580.439/639 Solutions to Homework #5

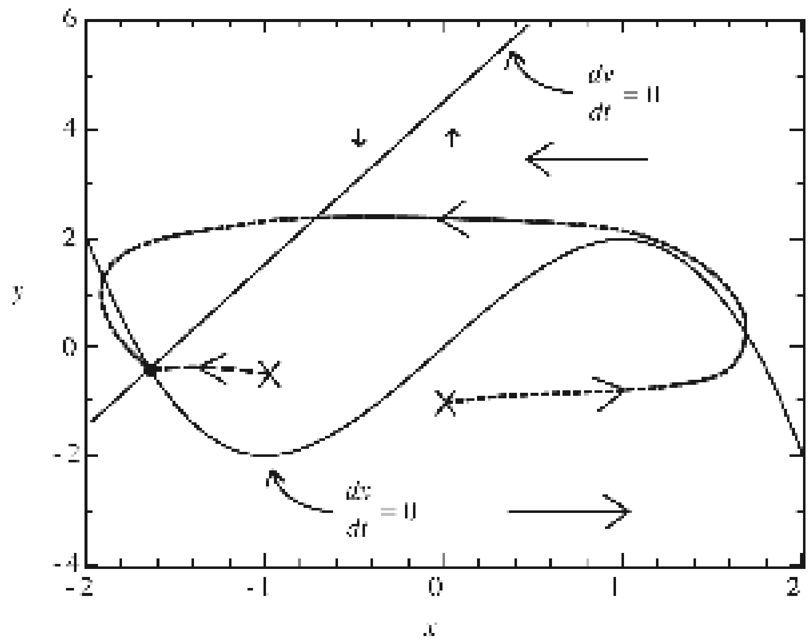
Problem 1

Part a) The isoclines for this system are the equations:

$$\frac{dx}{dt} = 0 \quad \Rightarrow \quad y = -x^3 + 3x$$

$$\frac{dy}{dt} = 0 \quad \Rightarrow \quad y = 3x + 4.5$$

The isoclines are plotted below (lines marked "$d()/dt$=0").



The arrows show the directions of flow in the phase plane relative to the two isoclines. Notice that the x-arrows are much larger than the y-arrows, as is (qualitatively) consistent with the problem statement (ε<<1). The equilibrium point at the intersection of the isoclines occurs at

$$x = -\sqrt[3]{4.5} = -1.65 \qquad y = 4.5 - 3\sqrt[3]{4.5} = -0.45$$

The Jacobian for this system is:

$$J = \begin{bmatrix} -\frac{1}{\varepsilon}\left(3x^2 - 3\right) & -\frac{1}{\varepsilon} \\ 3 & -1 \end{bmatrix}$$

from which it follows that the eigenvalues at a point *(x,y)* are the roots of:

$$\lambda^2 + \left(\frac{3x^2 - 3}{\varepsilon} + 1 \right) \lambda + \frac{3x^2}{\varepsilon} = 0$$

Using the quadratic formula:

$$\lambda = \frac{-\left(\frac{3x^2 - 3}{\varepsilon} + 1 \right)}{2} \pm \frac{\sqrt{\left(\frac{3x^2 - 3}{\varepsilon} + 1 \right)^2 - 4\frac{3x^2}{\varepsilon}}}{2}$$

Because $\varepsilon << 1$, the first term under the radical, which goes as $1/\varepsilon^2$, is large compared to the second term under the radical, which goes as $1/\varepsilon$. By factoring out the common expression outside and under the radical and ignoring the +1 component of the common expression (because $(3x^2-3)/\varepsilon >> 1$), the eigenvalues can be written as

$$\lambda = \frac{3x^2 - 3}{2\varepsilon} \left[-1 \pm \sqrt{1 - \frac{12x^2}{\left(3x^2 - 3\right)^2} \varepsilon} \right]$$

