Neural Networks and Biological Modeling

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ANSWERS TO QUESTION SET 4

Exercise 1: Inhibitory rebound

1.1 The effect of an applied current is to vertically shift the u-nullcline. Thus, as I becomes more negative, the fixed point moves away from the origin in the region $u, w < 0$.

1.2 For a long current pulse, the system will have settled at its fixed point at the moment the current is switched off. Thus at $t = 0$ the u-nullcline will instantaneously return to its original position and the system will move to the new fixed point $(u, w) = (0, 0)$. If I is large enough, it will do so by emitting an action potential (see Fig. 1).
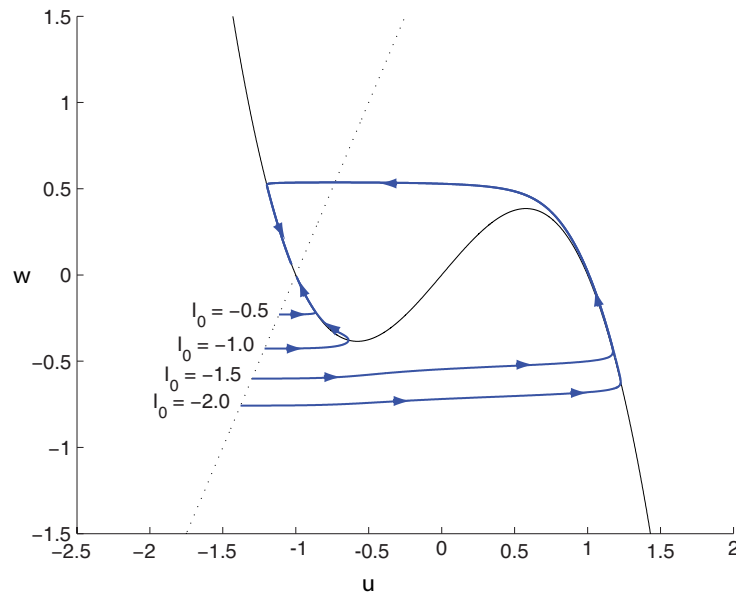

Figure 1: Response of the system of exercise 1 to the removal of a sustained inhibitory current. When the inhibitory current is large enough, a rebound spike occurs.

Exercise 2: Phase Plane Analysis

2.1 The flow arrows should qualitatively look like in figures 2(b) and 2(c)). For readability we split it into two figures. Note that the scales of the flow vectors are different across figures! Figure 2(a) shows a complete picture and a few trajectories.

2.2 From the phase plane (and more clearly from the flow vectors along the nullclines in figures 2(b) and 2(c)), we see an opposite dynamic for u and w at (u_2, w_2): small deviations of w are pushed back while small deviations of u will grow exponentially away from the fixed point. This is the signature of a saddle point. In figures 3(a), 3(b) and 3(c) we have plotted the flow vectors and a few trajectories in the

neighbourhood of each fixed point.

2.3 The key to analyze the stability of a *nonlinear* system is to do a linear approximation of the system at each fixed point and then apply the same techniques as discussed in question set 3 for linear systems. If you are not familiar with this strategy, you find a very clear introduction in chapter 6.2 in "Steven Strogatz, Nonlinear Dynamics and Chaos"; the book is available in the library).

We have the following system:

$$\begin{cases} \frac{d}{dt}u = F(u,w) = f(u) - w + I(t) \\ \frac{d}{dt}w = G(u,w) = \epsilon(g(u) - w) \end{cases} \tag{1}$$

with $\epsilon = 0.1$ and $I(t) = 0$.

The stability of the system in the neighbourhood of the fixed point 3 is analyzed by studying the eigenvalues of the Jacobian matrix at (u_3, w_3).

For completeness, we show, how you get the Jacobian matrix from linearizing the system at (u_3, w_3). The first order Taylor expansion of equation 1 is:

$F(u_3 + \Delta u, w_3 + \Delta w) \approx F(u_3, w_3) + \Delta u \frac{\partial F}{\partial u} + \Delta w \frac{\partial F}{\partial w}$

$G(u_3 + \Delta u, w_3 + \Delta w) \approx G(u_3, w_3) + \Delta u \frac{\partial G}{\partial u} + \Delta w \frac{\partial G}{\partial w}$

At the fixed point we have $F(u_3, w_3) = 0$ and $G(u_3, w_3) = 0$. Then, in matrix notation, we get

$$\begin{pmatrix} \frac{d}{dt}u \\ \frac{d}{dt}w \end{pmatrix} \approx \begin{pmatrix} \frac{\partial F}{\partial u} & \frac{\partial F}{\partial w} \\ \frac{\partial G}{\partial u} & \frac{\partial G}{\partial w} \end{pmatrix}_{|(u_3,w_3)} \begin{pmatrix} \Delta u \\ \Delta w \end{pmatrix}$$

