Solutions to Assignment 8 [*]

G4360 Introduction to Theoretical Neuroscience
Solutions (Spring 2019)

1 The inhibition-stabilized network (ISN)

a **For the I nullcline, compute the slope $\frac{\partial r_I}{\partial r_E}$.**

We can compute the slope of the I nullcline at the fixed point, by setting the equation for the linearized dynamics of r_I to zero.

$$\tau_I \frac{\partial}{\partial t}\delta r_I = J_{IE}\delta r_E - (1 + J_{II})\delta r_I + \delta i_I = 0$$

We are concerned with the no input deviation case, so $\delta \mathbf{i} = \mathbf{0}$.

$$(1 + J_{II})\delta r_I = J_{IE}\delta r_E$$

$$\frac{\delta r_I}{\delta r_E} = \frac{\partial r_I}{\partial r_E}^{(I)} = \frac{J_{IE}}{1 + J_{II}}$$

We'll use the superscript I to denote that this is the slope of the I nullcline.

b **Now for the E nullcline, compute the inverese of its slope.**

We can use the same strategy to compute the inverse slope of the E nullcline by setting the linearzed dynamics of r_E to zero.

$$\tau_E \frac{\partial}{\partial t}\delta r_E = (J_{EE} + -1)\delta r_E - J_{EI}\delta r_I + \delta i_E = 0$$

$$\delta i_E = 0$$

$$(J_{EE} - 1)\delta r_E = J_{EI}\delta r_I$$

$$\frac{\delta r_E}{\delta r_I} = \frac{\partial r_E}{\partial r_I}^{(E)} = \frac{J_{EI}}{J_{EE} - 1}$$

c **Show that the condition that Det $(J - 1) > 0$, which is necessary for stability is equivalent to the I nullcline having a larger slope than the E nullcline.**

$$\text{Det}\,(J - 1) = (J_{EE} - 1)(-J_{II} - 1) + J_{IE}J_{EI} > 0$$

$$(J_{EE} - 1)(-J_{II} - 1) > -J_{IE}J_{EI}$$

$$\frac{(J_{EE} - 1)}{J_{EI}} > \frac{J_{IE}}{(J_{II} + 1)}$$

[*]Solutions and codes are written by Sean Bittner.

$$\frac{\partial r_E}{\partial r_I}^{(E)} > \frac{\partial r_I}{\partial r_E}^{(I)}$$
$$\frac{\partial r_I}{\partial r_E}^{(E)} < \frac{\partial r_I}{\partial r_E}^{(I)}$$

d **First draw the I nullcline, which will be the same for both versions.**

Refer to the figure below. The students I nullcline should be monotonically increasing.

e **Now, draw the E nullcline, assuming a stable fixed point.**

Refer to the figure below. In the ISN plot, the E nullcline should start in the top left (high r_I, low r_E), and end at the bottom-right (low r_I, high r_E). At the crossing of the I nullcline, the E nullcline must have positive slope, which is less than the slope of the I nullcline.

f **Draw the arrows indicating the direction of flow in the different regions of the nullcline plane. Show that in negative-sloping regions of the E nullcline, if r_I is kept fixed, small perturbations of r_E off the nullcline will flow back to the nullcline; while in positive-sloping regions, it will flow away.**

Refer to the figure below. Students should have horizontally inward pointing arrows around negative sloping parts of the E nullcline, and outwardly pointing arrows around the positively sloping parts of the E nullcline.

g **Now, suppose you add a positive input to the I cells. Show that the resulting change in the I nullcline is to reduce r_E by the same amount for any given r_I , that is, to move the I nullcline leftward.**

$$\tau_I \frac{\partial}{\partial t}\delta r_I = J_{IE}\delta r_E - (1 + J_{II})\delta r_I + \delta i_I = 0$$
$$(1 + J_{II})\delta r_I = J_{IE}\delta r_E + \delta i_I$$
$$\delta r_I = \frac{J_{IE}(\delta r_E + \frac{\delta i_I}{J_{IE}})}{(1 + J_{II})}$$

