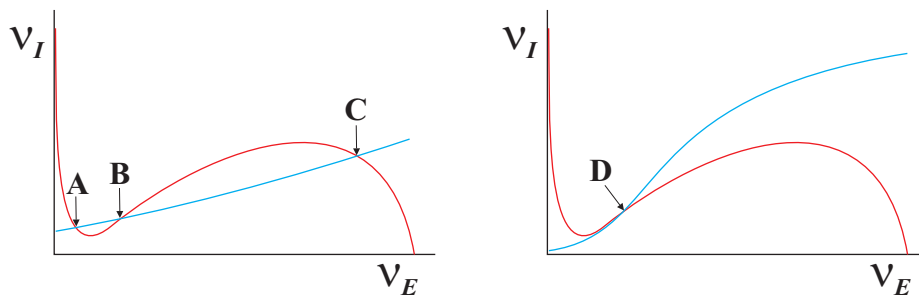
$$\tau \dot{\nu}_E = \phi_E(\nu_E, \nu_I) - \nu_E \quad (1a)$$

$$\tau \dot{\nu}_I = \phi_I(\nu_I, \nu_E) - \nu_I \quad (1b)$$

where the gain functions,  $\phi_E$  and  $\phi_I$ , are increasing functions of  $\nu_E$  and decreasing functions of  $\nu_I$  (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 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

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

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

$$\tau \frac{dz}{dt} = \phi(Jz - \theta) - z. \quad (3)$$

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

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

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

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  $\theta_i$ .

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

e. Let's go back to the case in which  $\theta_i = \theta$ , so that  $z$  evolves according to Eq. (3). Let  $\phi(y) = \tanh(y)$ . To model spike frequency adaptation, let  $\theta$  evolve according to

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

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

f. Show that the system exhibits bursting, and sketch  $z(t)$  and  $\theta(t)$  versus time. Here "bursting" just means a limit cycle in  $\theta$ - $z$  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 quickly from positive to negative or back.

## 3. Averages

Consider the quantity

$$\eta_i = \sum_j W_{ij} \nu_j, \quad (6)$$

with weights given by

$$W_{ij} = \frac{1}{K^{1/2}} \begin{cases} W_0 + w_{ij} & \text{with probability } K/N \\ 0 & \text{with probability } 1 - K/N. \end{cases} \quad (7)$$

Here  $K$  is the average number of connections per neuron and  $N$  is the number of neurons (so  $K < N$ ). Assume that the  $w_{ij}$  are drawn *iid* from a distribution  $p(w)$  with mean 0 and variance  $\sigma_w^2$ ,

$$\int dw w p(w) = 0 \tag{8a}$$

$$\int dw w^2 p(w) = \sigma_w^2. \tag{8b}$$

Treat  $\eta_i$  as a random variable with respect to the index  $i$ . Assuming  $W_{ij}$  and  $\nu_j$  are independent, compute the mean and variance of  $\eta_i$ .