Problem 1: The inhibition-stabilized network (ISN).

1a. Now for a steady-state input perturbation δi, write down the equation for the steady-state response δr.

Answer: the equation can be written as $T(1-J)^{-1}\frac{d}{dt}\delta r = -\delta r + \delta i(1-J)^{-1}$. Solving by exponential: $\delta r(t) = \delta i(1-J)^{-1} + (\delta r(0) - \delta i(1-J)^{-1})e^{\frac{-t}{T(1-J)^{-1}}}$ At steady state, $t \to \infty$, $\delta r = -(J-1)^{-1}\delta i$.

1b. Show that, for a stable fixed point, if a perturbation is given only to the I cells (δi ∝ [0 1]), the steady-state response is "paradoxical" (response to a positive input is negative; response to a negative input is positive) if and only if $j_{EE} > 1$.

Answer: $\delta r = \frac{1}{Det(J-I)}\begin{bmatrix} -j_{II}-1 & j_{EI} \\ -j_{IE} & j_{EE}-1 \end{bmatrix}\begin{bmatrix} 0 \\ \delta i \end{bmatrix}$

$= -\frac{\delta i}{Det(J-I)}\begin{bmatrix} j_{EI} \\ j_{EE}-1 \end{bmatrix}$

To let the term $-\frac{\delta i}{Det(J-I)}$ determines the paradoxical sign of δr (i.e. when δi >0, δr < 0 and vice versa.), $j_{EE} - 1 > 0$, thus $j_{EE} > 1$.

1c. Show that $j_{EE} > 1$ is precisely the condition that the E subpopulation alone is unstable: that is, if r_I were a fixed constant, fixed to its steady state value, so that the only dynamics were the E equation with the fixed r_I, then the fixed point would be unstable.

Answer: $Det(J-I) = -(j_{EE}-1)(j_{II}+1) + j_{EI}j_{IE}$. For Det(J-I) > 0, $(j_{EE}-1) < \frac{j_{EI}j_{IE}}{(j_{II}+1)}$ When r_I is fixed, this means that the excitatory population can no longer affect the inhibitory population, thus $j_{IE} = 0$. For the population to be stable, $j_{EE} - 1 < 0, or\ j_{EE} < 1$. Thus, if $j_{EE} > 1$, then $Det(J-I) < 0$, and the system becomes unstable.

2a. For the I nullcline, compute its slope, dr_I/dr_E; you should find that it is given by $\frac{j_{IE}}{1+j_{II}}$. This means that the nullcline always has positive slope.

Answer: Compute the I nucline $T\frac{dr_I}{dt} = -r_I + j_{IE}r_E - j_{II}r_I + i_I$.

$$Set\ \frac{dr_I}{dt} = 0,\ then\ r_I = \frac{j_{IE}}{1+j_{II}}r_E - \frac{i_I}{1+j_{II}}.$$

$$Thus\ the\ slope\ is\ \frac{j_{IE}}{1+j_{II}}.$$

2b. Now for the E nullcline, compute the inverse of its slope, dr_E/dr_I; you should find that this inverse slope is $\frac{j_{EI}}{j_{EE}-1}$. This means that the slope is positive if the E subnetwork is unstable, and negative if the E subnetwork is stable.

Answer: Compute the E nucline $T\frac{dr_E}{dt} = -r_E + j_{EE}r_E - j_{EI}r_I + i_E$.

$$Set\ \frac{dr_E}{dt} = 0,\ then\ r_E = \frac{j_{EI}}{j_{EE}-1}r_I - \frac{i_E}{j_{EE}-1}.$$

$$Thus\ the\ slope\ is\ \frac{j_{EI}}{j_{EE}-1}.$$

2c. 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. So for a fixed point to be stable, it is necessary that the I nullcline have a larger slope than the E nullcline at their crossing that defines the fixed point.

