MCN 2013: answer to Problem Set #1, Question #1

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1. Integrate and Fire Neurons

   (a) The frequency (F) of an integrate and fire neuron is equal to the inverse of the spike period ($F = P^{-1}$). Let $t = 0$ correspond to the beginning of an inter-spike interval (i.e. the point at which the neuron has just fired an action potential, and has been reset to V_R). At the end of the inter-spike interval, it follows that $t = P$ and $V = V_T$. The time constant of the neuron is invariant over time and is given by $\tau = C/g_L$; the steady-state membrane potential is also invariant and is given by $V_{ss} = (I + V_L g_L)/g_L$ (proof for these relations can be found in Dayan and Abbott). Because the time constant and steady- state voltage are constant, the membrane potential $V(t)$ can be expressed analytically as:

   $$V(t) = V_{ss} + (V_R - V_{ss})e^{-t/\tau},$$

   where we have substituted V_R for the initial condition. We also know the following: $V(t = P) = V_T$. Substituting this in, we can solve for F:

   $$V_T = V_{ss} + (V_R - V_{ss})e^{-P/\tau}$$
   $$V_T - V_{ss} = (V_R - V_{ss})e^{-P/\tau}$$
   $$\frac{V_T - V_{ss}}{V_R - V_{ss}} = e^{-P/\tau}$$
   $$-\tau * \ln \frac{V_T - V_{ss}}{V_R - V_{ss}} = P$$

$$F = \left(-\tau * \ln \frac{V_T - V_{ss}}{V_R - V_{ss}}\right)^{-1}$$

(b) The derivation is identical to the previous problem except

$$V_{ss} = \frac{V_L g_L + V_S g_S}{g_L + g_S}, \text{ and}$$

$$\tau = \frac{C}{g_L + g_S}.$$

(c) To determine the number of equilibrium points, we find the intersections of the V and W nullclines. The V nullcline is given by:

$$\frac{dV}{dt} = 0 = V^2 + I - W$$

$$V_{null}(V) = V^2 + I$$

The W nullcline is given by:

$$\frac{dW}{dt} = 0 = a(bV - W)$$

$$W_{null}(V) = bV$$

Now we find where these curves intersect:

$$V_{null} = W_{null}$$

$$V^2 + I = bV$$

$$V^2 - bV + I = 0$$

$$V = \frac{b \pm \sqrt{b^2 - 4I}}{2}$$

There are two real solutions when the discriminant is greater than zero, one degenerate solution when it equals zero, and no real solutions otherwise. Thus we conclude that there are two equilibrium points when $b > \left|\pm 2\sqrt{I}\right|$, one equilibrium point when $b = \pm 2\sqrt{I}$ (a bifurcation point), and no equilibria otherwise. Since we know

$W_{null}(V) = bV$, the equlibrium points are of the form (V, bV), specifically:

$$\left(\frac{b+\sqrt{b^2-4I}}{2}, \frac{b^2+b\sqrt{b^2-4I}}{2}\right), \text{and}$$

$$\left(\frac{b-\sqrt{b^2-4I}}{2}, \frac{b^2-b\sqrt{b^2-4I}}{2}\right)$$

To classify these equilibria points we use local linear analysis. The Jacobian matrix for the system is given by:

$$\begin{bmatrix} \frac{\delta\dot{V}}{\delta V} & \frac{\delta\dot{V}}{\delta W} \\ \frac{\delta\dot{W}}{\delta V} & \frac{\delta\dot{W}}{\delta W} \end{bmatrix},$$

where $\dot{V}$ and $\dot{W}$ denote the time derivatives for V and W. This is equal to:

$$\begin{bmatrix} 2V & -1 \\ ab & -a \end{bmatrix}.$$

Thus, the stability of each equlibrium point is only dependent on the value of V and does not depend on W. The eigenvalues of the Jacobian matrix can be found by solving the characteristic polynomial:

$$\lambda^2 - \mathrm{TRC}[J]\lambda + \mathrm{DET}[J],$$

where J denotes the Jacobian matrix, and the functions TRC[.] and DET[.] give the trace and determinant of a matrix. (NOTE: the nice form of the characteristic polynomial here is specific to 2-dimensional systems). The solutions to this quadratic are:

$$\lambda = \frac{\mathrm{TRC}[J] \pm \sqrt{\mathrm{TRC}[J]^2 - 4\mathrm{DET}[J]}}{2}.$$

If both solutions (eigenvalues) have negative real parts, then the fixed point is stable. The stability of equilibria are summarized in the image below (source: Izhikevitch (2007). *Dynamical Systems in Neuroscience*, pg. 104).

