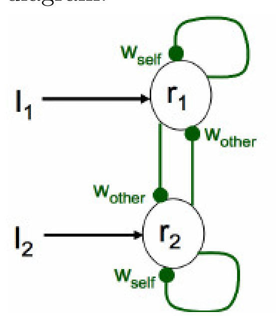
PROBLEM SET 2

METHODS IN COMPUTATIONAL NEUROSCIENCE 2015

1. Model circuit for selective amplification, neural integration, perceptual rivalry, or many other phenomena

Many neural networks, including the oculomotor neural integrator, consist of 2 populations of neurons whose effective connectivity is such that they provide self-excitation to neurons in their own population and inhibit neurons in the opposite population. A simple case of these circuits occurs when the connections are symmetric as in the following diagram:



Here, w_{self} gives the connection between either neuron population and itself and w_{other} gives the connection between the different neuron populations. In this problem, we will quite generally find the eigenvalues and eigenvectors for a circuit with this connectivity, and then apply our findings to several relevant cases.

a. Write down the equations describing this network, assuming the 2 neurons each decay to zero with time constant τ in the absence of input. Write them both as separate equations for dr_1/dt and dr_2/dt and as a single equation written compactly in terms of the firing rate vector $\mathbf{r} = [r_1, r_2]$ and a recurrent connectivity matrix $\mathbf{W}$.

b. Recalling that the eigenvectors of $\mathbf{W}$ are the patterns of inputs with the property that the outputs of the network will be a scaled version of this same pattern, and noting the symmetry of the network, try to *guess* the eigenvectors $\xi^{(1)}$ and $\xi^{(2)}$ of $\mathbf{W}$. (Use the convention that the first element of each eigenvector equals $+1$.) Confirm that you have found the correct direction by showing that $\mathbf{W}\xi = \lambda\xi$ for each eigenvector and give a formula for the corresponding eigenvalues λ_1 and λ_2.

c. Decompose the input vector $\mathbf{I}$ into a combination of the two eigenvectors $\mathbf{I} = b_1\xi^{(1)} + b_2\xi^{(2)}$ you found in part (b). Writing out this equation for each component, you should find that the coefficients b_1 and b_2, respectively, correspond to a part of the input that is common to both cells, I_{common}, and a part I_{diff} that gives the difference of each cell's input from this common value, i.e. that:

$$I_1 = I_{\text{common}} + I_{\text{diff}}$$
$$I_2 = I_{\text{common}} - I_{\text{diff}}$$

This implies that the common (or equivalently average) and difference portions of the input behave independently.

d. *Simple model of selective amplification of differences between inputs.* Suppose that each neuron excites itself ($w_{\text{self}} > 0$) and inhibits the other ($w_{\text{other}} < 0$) and that the inhibitory connections are stronger than the self-excitatory connections (i.e. $|w_{\text{other}}| > w_{\text{self}}$).
   (1) What will happen to inputs that are common to the two cells? (Will they be amplified or attenuated?) Show this by looking at the eigenvalue for the appropriate eigenvector.
   (2) What will happen to inputs that are opposite for the two cells?
   (3) Calculate the eigenvalues for $w_{\text{self}} = 0.2$ and $w_{\text{other}} = -0.7$.
   (4) Calculate the amplification factors $1/(1-\lambda)$ for each eigenvector, using the values in part (3) above.
   (5) If each cell in the network has an intrinsic time constant $\tau = 18$ ms, what will be the corresponding time constants τ_{eff} for each component? From this answer, do you expect the amplified component to change more or less quickly than the attenuated component?

e. Consider a network with $w_{\text{self}} = 0.2$ and $w_{\text{other}} = -0.7$, as in part (d). Suppose $I_1 = 63$ Hz and $I_2 = 57$ Hz.
   (1) Write these inputs in the form $\mathbf{I} = b_1\xi^{(1)} + b_2\xi^{(2)}$. What are b_1 and b_2?
   (2) Recall that the steady-state firing rate is obtained by simply scaling each component (b_1 or b_2) of $\mathbf{I}$ by the corresponding amplification factor ($(1-\lambda_1)^{-1}$ or $(1-\lambda_2)^{-1}$, respectively), and then adding together these components, i.e.

$$\mathbf{r} = \frac{b_1}{1-\lambda_1}\xi^{(1)} + \frac{b_2}{1-\lambda_2}\xi^{(2)}$$

   What will the steady-state firing rate vector $\mathbf{r}_\infty = [r_{\infty,1}, r_{\infty,2}]$ equal? For various initial conditions, sketch the expected trajectory of the firing rates as they approach this steady-state value.

f. Simulate the network by numerically solving the equations; the point is to "blindly" simulate these equations and confirm that you get the same answer you found analytically. For initial conditions, set $\mathbf{r}(t = 0) = \mathbf{I}$, i.e. start out the network at the firing rate values that would have been obtained in steady-state if there were no recurrent connections.

   Plot r_1 and r_2 as a function of time for long enough to see them reach steady state. On the same set of axes, plot the eigenvectors $\xi^{(1)}$ and $\xi^{(2)}$. Check that the steady state values that you get are the same as those you calculated analytically.

g. Modify the above network so that it integrates a quantity proportional to the difference between I_1 and I_2 . What is the condition on w_{self} and w_{other} for this to occur? Also observe what happens when the inputs I_1 and I_2 equal zero. Do you observe persistent neural activity? (For comparison, set I_1 and I_2 equal to zero in part (f)). For this question, don't worry that firing rates can become negative. You can consider $\mathbf{r}$ to be the firing rate relative to a background level.

h. *Winner-take-all networks.* For a more extreme example of the rivalry between inputs observed in part (f), see what happens if w_{other} is a large negative value. For this network, add constraints on your neurons such that firing rates that become negative get thresholded to zero. Experiment with various initial conditions and input values.
   (i) Such a network is called a *winner-take-all network* because the loser becomes zero and the winner achieves a large value determined by its external input $\mathbf{I}$ and by w_{self}. What is the condition for one of the neurons to be driven to zero firing rate? What additional condition (on the synaptic weights) will lead the winner to exhibit runaway growth? (If you wish to explore this part of the model's parameter space, you can prevent runaway growth from occurring by adding saturation to the model. This is most simply done by imposing a maximum firing rate constraint such that neurons do not increase their firing rates beyond a fixed level $r_{\max}$).
   (ii) *Extra Credit.* This model is commonly used as a simple description of phenomena such as perceptual rivalry. A fundamental property of perceptual rivalry is that the percept remains stable for awhile and then stochastically switches to the other possibility. Can you find a way to modify the previous model to reproduce this behavior?