Answer: The I nullcline has a positive slope and is always stable, but for E nullcline it needs a negative slope to be stable. Thus, the I nullcline will always have a larger slope than the E nullcline. For $\frac{j_{EI}}{j_{EE}-1} < 0,\ it\ requires\ j_{EE} - 1 < 0,\ thus\ j_{EE} < 1.$ This is the same condition for Det (J − 1) > 0.

2d. Graph two versions of the nullclines. Answer: see below.

2e. Now, suppose you add a positive input to the I cells. Show that the resulting change in the I nullcline is to reduce rE by the same amount for any given rI, that is, to move the I nullcline leftward.

Answer: When input current is zero, the I nullcline is effectively $r_I = \frac{j_{IE}}{1+j_{II}}r_E$. With positive input current, the I nullcline becomes $r_I = \frac{j_{IE}}{1+j_{II}}r_E + \frac{i_I}{1+j_{II}}$. Thus, the curve shifts upwards, and for a sinusoidal curve, that's the same as shifting leftwards.

2d. Show on the plot that, for a stable fixed point, if the network is an ISN, the result is to decrease both rE and rI in moving to the new fixed point; while for a non-ISN, the result is to decrease rE but increase rI.

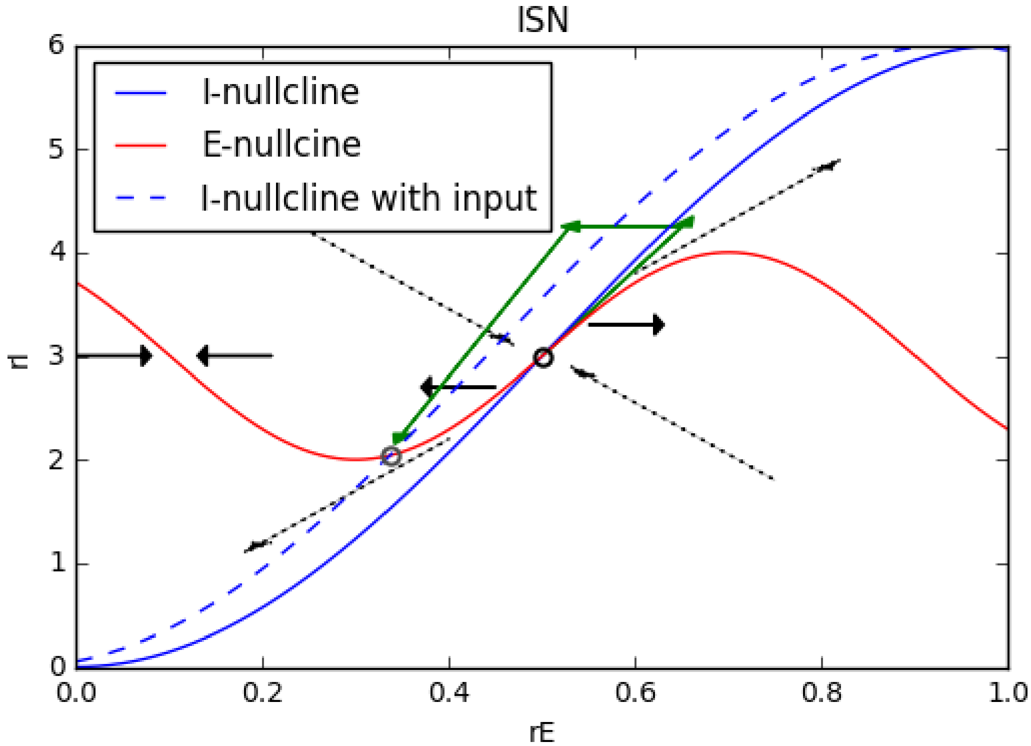
Answer: As shown below by the position of the new fixed point, rE is reduced for both cases, but ISN has smaller rI, while non-ISN has bigger rI.