Because $\varepsilon << 1$, the radical can be approximated as $\sqrt{1+\varepsilon} \approx 1+\varepsilon/2$, and after some algebra,

$$\lambda \approx -\frac{3x^2 - 3}{\varepsilon} \qquad -\frac{3x^2}{3x^2 - 3}$$

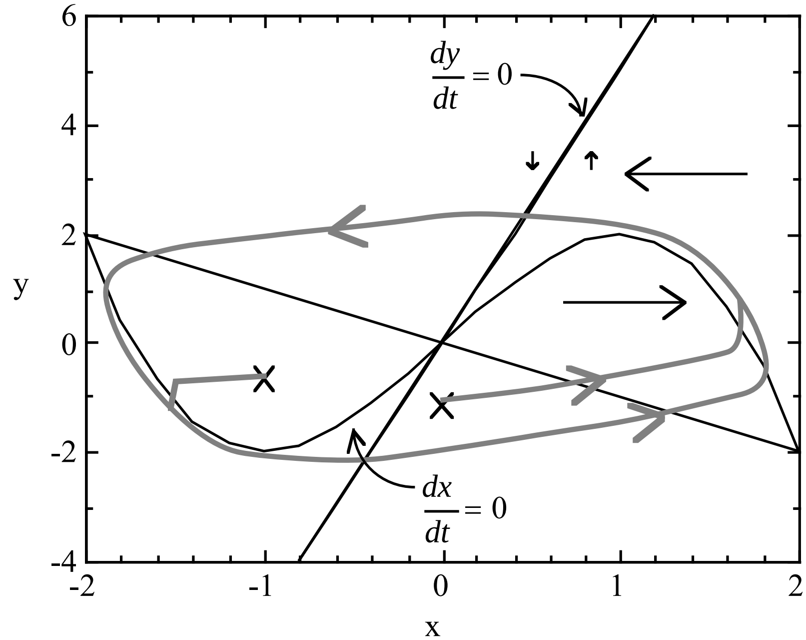
At the equilibrium point, $\lambda \approx -5.18/\varepsilon$ and $\lambda \approx -1.58$. Both eigenvalues are real and negative, so the equilibrium point is stable.

If there were a limit cycle, it would have to surround the equilibrium point, but there is no way to draw a limit cycle consistent with the direction of trajectories in the phase plane for the region *y < eq. pt* and *x ~ eq. pt.* The approximate trajectories are drawn in the figure above.

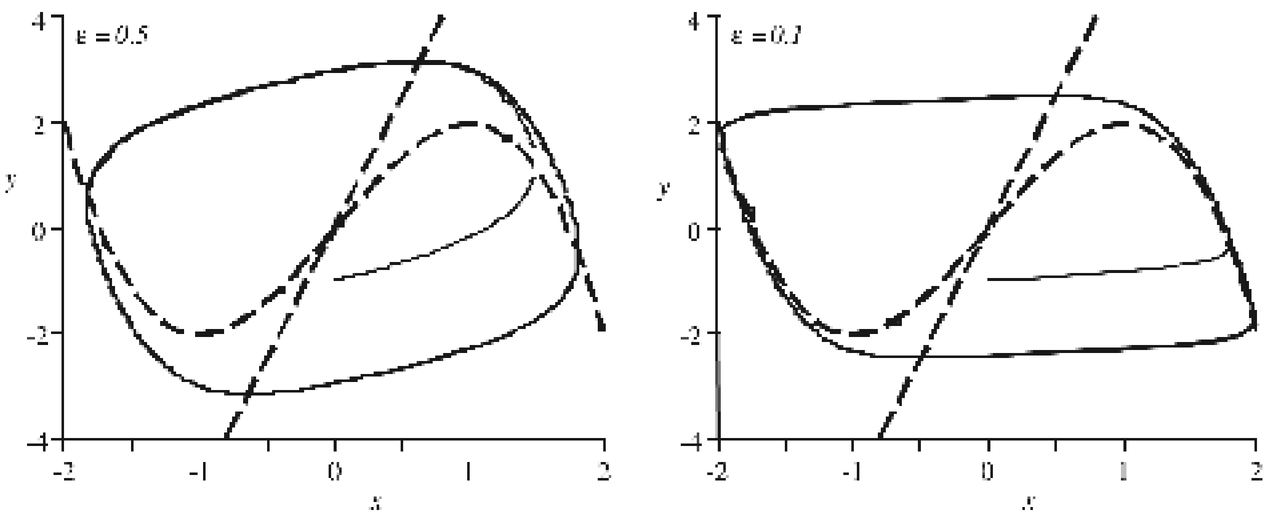
Part b) The phase space for this case is drawn below. In this case, the equilibrium point is (0,0). Carrying out the same calculations as above yields the following eigenvalues at the equilibrium point:

$$\lambda \approx -\frac{3x^2-3}{\varepsilon} \qquad -\frac{3x^2+2}{3x^2-3}$$

from which it follows that at (0,0), $\lambda \approx 3/\varepsilon$ and 2/3, both positive and real, and the equilibrium point is unstable. The Poincare-Bendixson theorem applies here and the system has a limit cycle. Approximate trajectories from the two initial conditions are shown in the figure (fuzzy lines). These should merge with the stable limit cycle (also fuzzy), which can be demonstrated by simulation.



The phase plane plots below show the limit cycle of the system computed by simulation with the relative time scale parameter ε set to two values, 0.5 and 0.1. In the first case, the difference in time scale of the differential equations is small and the actual trajectories are not well approximated by the assumed trajectories drawn above. In the second case, the trajectories follow the dx/dt=0 nullcline quite closely.

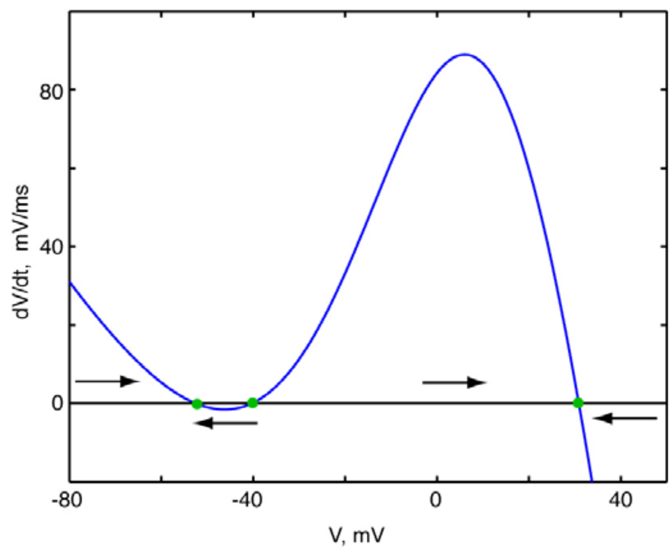


Problem 2

Part a) For the model described in the problem statement, there is only one differential equation:

$$C\frac{dV}{dt} = I_{ext} - G_{Na}m_\infty(V)\big(V - E_{Na}\big) - G_L(V - E_L)$$

Part b) The phase plane for this system with I_{ext}=0 is shown at right. The equilibrium points are the points where *dV/dt* = 0, at the green dots. These can be found graphically or with a zero-finding program (like fzero() in Matlab) to be -52.5, -40.3, and 30.9.

