Piecewise Linear Analysis of One-Column Microcircuit

The original equations are

$$\begin{aligned}
\tau_{E1}\frac{dr_E}{dt} &= -r_E + F_E(I_E) \\
\tau_{I1}\frac{dr_I}{dt} &= -r_I + F_I(I_I) \\
\frac{dS_E}{dt} &= -\frac{S_E}{\tau_E} + (1 - S_E)\alpha r_E \\
\frac{dS_I}{dt} &= -\frac{S_I}{\tau_I} + r_I \\
F_E(I_E) &= \frac{c_E I_E - I_{thE}}{1 - e^{-g(c_E I_E - I_{thE})} + \frac{\tau_{re}}{1000}(c_E I_E - I_{thE})} \\
F_I(I_I) &= \frac{c_I I_I - I_{thI}}{1 - e^{-g(c_I I_I - I_{thI})} + \frac{\tau_{ri}}{1000}(c_I I_I - I_{thI})} \\
I_E &= J_{EE}S_E - J_{IE}S_I + I_{stim} + I_o \\
I_I &= J_{EI}S_E - J_{II}S_I + I_o
\end{aligned}$$

Note that r_I does not have a coefficient in $\frac{dS_I}{dt}$, consistent with Wong and Wang 2006. (I carried out my calculations without a coefficient.)

Assuming the firing dynamics are fast, so τ_{E1} and τ_{I1} are small, thus

$$\begin{aligned}
\frac{dS_E}{dt} &= -\frac{S_E}{\tau_E} + (1 - S_E)\alpha F_E(I_E) \\
\frac{dS_I}{dt} &= -\frac{S_I}{\tau_I} + F_I(I_I)
\end{aligned}$$

Piecewise linearization of the input-output function, linearized around $I_E = \frac{I_{thE}}{c_E}$ and I_2, where $F_E(I_E)$ approximately plateaus.

$$F_E(I_E) = \begin{cases} b_1 & I_E < \frac{I_{thE}}{c_E} \\ k_1(I_E - \frac{I_{thE}}{c_E}) + b_1 & \frac{I_{thE}}{c_E} < I_E < I_2 \\ k_3(I_E - I_2) + b_1 + k_1(I_2 - \frac{I_{thE}}{c_E}) & I_E > I_2 \end{cases}$$

where b_1 is a small nonzero constant. And

$$F_I(I_I) = k_2 I_I$$

$F_I(I_I)$ can be approximated by a single slope as we are only considering low quantities of input.

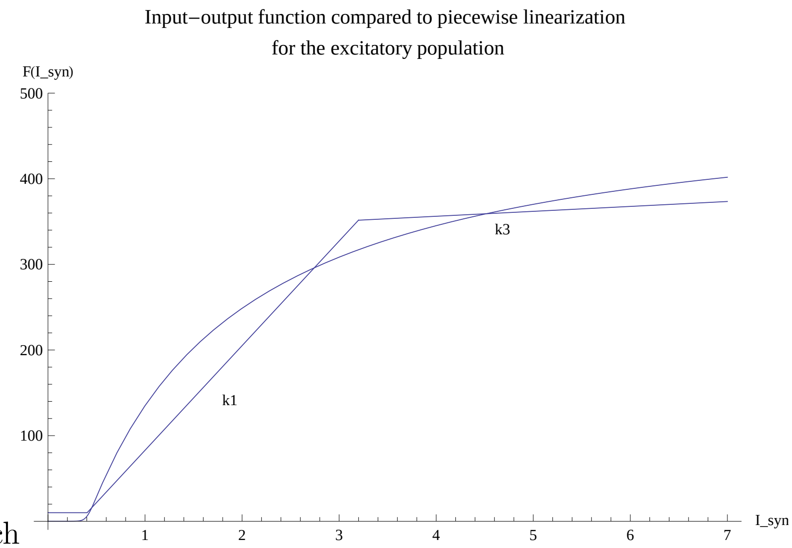

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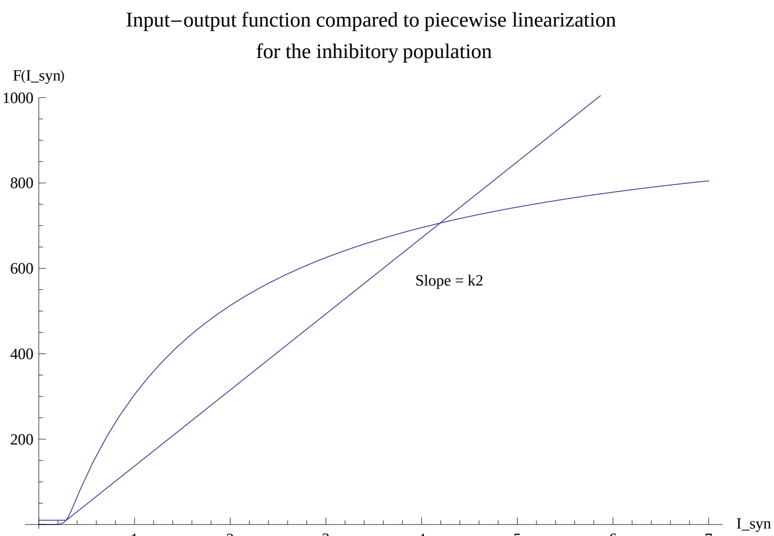
Figure 1: (Apologies for the “chch” before the graphs. I have not located the exact source yet, but it must come from the compiler.)



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Thus we obtain a linear system of equations,

$$\frac{dS_E}{dt} = \begin{cases} -\frac{S_E}{\tau_E} + \alpha(1-S_E)b_1 & S_E < S_1 \\ -\frac{S_E - S_1}{\tau_E} + k_1(1 - S_E + S_1)[\alpha((I_{stim}+I_o) - \frac{I_{thE}}{c_E}) + \alpha J_{EE}(S_E - S_1) - \alpha J_{IE} S_I] + b_2 & S_1 < S_E < S_2 \\ -\frac{S_E - S_2}{\tau_E} + k_3(1 - S_E + S_2)[\alpha((I_{stim}+I_o) - I_2) + \alpha J_{EE}(S_E - S_2) - \alpha J_{IE} S_I] + b_3 & S_E > S_2 \end{cases}$$

Where $b_2 = \frac{dS_E}{dt}|_{S_1}$ and $b_3 = \frac{dS_E}{dt}|_{S_2}$.

$$\frac{dS_I}{dt} = -\frac{S_I}{\tau_I} + k_2[I_o - \frac{I_{thI}}{c_I} + J_{EI}S_E - J_{II}S_I]$$

Where $S_1 = \frac{1}{J_{EE}}(\frac{I_{thE}}{c_E} + J_{IE}S_I - I_{stim} - I_o)$ and $S_2 = \frac{1}{J_{EE}}(I_2 + J_{IE}S_I - I_{stim} - I_o)$, as determined by $I_E = J_{EE}S_E - J_{IE}S_I + I_{stim} + I_o$.

Group together constants

$$\frac{dS_E}{dt} = \begin{cases} -\frac{S_E}{\tau_E} + \alpha(1 - S_E)b_1 & S_E < S_1 \\ -\frac{S_E - S_1}{\tau_E} + k_1(1 - S_E + S_1)[C_1 + C_2(S_E - S_1) - C_3S_I] + b_2 & S_1 < S_E < S_2 \\ -\frac{S_E - S_2}{\tau_E} + k_3(1 - S_E + S_2)[C_{12} + C_2(S_E - S_2) - C_3S_I] + b_3 & S_E > S_2 \end{cases}$$

$$\frac{dS_I}{dt} = -\frac{S_I}{\tau_I} + k_2[C_4 + C_5S_E - C_6S_I]$$

Where $C_1 = \alpha[(I_{stim} + I_o) - \frac{I_{th(E)}}{c_E}], C_{12} = (I_{stim} + I_o) - I_2, C_2 = \alpha J_{EE}, C_3 = \alpha J_{IE}, C_4 = I_o - \frac{I_{th(I)}}{c_I}, C_5 = J_{EI}, C_6 = J_{II}$.