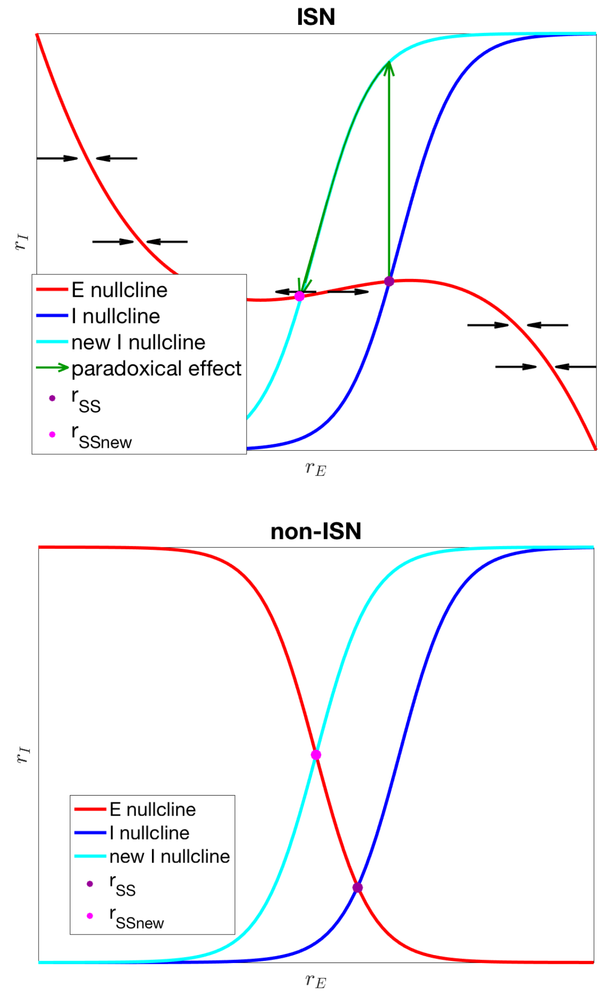
In response to a positive input δi_I, there is a constant leftward shift of the I nullcline by $\frac{\delta i_I}{J_{IE}}$ which is independent of r_I.

Refer to the figure below for how the students should demonstrate the ISN and non-ISN responses to inhibitory input. In the ISN, the new fixed point (at the intersection of the E and I nullclines) should be at a more negative r_E and r_I than before the input. For the non-ISN, r_E should decrease, while r_I should increase at the new fixed.

h **In the ISN case, draw the dynamical path followed by r_E, r_I from the old fixed point to the new fixed point after adding the positive input to I.**

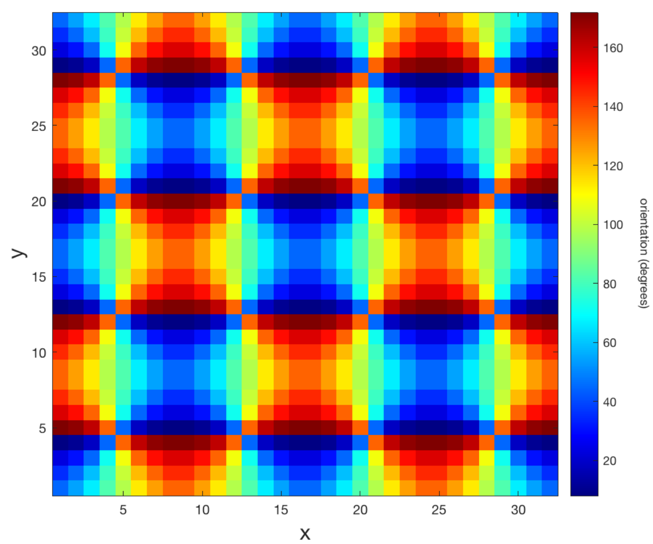
Refer to the figure below. The students should demonstrate that the state goes up initially, then goes down and to the left to relax at the new fixed point at a lower r_E and r_I.