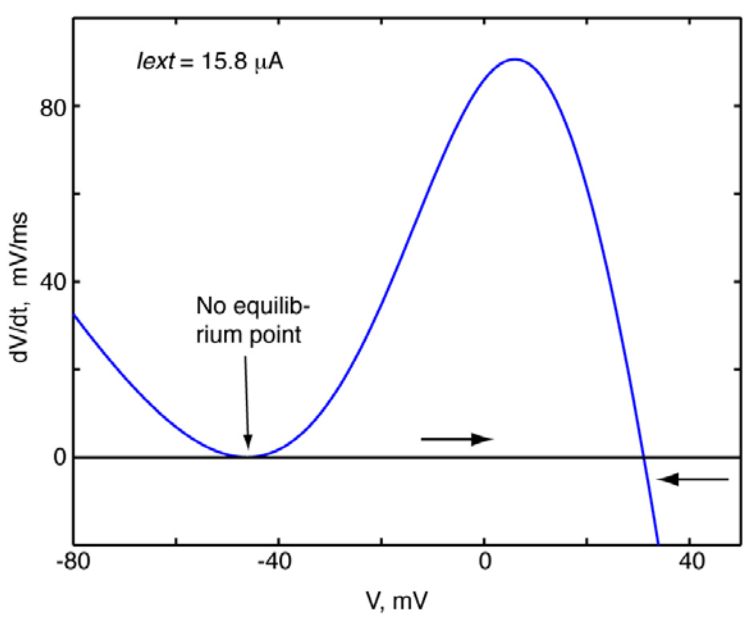


Part c) The arrows in the phase plane plot show the direction that the system will move along the *V* axis. From these, it is clear that the equilibrium points at -52.5 and 30.9 are stable whereas the one at -40.3 is unstable. A qualitative argument for these conclusions, from the arrows, is that the system will asymptotically approach one of the outer two equilibrium points from any point along the *V* axis. The point at -40.3 is unstable because trajectories move away from it for all nearby points.

The Jacobian of this system is a scalar, equal to the derivative w.r.t. *V* of the r.h.s. of the differential equation:

$$Jac = \left.\frac{d\big[I_{ext} - G_{Na}m_\infty(V)\big(V - E_{Na}\big) - G_L(V - E_L)\big]}{dV}\right|_{Eqpt}$$

The equilibrium point is stable if *Re[Jac]*<0, meaning a negative slope of the plot above at the equilibrium point and vice-versa. Since the Jacobian is just the slope of the r.h.s. of the differential equation at the equilibrium point, these two arguments say the same thing.

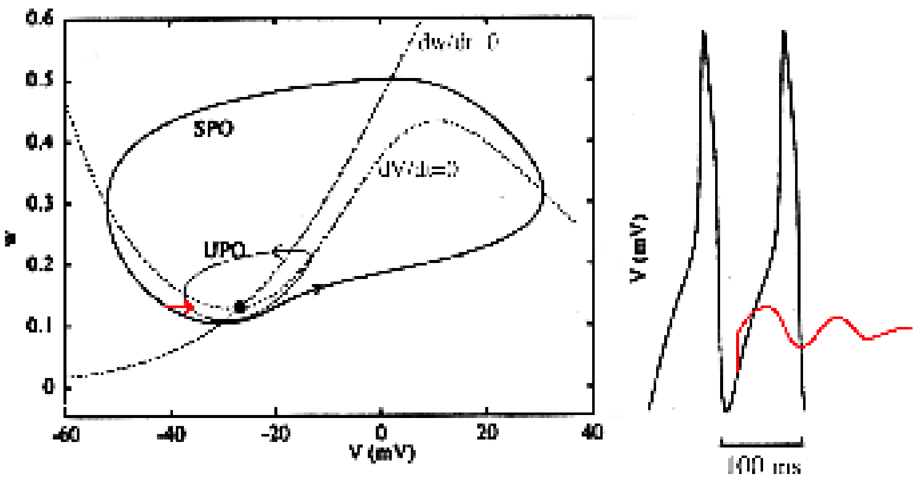


Part d) As I_{ext} increases, the *dV/dt* plot moves vertically. When $I_{ext} \approx$ 15.8, the two equilibrium points between -40 and -50 meet and disappear. Then the only stable equilibrium point is at 31.1. This is like a saddle-node bifurcation. Izhikevich argues that this is a model for the rising phase of an action potential. If the model were suddenly depolarized by such a current, the membrane potential would jump from ~-50 mV to ~-30 mV (assuming it started at -50 mV).