That matrix of partial derivatives is the Jacobian of the system. We now plug the actual expressions from 1 into J and evaluate them at (u_3, w_3).

$$J = \begin{pmatrix} \frac{d}{du}f(u) & -1 \\ \epsilon \frac{d}{du}g(u) & -\epsilon \end{pmatrix}_{|(u_3,w_3)}$$

The functions $f(u)$ and $g(u)$ are not given explicitly. But the only thing we need to know is their rate of change with respect to u at (u_3, w_3). We can estimate those values from the figure: We first note that the given function graphs of the two nullclines actually correspond to $w = f(u)$ and $w = g(u)$ respectively. Then, we try to estimate the slopes of f and g at (u_3, w_3). Note that the scales in the u- and w direction are slightly different. From the figure, we estimate the following values: $\frac{d}{du}f(u)|_{u_3} \approx 0.5$ and $\frac{d}{du}g(u)|_{u_3} \approx 2.3$.

We can now use these values and calculate the eigenvalues λ_{+-} of J:

$$det(J - \lambda I) = det \begin{pmatrix} 0.5 - \lambda & -1 \\ 0.1 \times 2.3 & -0.1 - \lambda \end{pmatrix} \overset{!}{=} 0 \text{ (This is the \textit{characteristic equation} of J)}$$

$\Rightarrow \lambda^2 - 0.4\lambda + 0.18 = 0$ (The left hand side is the *characteristic polynomial* of J)

$\Rightarrow \lambda_{+-} \approx 0.2 \pm 0.75i$

We have complex eigenvalues with $Re\{\lambda\} > 0$. Therefore, (u_3, w_3) is unstable and a small perturbation will spiral (because λ is complex) outwards (see figure 3(c)).

Note that, for the stability analysis, we do not need exact values for λ. Therefore there is no need to do the numeric calculation exactly or to estimate the derivatives very precisely from the figure.

2.4

(i) The injected pulse immediately moves the membrane voltage to u_3. Because the current is very short with respect to the systems dynamics, we can assume that the nullclines do not move. The resulting trajectory is shown in figure 2(a) (the one starting at (u_3, w_1)).
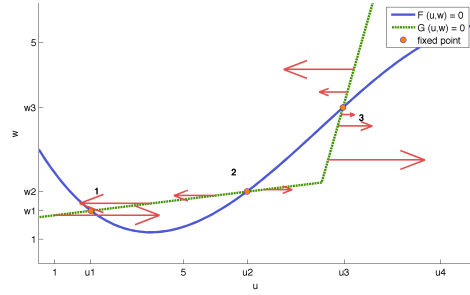
(ii) We plot $u(t)$ in figure 4. Note the regions of fast and slow voltage changes.
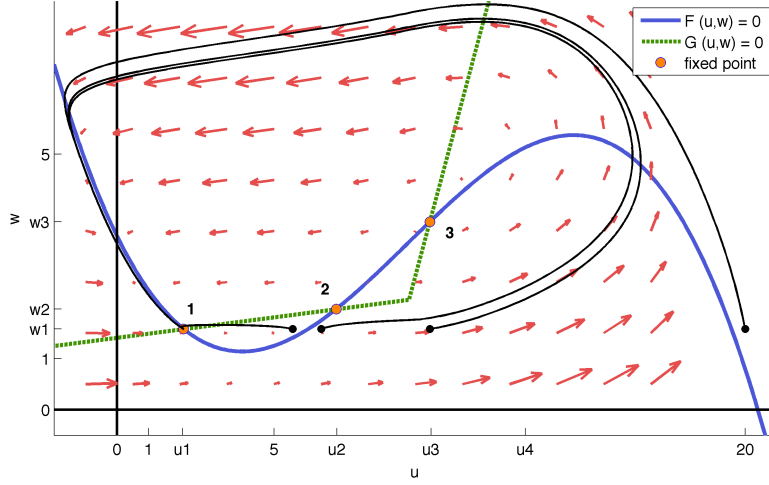
(a) Phase Plane with flow vectors and four trajectories
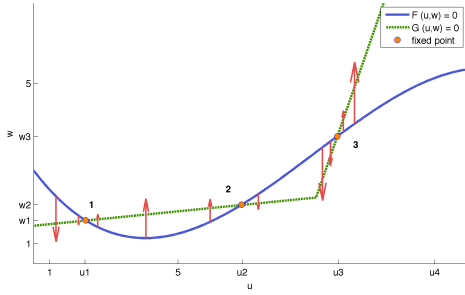
(b) Flow vectors along the u-nullcline

(c) Flow vectors along the w-nullcline

Figure 2: Flow vectors along the nullclines. For readability, the scales of the flow vectors are different across figures!