Figure 1: Pardoxical effect in the ISN

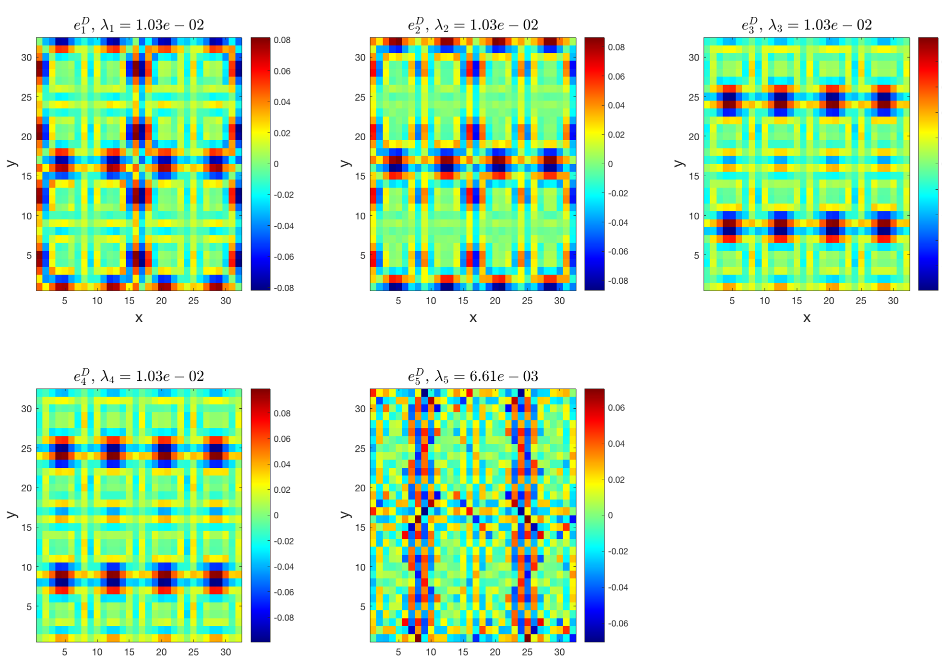


2 Eigenvectors, Schur Vectors and Non-Normal Dynamics in Higher Dimensions

The orientation map

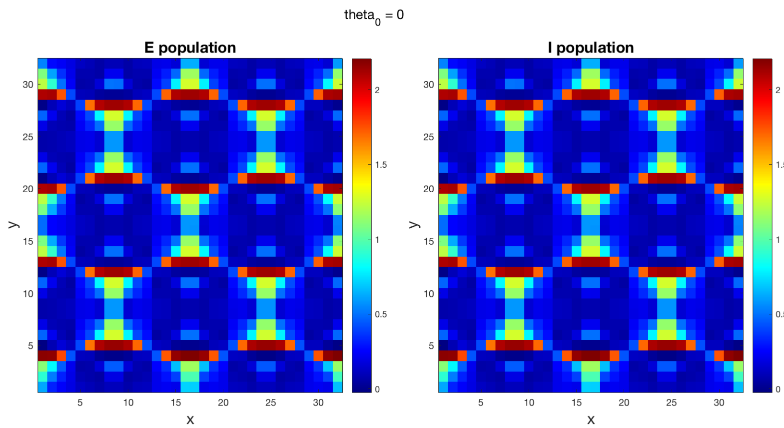


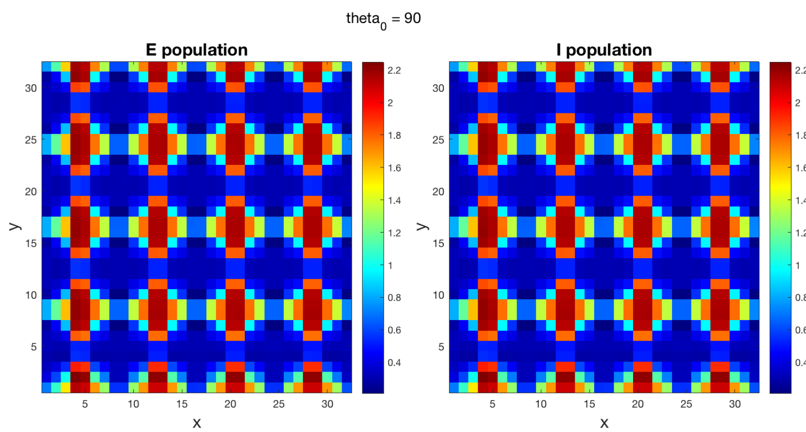
a **Compute and plot the 5 eigenvectors $\mathbf{e}_i^D$ with the largest eigenvalues (the eigenvalues will be real, because $\mathbf{W}^E - \mathbf{W}^I$ is symmetric) and note their corresponding eigenvalues.**