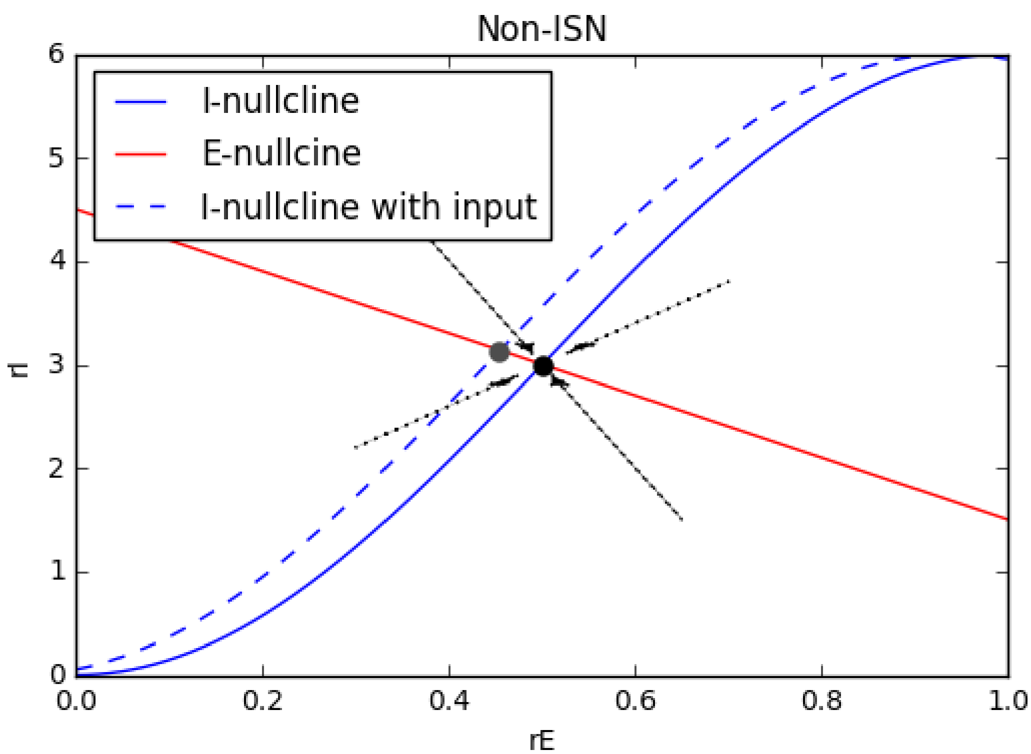
In [547]:

```
import numpy as np
import matplotlib.pyplot as plt

# ISN
# creating fake data that looks like nullclines
t = np.arange(0,1,0.001)
rI = 3*np.cos(np.pi*1*t+np.pi) +3
rE = - np.sin(np.pi*2.5*t-np.pi/4) +3

rI2 = 3*np.cos(np.pi*1*(t+0.06)+np.pi) +3

# find new fix point by looking for interception
idx = np.argwhere(np.diff(np.sign(rI2 - rE)) != 0).reshape(-1) + 0

plt.plot(t,rI,'b')
plt.plot(t,rE,'r')
plt.plot(t,rI2,'b--')
plt.plot(0.5, 3, 'o', mfc='none', mew = 1.5) #initial fixed point
plt.plot(t[idx], rI2[idx], 'o', mfc='none', mew = 1.5, mec = '0.3') # fixed po
int with input current

#Draw the arrows indicating the direction of flow in the different regions of
 the nullcline plane
```

```
plt.arrow(0.6, 3.8, 0.2, 1, head_width=0.02, head_length=0.1, fc='k', ec='k',
linestyle=':')
plt.arrow(0.4, 2.2, -0.2, -1, head_width=0.02, head_length=0.1, fc='k',
ec='k', linestyle=':')
plt.arrow(0.25, 4.2, 0.2, -1, head_width=0.02, head_length=0.1, fc='k',
ec='k', linestyle=':')
plt.arrow(0.75, 1.8, -0.2, 1, head_width=0.02, head_length=0.1, fc='k',
ec='k', linestyle=':')

# plotting to show: in negative-sloping regions of the E nullcline, if rI is k
ept fixed, small perturbations off the E nullcline will flow back to the nullc
line;
plt.arrow(0, 3, 0.07, 0, head_width=0.2, head_length=0.01, fc='k', ec='k')
plt.arrow(0.21, 3, -0.07, 0, head_width=0.2, head_length=0.01, fc='k', ec='k')
# plotting to show: while in positive-sloping regions, it will flow away.
plt.arrow(0.45, 2.7, -0.07, 0, head_width=0.2, head_length=0.01, fc='k',
ec='k')
plt.arrow(0.55, 3.3, 0.07, 0, head_width=0.2, head_length=0.01, fc='k',
ec='k')

# plot the dynamic path
## Dear TA: I'm not sure how to plot arcs,so I made straight arrows. Please im
agine the green arrows linked with curved corners.
plt.arrow(0.5, 3, 0.15, 1.25, head_width=0.02, head_length=0.1, fc='g', ec='g'
 )
plt.arrow(0.65, 4.25, -0.11, -0, head_width=0.1, head_length=0.02, fc='g',
ec='g')
plt.arrow(0.65-0.12, 4.25, -0.18, -2, head_width=0.02, head_length=0.1,
fc='g', ec='g')


plt.xlim([0,1.0])
plt.xlabel('rE')
plt.ylabel('rI')
plt.title('ISN')
plt.legend(['I-nullcline','E-nullcine','I-nullcline with input'],loc='best')
plt.show()


# non-ISN
plt.figure()
# creating fake data that looks like nullclines
t = np.arange(0,1,0.001)
rI = 3*np.cos(np.pi*1*t+np.pi) +3
rE = -3*(t-0.5) +3

rI2 = 3*np.cos(np.pi*1*(t+0.06)+np.pi) +3 # shifted inhibitory nullcline if cu
rent is injected into the inhibitory cells.

# find new fix point by looking for interception
idx = np.argwhere(np.diff(np.sign(rI2 - rE)) != 0).reshape(-1) + 0

plt.plot(t,rI,'b')
plt.plot(t,rE,'r')
plt.plot(t,rI2,'b--')
plt.plot(0.5, 3, 'ko', mew = 1.5) # initial fixed point
plt.plot(t[idx], rI2[idx], 'o', mfc= '0.3', mew = 1.5, mec = '0.3' )  # fixed
```

```
 point with input current

#Draw the arrows indicating the direction of flow in the different regions of
 the nullcline plane
plt.arrow(0.7, 3.8, -0.15, -0.6, head_width=0.02, head_length=0.1, fc='k',
ec='k', linestyle=':')
plt.arrow(0.3, 2.2, 0.15, 0.6, head_width=0.02, head_length=0.1, fc='k',
ec='k', linestyle=':')
plt.arrow(0.35, 4.5, 0.13, -1.3, head_width=0.02, head_length=0.1, fc='k',
ec='k', linestyle=':')
plt.arrow(0.65, 1.5, -0.13, 1.3, head_width=0.02, head_length=0.1, fc='k',
ec='k', linestyle=':')

plt.xlim([0,1.0])
plt.xlabel('rE')
plt.ylabel('rI')
plt.title('Non-ISN')
plt.legend(['I-nullcline','E-nullcine','I-nullcline with input'],loc='best')
plt.show()
```