2.5 Look at the four trajectories in figure 2(a). The starting points are the results of pulse currents of different amplitude. We see that the neuron elicits a spike if the depolarization is large enough. From figure 2(a) one could make the (wrong) conclusion that we get a spike by crossing the u-nullcline. Looking more closely at figure 3(b) we see that crossing the nullcline is not sufficient. The line we have to cross is the stable manifold of the saddle point. That line is not shown in the figure but you can see from the trajectories in 3(b) that there is a boundary separating trajectories evolving towards the left and the right.

2.6 For $t > t_0$ the system is described by

$$
\begin{cases}
\frac{d}{dt}u = F(u,w) = f(u) - w + 3 \\
\frac{d}{dt}w = G(u,w) = \epsilon(g(u) - w)
\end{cases}
\tag{2}
$$

(i) The u-nullcline then is $\frac{d}{dt}u = 0 = f(u) - w + 3 \Rightarrow w = f(u) + 3$. The u-nullcline is shifted by $+3$. This changes the dynamics of the system as we can see from figure 5.

(ii) The resting state of the neuron is at (u_1, w_1) which is its only stable fixed point. When we inject a current at $t > 0$, the u-nullcline is shifted as an effect of $I(t)$ and (u_1, w_1) is no longer a fixed point. Instead, the neuron evolves according to the new dynamics. The trajectory is shown if figure 5. We observe that the new system does not have a stable fixed point. Instead it keeps evolving along a closed trajectory, called a limit cycle. For the neuron, this oscillation corresponds to a regular firing.

For completeness, we have added a second trajectory, starting near the unstable fixed point. We see that

(a) Flow vectors at fixed point 1   (b) Flow vectors at fixed point 2   (c) Flow vectors at fixed point 3
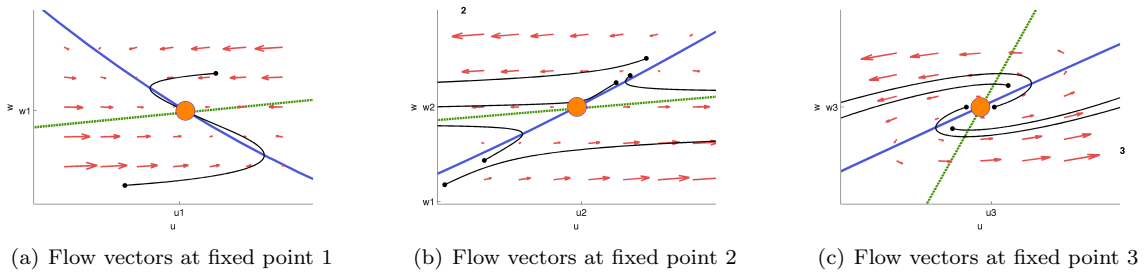
Figure 3: Flow vectors in the neighbourhood of the fixed points. Black lines indicate a few trajectories when the system evolves from one of the small black points.
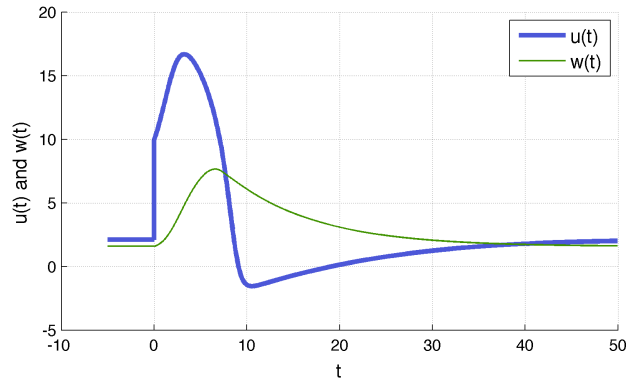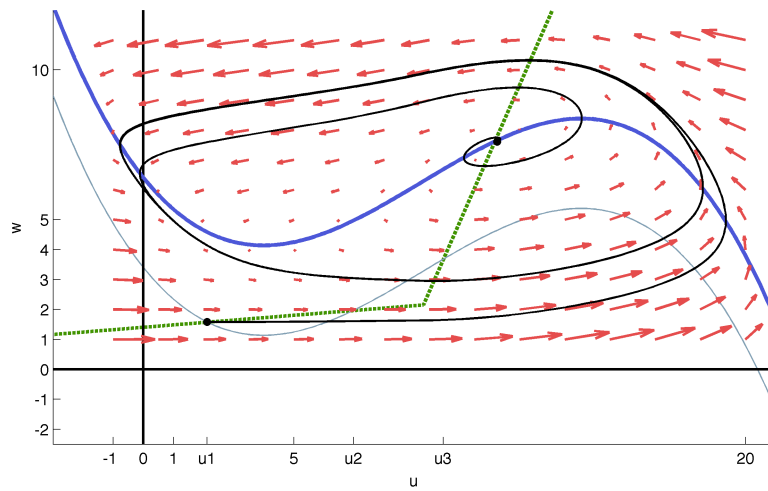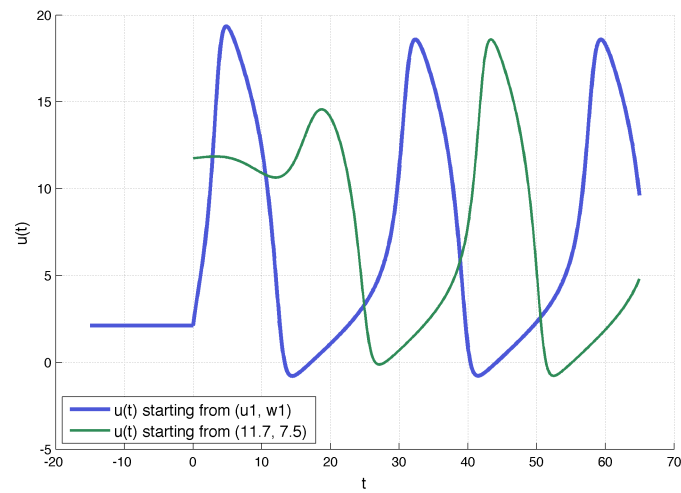