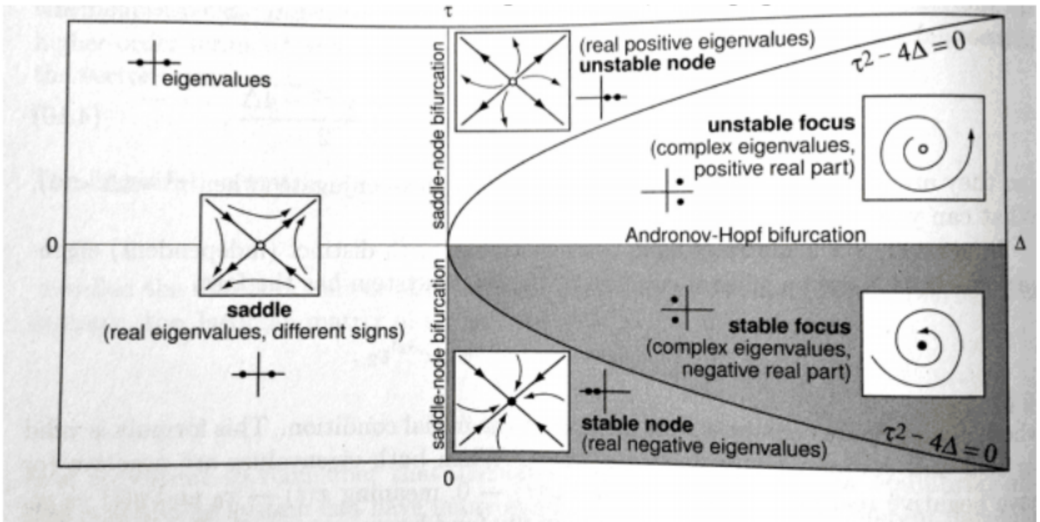

Figure 4.15: Classification of equilibria according to the trace (τ) and the determinan (Δ) of the Jacobian matrix L. The shaded region corresponds to stable equilibria.

Now we calculate the trace and determinant of the Jacobian matrix around an equilibrium point ($\bar{V}$,$\bar{W}$). Recall that

$$\bar{V} = \frac{b \pm \sqrt{b^2 - 4I}}{2}.$$

This implies:

$$\mathrm{TRC}[J] = 2\bar{V} - a$$

$$\mathrm{TRC}[J] = b \pm \sqrt{b^2 - 4I} - a.$$

In addition:

$$\mathrm{DET}[J] = ab - 2a\bar{V}$$

$$\mathrm{DET}[J] = ab - a\left(b \pm \sqrt{b^2 - 4I}\right).$$

$$\mathrm{DET}[J] = \pm a\sqrt{b^2 - 4I}.$$

We are interested in finding the values at which the trace and determinant change sign (i.e. bifurcation points), subject to the condition that $a > 0$. These transition points can be derived by finding values of b and I, where the determinant and trace are equal to zero. First consider the determinant:

$$\mathrm{DET}[J] = 0$$

$$\pm a\sqrt{b^2 - 4I} = 0$$
$$b^2 - 4I = 0$$
$$b = \pm 2\sqrt{I}$$

This relation between b and I describes the location of saddle-node bifurcations in parameter space. When $b > \pm 2\sqrt{I}$, there are two equilibria: one has $\mathrm{DET}[J] > 0$ (a node), and the other has $\mathrm{DET}[J] < 0$ (a saddle). When $b < \pm 2\sqrt{I}$, there are no equilibria (see above).

Now consider the trace of the Jacobian matrix. When the trace is equal to zero, we are at a Hopf bifurcation point:

$$\mathrm{TRC}[J] = 0$$

$$b \pm \sqrt{b^2 - 4I} - a = 0$$
$$a - b = \pm\sqrt{b^2 - 4I}$$
$$a^2 - 2ab + b^2 = b^2 - 4I$$
$$a^2 - 2ab = -4I$$
$$a^2 + 4I = 2ab$$
$$b = \frac{a^2 + 4I}{2a}$$

We can now find where these two curves (for the Hopf and saddle-node bifurcations) meet:

$$b = \frac{a^2 + 4I}{2a} = \pm 2\sqrt{I}$$

$$a^2 + 4I = \pm 4a\sqrt{I}$$
$$(a^2 + 4I)^2 = 8a^2 I$$
$$a^4 + 8a^2 I + 16I^2 = 8a^2 I$$
$$a^4 + 16I^2 = 0$$
$$a^2 = 4I$$
$$a = 2\sqrt{I}$$

This point in parameter space corresponds to a *Bogdanov-Takens* bifurcation. This is one of the two ways a system can simultaneously undergo a saddle-node and a Hopf bifurcation (the other, a *Fold-Hopf* bifurcation, occurs in systems that are at least three-dimensional).