ISN
I-nullcline
E-nullcine
I-nullcline with input
rI
rE
0
1
2
3
4
5
6
0.0
0.2
0.4
0.6
0.8
1.0


Non-ISN
I-nullcline
E-nullcine
I-nullcline with input
rI
rE
0
1
2
3
4
5
6
0.0
0.2
0.4
0.6
0.8
1.0

Problem 2: Non-normal dynamics

2a. Verify that the (unnormalized) eigenvectors are $\begin{bmatrix} 1 \\ 1 \end{bmatrix}$ with eigenvalue $\lambda_1 = -x$, and $\begin{bmatrix} \frac{w_1+x}{w_2} \\ 1 \end{bmatrix}$ eigenvalue $\lambda_2 = w_1 - w_2$.

Answer: $T\frac{d}{dt}r = -r + Wr + i$. For Eigen value λ, Wr = λIr. (W- λI)r = 0. If (W- λI) is invertible, then there's no solution. Thus (W- λI) needs to be non-invertible, i.e. det(W- λI) = 0.

$\lambda = \frac{w_1-w_2-x \pm \sqrt{(w_1-(w_2+x))^2 - 4(w_1w_2 - w_1x + w_2w_1 + w_2x)}}{2}$. $\lambda = \frac{w_1-w_2-x\pm(w_2-w_1-x)}{2}$, $\lambda_1 = -x,\ \lambda_2 = w_1 - w_2.$

$\lambda_1 \begin{bmatrix} 1 \\ 1 \end{bmatrix} = \begin{bmatrix} -x \\ -x \end{bmatrix}$. $W\begin{bmatrix} 1 \\ 1 \end{bmatrix} = \begin{bmatrix} w_1 - (w_1+x) \\ w_2 - (w_2+x) \end{bmatrix} = \begin{bmatrix} -x \\ -x \end{bmatrix}. Verfitied$

$\lambda_2 \begin{bmatrix} \frac{w_1+x}{w_2} \\ 1 \end{bmatrix} = \begin{bmatrix} \frac{(w_1+x)(w_1-w_2)}{w_2} \\ (w_1-w_2) \end{bmatrix}$. $W\begin{bmatrix} \frac{w_1+x}{w_2} \\ 1 \end{bmatrix} = \begin{bmatrix} \frac{(w_1+x)w_1}{w_2} - (w_1+x) \\ \frac{(w_1+x)w_2}{w_2} - (w_2+x) \end{bmatrix} = \begin{bmatrix} \frac{(w_1+x)(w_1-w_2)}{w_2} \\ (w_1-w_2) \end{bmatrix}. Veri$

2b. Schur transformation.We'll choose our (normalized) Schur basis vectors to be $s_1 = \frac{1}{\sqrt{2}}\begin{bmatrix} 1 \\ 1 \end{bmatrix}$, and a vector orthogonal to it, $s_2 = \frac{1}{\sqrt{2}}\begin{bmatrix} 1 \\ -1 \end{bmatrix}$.Since the component of a vector along an orthonormal basis vector is just given by the dot product of the vector with the basis vector, show that r has components $\begin{bmatrix} r_1 \\ r_2 \end{bmatrix} = \begin{bmatrix} \frac{r_E+r_I}{\sqrt{2}} \\ \frac{r_E-r_I}{\sqrt{2}} \end{bmatrix}$ in the s1, s2 basis, that is, the components r1 and r2 represent the sum and difference of E and I activities, respectively.

Answer: $r = (r_E\, r_I),\ r_1 = r\cdot s_1 = (r_E\, r_I)\frac{1}{\sqrt{2}}\begin{bmatrix} 1 \\ 1 \end{bmatrix} = \frac{r_E+r_I}{\sqrt{2}}$

$r_2 = r\cdot s_2 = (r_E\, r_I)\frac{1}{\sqrt{2}}\begin{bmatrix} 1 \\ -1 \end{bmatrix} = \frac{r_E-r_I}{\sqrt{2}}.$

Thus, $\begin{bmatrix} r_1 \\ r_2 \end{bmatrix} = \begin{bmatrix} \frac{r_E+r_I}{\sqrt{2}} \\ \frac{r_E-r_I}{\sqrt{2}} \end{bmatrix}$

2c. You already know that $Ws_1 = -xs_1$. Show that $Ws_2 = (w_1+w_2+x)s_1 + (w_1-w_2)s_2$.