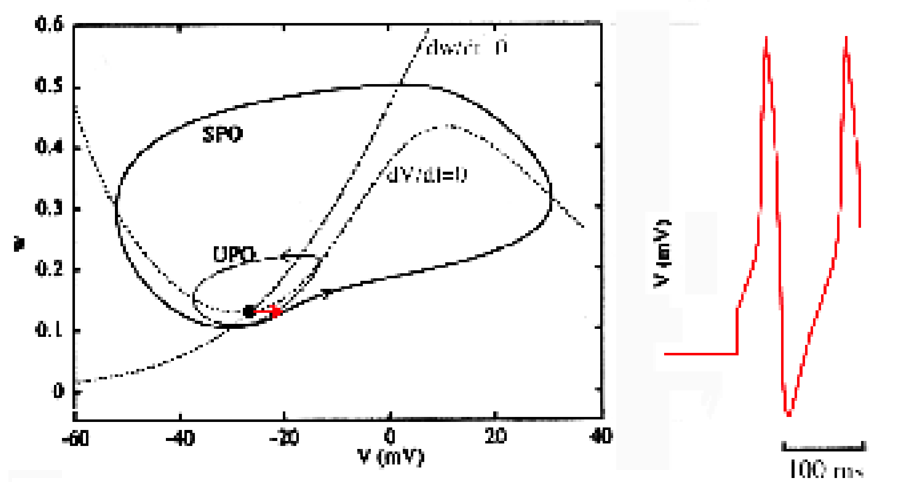
Problem 3

More details on these manipulations can be found in the Rinzel and Ermentrout chapter. Answers are shown as red lines below.

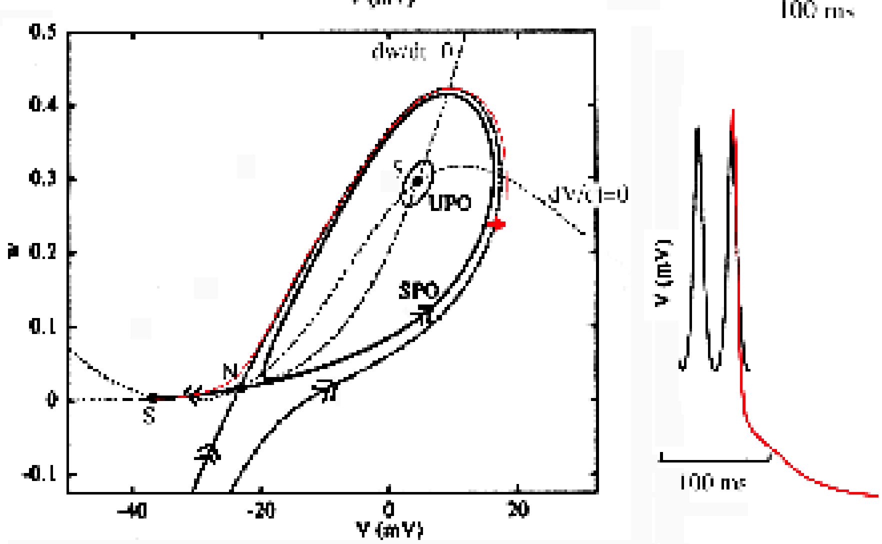
Part a) The depolarizing pulse should be applied as shown to move the trajectory across the UPO, which serves to separate the stable equilibrium point from the limit cycle. The ringing is caused by the fact that the equilibrium point is a stable spiral in this case. (The ringing is not a necessary part of the answer since you had no way of knowing about it.)



Part b) In this case, the voltage trajectory must carry across the UPO into the region of the limit cycle.

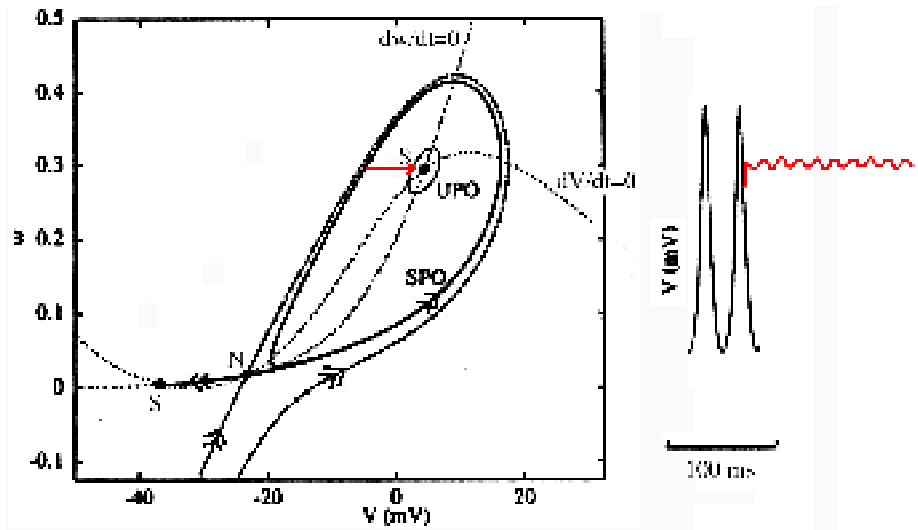


Part c) The voltage step can be placed at many points along the right side of the limit cycle. Its goal is to move the trajectory across the stable manifold of the saddle node, which moves the trajectory into the region of attraction of the resting potential. One such trajectory is shown in the phase plane at right along with the

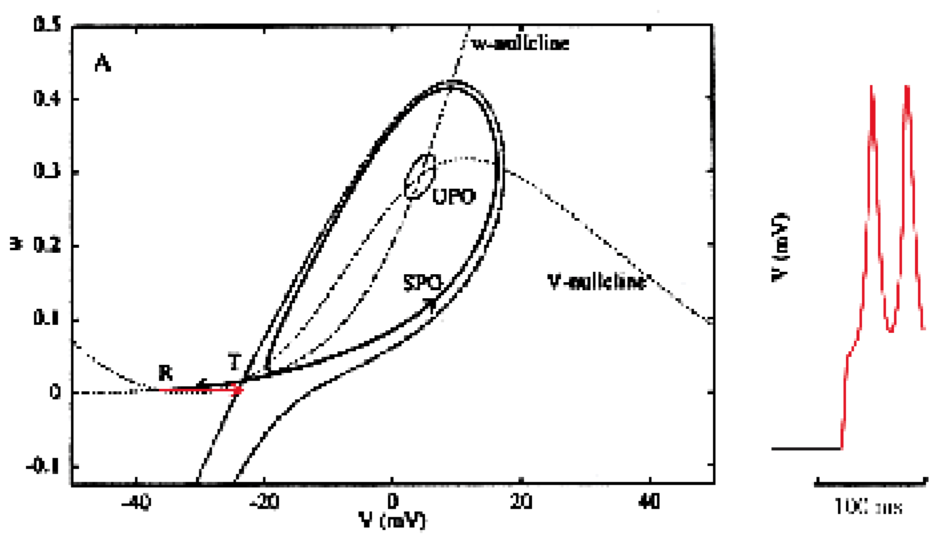


accompanying voltage waveform. Notice that only a very small voltage displacement is necessary (arrow in the phase plane).

Part d) This case is essentially the same as part a), where the voltage step is applied so as to transfer the trajectory across the UPO into the vicinity of the high-voltage equilibrium point. In this case, the equilibrium point is a spiral, so the trajectory oscillates after the transfer.



Part e) In this case, the goal is to move the trajectory across the stable manifold of the saddle node.



Part f) A depolarizing pulse can only make transfers like that shown in part e) above. At small currents (smaller than used in part e), the trajectory will return to rest; larger currents, like the one in e), put the trajectory into the limit cycle (SPO); larger current pulses that transfer the trajectory across both stable manifolds produce an action potential followed by a return of the trajectory to rest. So, it is not possible to transfer from the resting potential directly to the upper equilibrium point with a single depolarizing pulse.

From the upper equilibrium point, a depolarizing pulse which moves the trajectory across the UPO, the SPO, and the stable manifold (to a point similar to the endpoint of the arrow in part c) would produce an action potential followed by a return to the rest potential. Thus a transfer to the upper equilibrium point to the resting potential is possible with a single pulse.