(d) Fun with planar dynamics

i. An equilibrium point is stable if and only if all eigenvalues of the Jacobian matrix have negative real parts. In this system the Jacobian is expressed as:

$$\begin{bmatrix} \frac{\delta f(V,W)}{\delta V} & \frac{\delta f(V,W)}{\delta W} \\ \frac{\delta g(V,W)}{\delta V} & \frac{\delta g(V,W)}{\delta W} \end{bmatrix} = \begin{bmatrix} f_V & f_W \\ g_V & g_W \end{bmatrix}.$$

The problem states that "we assume the standard potassium/voltage scenario so that $f_W < 0,\ g_W < 0,\ g_V > 0$." These three conditions respectively imply that potassium currents are hyperpolarizing, potassium activation decays towards a steady state, and that potassium currents are activated by depolarizing the membrane potential. If we additionally suppose that $f_V < 0$, we can show that the equilibrium is stable. Let us express the Jacobian matrix in terms of three postive constants a,b,c,d:

$$\begin{bmatrix} -a & -b \\ +c & -d \end{bmatrix}$$

There are several ways we can prove that this matrix has negative, real eigenvalues. Perhaps the easiest is to recall the relationship between the sum/product of the eigenvalues of a matrix with its trace/determinant:

$$\mathrm{TRC}[M] = \sum \lambda_i$$

$$\mathrm{DET}[M] = \prod \lambda_i.$$

In this case, we know that the trace is negative ($-a - d < 0$, by necessity). We also know that the determinant is positive

($ad + bc > 0$, again by necessity). This implies the following two relationships for the eigenvalues λ_1 and λ_2:

$$\lambda_1 + \lambda_2 < 0, \text{and}$$

$$\lambda_1 \lambda_2 > 0,$$

which can only be satisfied if λ_1 and λ_2 are negative.

ii. A. Let $\Psi(V)$ denote the V-nullcline in the phase plane, on which $dV/dt = f(V, W) = 0$. On the middle branch of the nullcline, this function is increasing: $d\Psi/dV > 0$. We can prove the result as follows:

$$f(V, \Psi(V)) = 0$$

$$\frac{df(V, \Psi(V))}{dV} = 0$$

$$\frac{\delta f}{\delta V} + \frac{\delta f}{\delta W} \frac{\delta W}{\delta V}\bigg|_{W=\Psi(V)} = 0$$

We are given that $f_W < 0$ for all (V, W), and furthermore, because the middle branch of the nullcline is increasing, we know that:

$$\frac{\delta W}{\delta V} > 0.$$

Thus, we know that:

$$\frac{\delta f}{\delta W} \frac{\delta W}{\delta V}\bigg|_{W=\Psi(V)} < 0,$$

which directly implies that:

$$\frac{\delta f}{\delta V} = f_V > 0.$$

B. Let $\Omega(V)$ denote the W-nullcline, which is monotonically increasing: $d\Omega/dV > 0$. Following the logic in the previous question, we have:

$$\frac{df(V, \Psi(V))}{dV} = \frac{\delta f}{\delta V} + \frac{\delta f}{\delta W} \frac{\delta W}{\delta V}\bigg|_{W=\Psi(V)} = 0$$

$$\frac{dg(V,\Omega(V))}{dV} = \frac{\delta g}{\delta V} + \frac{\delta g}{\delta W}\frac{\delta W}{\delta V}\bigg|_{W=\Omega(V)} = 0$$

To determine the stability of the equilibrium points on the middle branch, we must compute the trace and determinant of the jacobian matrix.

$$\mathrm{TRC}[J] = f_V + g_W$$

$$\mathrm{DET}[J] = f_V g_W - g_V f_W$$

The problem considers a saddle-node bifurcation, which occurs when the determinant switches sign. To find these bifurcation points we set the determinant to zero:

$$f_V g_W - g_V f_W = 0.$$

Note that $f_V g_W$ is always negative since $f_V > 0$ on the middle branch and $g_W > 0$. Thus, for the determinant to equal zero the following must hold:

$$g_V f_W < 0.$$