Answer:

$$Ws_2 = \frac{1}{\sqrt{2}}\begin{bmatrix} w_1+w_1+x \\ w_2+w_2+x \end{bmatrix} = \frac{1}{\sqrt{2}}\begin{bmatrix} w_1+w_2+x+(w_1-w_2) \\ w_1+w_2+x-(w_1-w_2) \end{bmatrix} = (w_1+w_2+x)s_1 + (w_1-w_2)s_2.$$

2d. Show this also in the rE; rI basis: if wFF = w1 + w2 + x = 0, then the matrix W in this basis becomes a symmetric matrix, $W = W^T$, and therefore is normal; and the eigenvectors become orthogonal, i.e. the second eigenvector becomes $\begin{bmatrix} 1 \\ 1 \end{bmatrix}$.

Answer: $if\ w_F F = w_1 + w_2 + x = 0,\ then\ W = \begin{bmatrix} w_1 & -(w_1 + x) \\ w_2 & -(w_2 + x) \end{bmatrix} = \begin{bmatrix} w_1 & w_2 \\ w_2 & w_1 \end{bmatrix} = W^T.\ Shown.$

2e.Solve the linear dynamics $\tau \frac{d}{dt} r = -r + Wr + i$ for constant i in the s_1, s_2 basis. You will have to first solve for $r_2(t)$, then solve for $r_1(t)$ with $w_{FF} r_2(t)$ as one of the inputs.

Answer:

$\tau \frac{d}{dt} r_2 = -r_2 + W r_2 + i_2 = -r_2 + \lambda_2 r_2 + i_2.$

$\frac{\tau}{1-\lambda_2} \frac{d}{dt} r_2 = -r_2 + \frac{i_2}{1-\lambda_2}.$

$Solving\ the\ equation:\ r_2(t) = \frac{i_2}{1-\lambda_2} + (r_2(0) - \frac{i_2}{1-\lambda_2}) e^{-\frac{(1-\lambda_2)t}{\tau}} = r_2(0) e^{-\frac{(1-\lambda_2)t}{\tau}} + \frac{i_2}{1-\lambda_2}(1 - e^{-\frac{(1-\lambda_2)t}{\tau}})$

$\tau \frac{d}{dt} r_1 = -r_1 + W r_1 + i_1 = -r_1 + \lambda_1 r_1 + w_{FF} r_2 + i_1.$

$\frac{\tau}{1-\lambda_1} \frac{d}{dt} r_1 = -r_1 + \frac{w_{FF} r_2 + i_1}{1-\lambda_1}.$

$Solving\ the\ equation:\ r_1(t) = \frac{w_{FF} r_2(t) + i_1}{1-\lambda_1} + (r_1(0) - \frac{w_{FF} r_2(t) + i_1}{1-\lambda_1}) e^{-\frac{(1-\lambda_1)t}{\tau}} = r_1(0) e^{-\frac{(1-\lambda_1)t}{\tau}} + \frac{w_{FF} r_2(t) +}{1-\lambda_1}$

$Substitute\ r_2(t)\ into\ the\ equation: r_1(t) = r_1(0) e^{-\frac{(1-\lambda_1)t}{\tau}} + \frac{i_1 + w_{FF} i_2}{(1-\lambda_2)(1-\lambda_1)}(1 - e^{-\frac{(1-\lambda_1)t}{\tau}}) + w_{FF}(r_2(0)$

2e: Graph the function $\frac{e^{-\frac{(1-\lambda_1)t}{\tau}} - e^{-\frac{(1-\lambda_2)t}{\tau}}}{\lambda_1 - \lambda_2}$ for some choice of λ_1 and λ_2 as real numbers less than 1 (they can be negative).

Anwser: see below

Dear TA, I stopped here as the rest is optional.