b **Can you say anything about how the spatial structure of these eigenvectors reflects the**

spatial structure of the connectivity? For comparison, compute and plot the steady-state response of linear rate dynamics to an oriented full-field input of orientation $\theta_0 = 0^o$, and the steady-state response to input of orientation $\theta_0 = 90^o$, where the input to the E and I neurons at position x is given by $4e^{-\frac{(\theta_0-\theta(\mathbf{x}))^2}{2(20^o)^2}}$.





The difference eigenvectors reflect the periodice structure of tuning across space, yet the crossing patterns do not explain the evoked responses well. Perhaps, the sum eigenvectors will explain the responses more effectively.

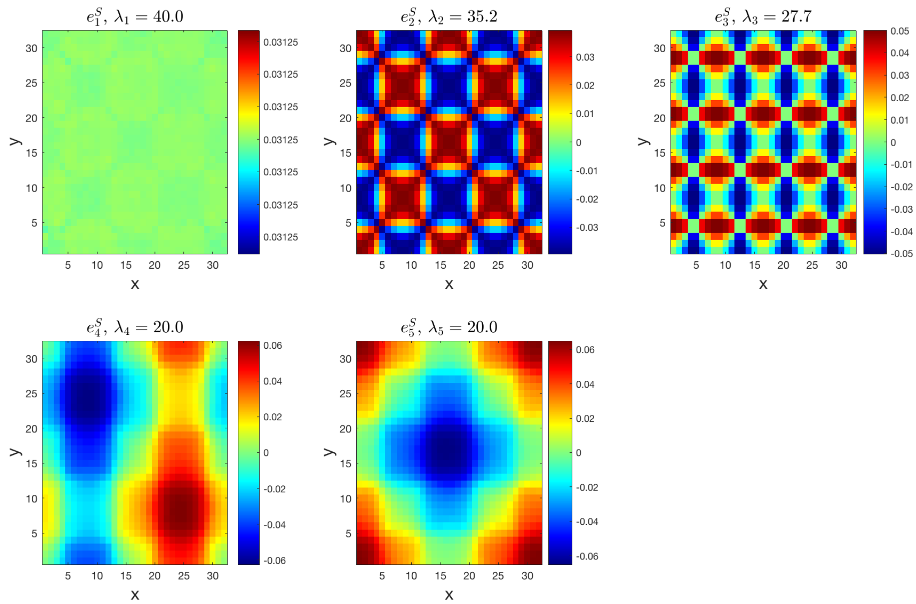
c **Compute the correlation coefficient of each eigenvector with each orientation response.**

```
Ori 0, Eig 1: corr = 0.000717
Ori 0, Eig 2: corr = -0.016422
Ori 0, Eig 3: corr = -0.006191
Ori 0, Eig 4: corr = -0.006191
Ori 0, Eig 5: corr = 0.001020

Ori 90, Eig 1: corr = -0.000755
Ori 90, Eig 2: corr = -0.001126
Ori 90, Eig 3: corr = -0.000730
Ori 90, Eig 4: corr = -0.000730
Ori 90, Eig 5: corr = -0.001395
```

Each difference eigenvector has near-zero correlation with the evoked responses.

d **Now plot the 5 leading $\mathbf{e}_i^S$ (those with the largest λ_i^S), and note their corresponding λ_i^S.**



e **Again, what can you say about how the spatial structure of the e_i^S relates to the spatial structure of the connectivity and the evoked orientation responses?**

The first three sum eigenvectors are periodic and reflect the orientation structure. The second and third eigenvectors reflect co-activation of neurons with similar orientation tuning. Specifically, the second eigenvector shows coactivation of neurons with orientations less than 90 degrees, with a peak at 45 degrees, and reduced activation of neurons with greater than 90 degrees, with a trough at 135 degrees. The third eigenvector shows coactivation of neurons with orientations from 135 to 45 degrees (wrapping around), with a peak at 0 degrees, and reduced activation of other neurons with a trough at 90 degrees.

We expect the 0 degree evoked response to be correlated with both the second and third eigenvectors, since 0 degree tuned neurons are included in both eigenvector sets of activated neurons. We expect the 90 degree evoked response to be uncorrelated with the second eigenvector, and to be highly anti-correlated with the third eigenvector. This is what we see in f.).

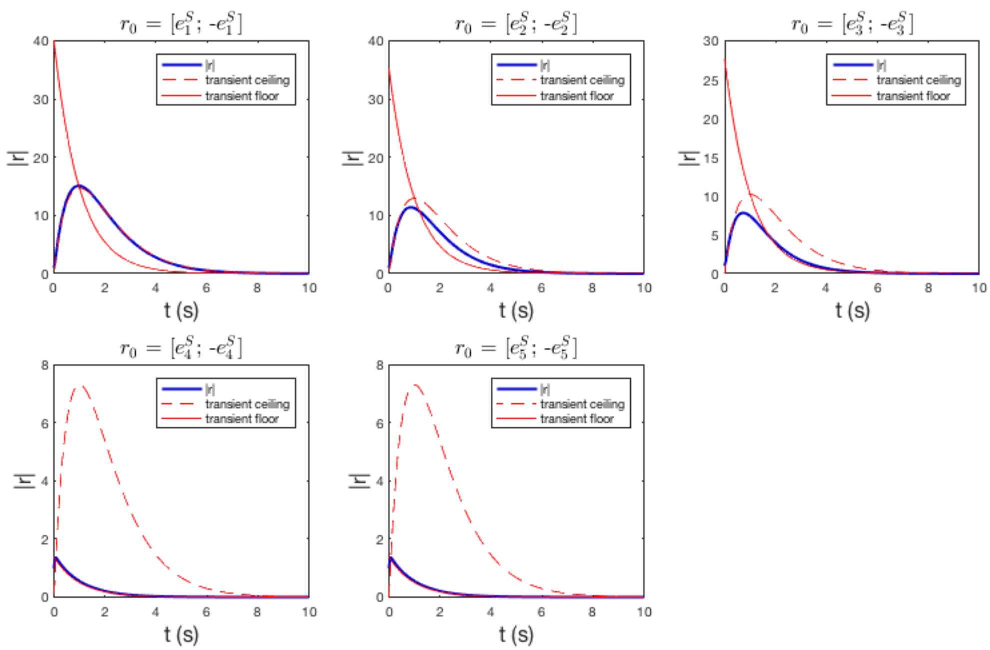
f **Compute the correlation coefficient of each eigenvector $\mathbf{e}_i^S$ with each orientation response.**

```
Ori 0, Eig 1: corr = -0.437235
Ori 0, Eig 2: corr = 0.471213
Ori 0, Eig 3: corr = 0.532500
Ori 0, Eig 4: corr = 0.008053
Ori 0, Eig 5: corr = 0.008053

Ori 90, Eig 1: corr = 0.009791
```

```
Ori 90, Eig 2: corr = -0.000169
Ori 90, Eig 3: corr = -0.902647
Ori 90, Eig 4: corr = -0.012195
Ori 90, Eig 5: corr = -0.012195
```

g **Finally, examine the dynamics of the non-normal amplification in this model. For each of the 5 leading $\mathbf{e}_i^S$, start the dynamics with an initial condition $\begin{pmatrix} \mathbf{r}_E \\ \mathbf{r}_I \end{pmatrix} = \frac{1}{\sqrt{2}} \begin{pmatrix} \mathbf{e}_i^S \\ -\mathbf{e}_i^S \end{pmatrix}$. The dynamics is given by $\tau \frac{d\mathbf{r}}{dt} = -\mathbf{r} + \mathbf{W}\mathbf{r}$ (the external input is zero). Plot the time course of $|\mathbf{r}|$.**



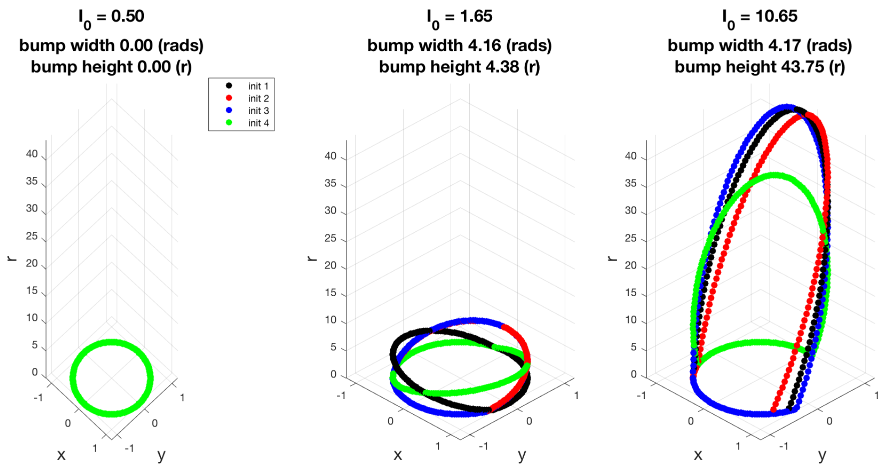
h **For each of the 5 $\mathbf{e}_i^S$, plot the time course of $|\mathbf{r}|$ along with the functions $\lambda_i^S e^{-t/\tau}$ and $\lambda_i^S t e^{-t/\tau}$.**

Refer to previous figure.

3 Ring networks: Bump attractors or an SSN

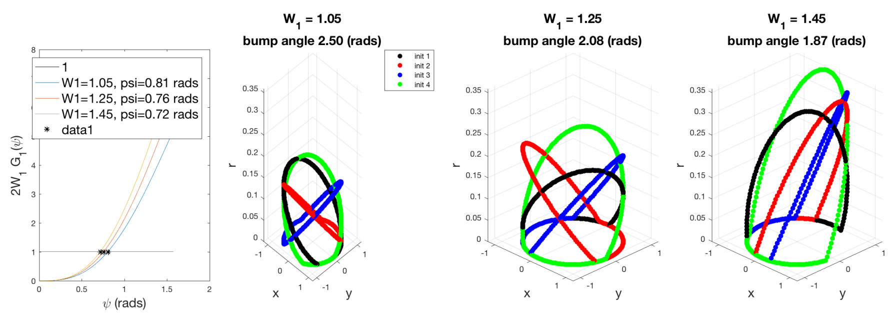
Bump attactors

a **First consider a uniform input, $i_1 = 0$. Verify that for $i_0 < v_{th}$, even if you start with a random initial condition of positive activations, the dynamics will decay to $\mathbf{r} = 0$. Simulate for a couple of values of $i_0 > v_{th}$, say $i_0 = v_{th} + 1$ and $i_0 = v_{th} + 10$. Verify that if your initial condition has any nonzero (positive) noise, no matter how small, the dynamics will evolve to a bump solution. How do the shape and height change for different values of i_0?**



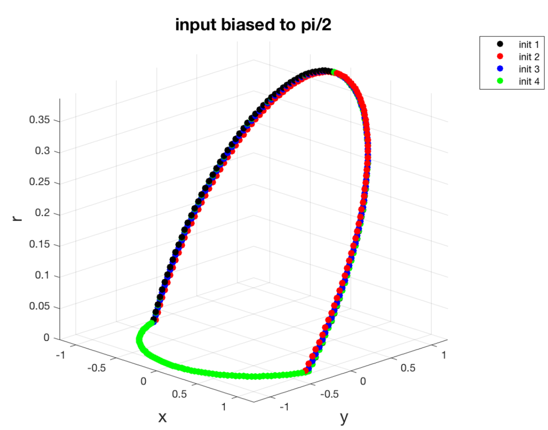
The height of the bump increases with the amount of non-specific current, while the width of the bump remains unchanged.

b **Does this appear to agree with your simulations?**



While the simulation replicates the decrease in bump width with increasing W_1, the values do not match up well. I'll attribute this to the discretization of the simulation. Be lenient on student's ability to reproduce those theoretically predicted values.

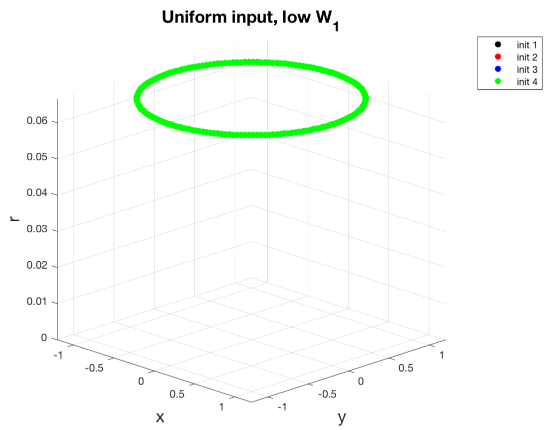
c **Now add a weak tuned input i_1, say $i_1 = 0.1(i_0 - v_{th})$. Does this choose the bump location? Does the bump appear to be otherwise similar or identical?**



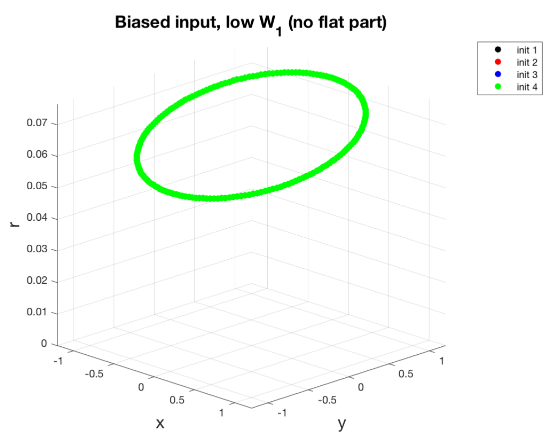
Across all 4 initializations, the bump was always centered at $\pi/2$ for input current tuned to $\pi/2$.

d **Finally, simulate with the same parameters except $0 < W_1 < 1$. Now you should find that the uniform solution is stable, and there is no bump solution to a uniform input. What steady state do you arrive at for a non-uniform input (nonzero i_1), and how does it compare to the bump solution for $W_1 > 1$?**

There is no bump for low W_1 with uniform input.



The steady state solution is tuned to $\pi/2$, but has no zero-values. The entire network is still firing.



SSN

a **First, for a single stimulus of orientation of your choice θ_0, simulate the response, starting from an initial condition $\mathbf{r} = 0$, for $c = \{1.25, 2.5, 5, 10, 20, 40\}$. Again, use first-order Euler, a time constant of $1ms$ should be fine. For each c, simulate until a steady state is reached by some criterion (change per timestep gets sufficiently small). For the steady state, for the E unit and the I unit at the stimulus center, plot, as a function of c:**

- **Their firing rate;**
- **Their feedforward input, their net recurrent input ($E - I$, where E is the recurrent excitatory input and I is the recurrent inhibitory input, taken to have a positive sign), and their total input (feedforward + net recurrent).**

- **The percent of the unit's input that is feedforward or is recurrent, counting recurrent input now as $E + I$ and total input as $FF + E + I$**
- **For the recurrent input, the percent of it that is excitatory:** $\frac{E}{E+I}$

b **Simulate response to the twtimuli shown at the same time, again for the given values of** c**, (same** c **for both stimuli).**

c **For at least some, if not all, of the** c **values, you probably want to ot, with preferred orientation from** 0^o **to** 180^o **on the x axis, the sum of the responses of the E unit to each stimulus shown alone, and its response to the two stimuli shown together; and the same for the I unit.**