From these equations we calculate the Jacobian matrix around the fixed point. Assuming that the fixed point takes place between S_1 and S_2, we can approximate $F_E(I_E)$ and $F_I(I_I)$ with slopes k_1 and k_2, respectively.

$$\begin{pmatrix} -\frac{1}{\tau_E} + k_1C_2 - 2k_1C_2S_E - k_1C_1 + k_1C_3S_I + 2k_3C_2S_1 & -k_1(1 - S_E)C_3 - k_1C_3S_1 \\ k_2C_5 & -\frac{1}{\tau_I} - k_2C_6 \end{pmatrix}$$

The eigenvalues are the roots of the characteristic polynomial

$$(-\frac{1}{\tau_E}+k_1C_2-2k_1C_2S_E-k_1C_1+k_1C_3S_I+2k_3C_2S_1-\lambda)(-\frac{1}{\tau_I}-k_2C_6-\lambda)+k_2C_5(k_1C_3(1-S_E+S_1)) = 0$$

Solving for λ, we obtain

$$\lambda = \frac{-C_7 \pm \sqrt{C_7^2 - 4C_8}}{2}$$

Where

$$C_7 = \frac{1}{\tau_E} - k_1C_2 + 2k_1C_2S_E + \frac{1}{\tau_I} + k_2C_6 + k_1C_1 - k_1C_3S_I - 2k_3C_2S_1$$

$$\begin{aligned} C_8 = \frac{1}{\tau_I\tau_E} + \frac{k_2C_6}{\tau_E} - \frac{k_1C_2}{\tau_I} - k_1C_2k_2C_6 + \frac{2k_1C_2S_E}{\tau_I} + k_1k_2C_3C_5 + 2k_1k_2C_2C_6S_E - k_1k_2C_3C_5S_E \\ + \frac{k_1C_1}{S_I} + k_1C_1k_2C_6 - \frac{k_1C_3S_I}{\tau_I} - k_1C_3k_2C_6S_I + k_1k_2C_3C_5S_1 - 2k_3C_2S_1(\frac{1}{\tau_I} + k_2C_6) \end{aligned}$$

Where S_E and S_I are evaluated at the fixed points satisfying

$$S_E = \frac{\alpha F_E(I_E)}{\frac{1}{\tau_E} + \alpha F_E(I_E)}$$

$$S_I = \tau_I F_I(I_I)$$

In order to obtain a Hopf bifurcation, we need a parametrization that produces a pair of purely imaginary complex conjugate eigenvalues for the Jacobian matrix at the fixed point. Therefore, such a parametrization must satisfy $C_7 = 0$ and $C_8 > 0$.

Another interesting scenario would be producing damped oscillations. In this case, the parametrization must result in a pair of complex eigenvalues whose real parts are negative, thus forming a stable attractor. For both stable limit cycles and damped oscillations, the imaginary part of the eigenvalues, divided by 2π, gives the frequency of oscillation.

The parametrization leading to a trapping region must allow solution vectors to flow into the region. Thus, on the S_I S_E phase plane, $\frac{dS_E}{dt}$ must be negative along the line $S_E = 1$ and positive along $S_E = 0$, and $\frac{dS_I}{dt}$ must be negative along $S_I = 1$ and positive along $S_I = 0$, leading to the following relations

$$\begin{aligned} C_1 - C_3 S_I &> 0 \ (S_E = 0) \\ -\frac{1}{\tau_I} + k_2(C_4 + C_5 S_E - C_6) &< 0 \ (S_I = 1) \\ -\frac{1}{\tau_E} &< 0 \ (S_E = 1) \\ C_4 + C_5 S_E &> 0 \ (S_I = 0) \end{aligned}$$

Where S_E, $S_I \in [0, 1]$.

Since the above inequalities are all linear in either S_E or S_I, we can simplify these conditions by checking only at the extreme points.

$$S_E = 0 : \begin{cases} C_1 - C_3 > 0 & S_I = 1 \\ C_1 > 0 & S_I = 0 \ C_1 = \alpha((I_{stim} + I_o) - \frac{I_{thE}}{c_E}) < 0 \text{ for } I_{stim} + I_o \text{ small. } C_3 \text{ is positive.} \end{cases}$$

$$S_I = 1 : \frac{1}{\tau_I} + k_2 C_6 > k_2(C_4 + C_5) \ S_E = 1 \ (C_5 \text{ is always positive})$$

$$S_I = 0 : C_4 > 0 \ S_E = 0 \ (C_4 = I_o - \frac{IthI}{cI} \text{ can be negative for small } I_o\text{; but } C_5 \text{ is always positive})$$

For $S_E = 1$, the condition $-\frac{1}{\tau_E} < 0$ is automatically satisfied as τ_E is positive.

To check the stability around a fixed point, we approximate the values of the derivatives and function values of the input-output functions. The Jacobian matrix for the nonlinear system is

$$\begin{pmatrix} -\frac{1}{\tau_E} - \alpha F_E(I_E) + \alpha(1 - S_E)\frac{\partial F_E(I_E)}{\partial S_E} & \alpha(1 - S_E)\frac{\partial F_E(I_E)}{\partial S_I} \\ \frac{\partial F_I(I_I)}{\partial S_E} & -\frac{1}{\tau_I} + \frac{\partial F_I(I_I)}{\partial S_I} \end{pmatrix}$$

where

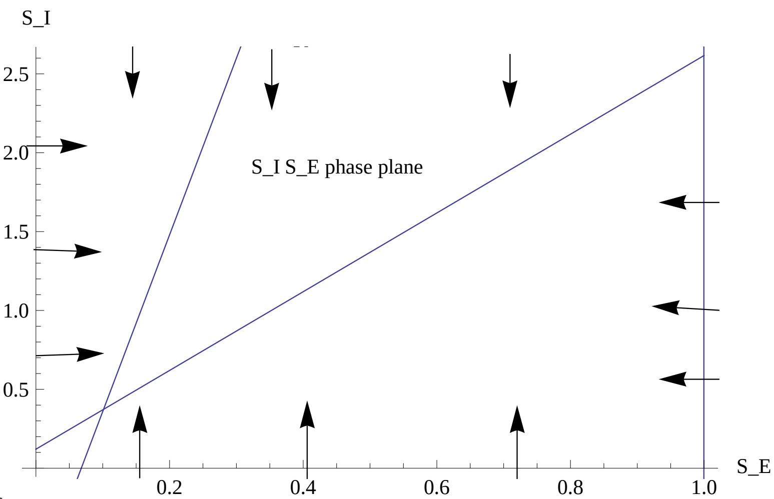

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Figure 2: Vector flow of S_E and S_I solutions. Note that the direction of $\frac{dS_E}{dt}$ along $S_I = 0, 1$ and $\frac{dS_I}{dt}$ along $S_E = 0, 1$ depends on the orientation of the limit cycle. Also note that the top vectors represent the direction of $\frac{dS_I}{dt}$ along $S_I = 1$.

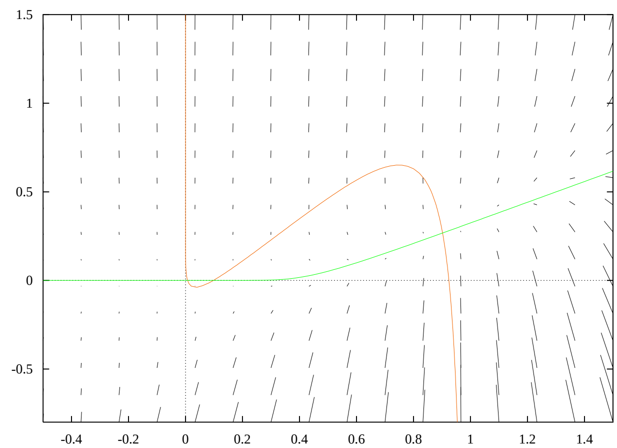

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Figure 3: A parametrization produced three fixed points in this phase plane. The first and and third fixed points are stable, and the middle one is an unstable saddle. If the nullclines shift such that the third fixed point becomes unstable, and the first two collide and annihilate each other, a saddle-node bifurcation could form at this saddle-node. At this point, one of the eigenvalues of the Jacobian matrix is zero while the rest have nonzero real parts. In this case, a limit cycle can arise if the third fixed point is unstable.

$$\frac{\partial F_E}{\partial S_I} = -\frac{(c_E(I_o + I_{stim} + J_{EE}S_E - J_{IE}S_I) - I_{thE})(c_E e^{-g_E(c_E(I_o+I_{stim}+J_{EE}S_E-J_{IE}S_I)-I_{thE})} g_E J_{EE} + \frac{c_E J_{EE}\tau_{re}}{1000})}{(1 - e^{-g_E(c_E(I_o+I_{stim}+J_{EE}S_E-J_{IE}S_I)-I_{thE}+)} + (c_E(I_o + I_{stim} + J_{EE}S_E - J_{IE}S_I) - I_{thE})\frac{\tau_{re}}{1000})^2} + \frac{c_E J_{EE}}{1 - e^{-g_E(c_E(I_o+I_{stim}+J_{EE}S_E-J_{IE}S_I)-I_{thE})} + (c_E(I_o + I_{stim} + J_{EE}S_E - J_{IE}S_I) - I_{thE})\frac{\tau_{re}}{1000}}$$

$$\frac{\partial F_E}{\partial S_I} = -\frac{(c_I(I_o + J_{EI}S_E - J_{II}S_I) - I_{thI})(-c_I e^{-g_I(c_I(I_o+J_{EI}S_E-J_{II}S_I)-I_{thI})} g_I J_{II} - \frac{c_I J_{II}\tau_{ri}}{1000})}{(1 - e^{-g_I(c_I(I_o+J_{EI}S_E-J_{II}S_I)-I_{thI})} + ((c_I(I_o + J_{EI}S_E - J_{II}S_I) - I_{thI})\frac{\tau_{ri}}{1000})^2} - \frac{c_I J_{II}}{1 - e^{-g_I(c_I(I_o+J_{EI}S_E-J_{II}S_I)-I_{thI})} + ((c_I(I_o + J_{EI}S_E - J_{II}S_I) - I_{thI})\frac{\tau_{ri}}{1000}}$$

The characteristic polynomial of the Jacobian matrix is

$$(-\frac{1}{\tau_E} - \alpha F_E(I_E) + \alpha(1 - S_E)\frac{\partial F_E(I_E)}{\partial S_E} - \lambda)(-\frac{1}{\tau_I} + \frac{\partial F_I(I_I)}{\partial S_I} - \lambda) + \frac{\partial F_I(I_I)}{\partial S_E}\alpha(1 - S_E)\frac{\partial F_E(I_E)}{\partial S_I}$$

The root of which gives the eigenvalues. Again, S_E and S_I are the coordinates at the fixed points with the same expressions as mentioned above.

Linearizing $F_E(I_E)$ and $F_I(I_I)$ at a given point prior to calculating the eigenvalues assumes a fixed slope, which is not necessarily the slope at the fixed point. Therefore, as calculations have shown, the parameter sets that satisfy the above conditions in the linearized system do not necessarily satisfy the same conditions in the nonlinear system.