Figure 4: u(t) and (for completeness) w(t) after a pulse current is injected at t_0

this trajectory approaches, from "inside", the same limit cycle. The system has a stable limit cycle.

(a) Phase Plane, $I(t) = 3$. The u-nullcline is shifted by $+3$ (blue line). Two trajectories are shown in black.

(b) $u(t)$ for the two different trajectories shown in figure 5(a)

Figure 5: Phase plane and u(t).

Exercise 3: Impulse response

Two typical trajectories are shown on Fig. 6. Since the dynamics of u is much faster than that of w, the state of the system moves almost horizontally in the phase plane. The vertical component of the velocity of the system has a non-negligible effect only on the u-nullcline. If the initial pulse is strong enough to cross the middle branch of the u-nullcline, then the system will come back to the stable fixed point with a long detour, by initially following the u-nullcline and then moving horizontally. This trajectory corresponds to a spike. In the limit $\epsilon \ll 1$, the middle branch of the u-nullcline acts as the spiking threshold when the system is subjected to short current pulses.
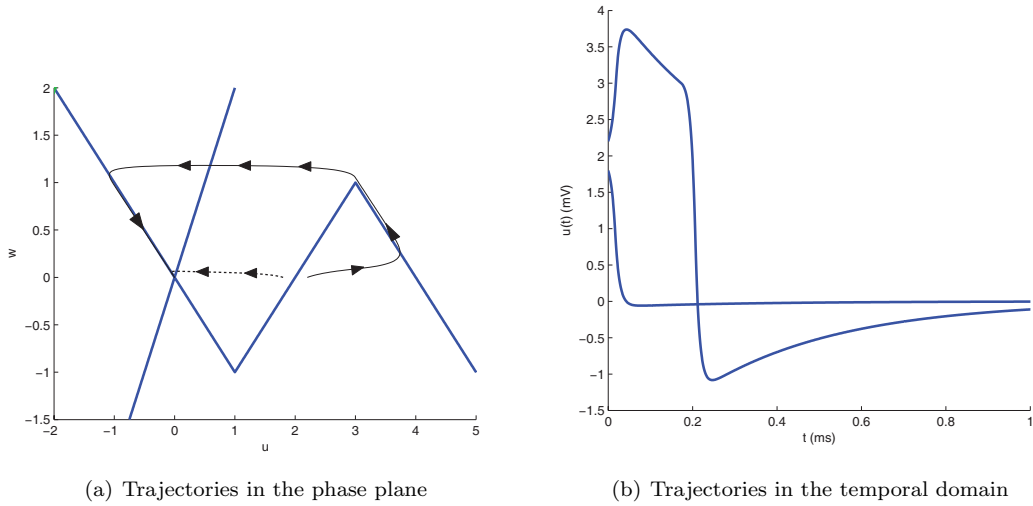

(a) Trajectories in the phase plane

(b) Trajectories in the temporal domain

Figure 6: