Mathematical Neuroscience

Homework Set 5 - due 4/26/04

Problems that are marked with a (*) are required only for graduate students in the class. Problems marked with (**) are required only for undergraduates (although graduate students should consider doing these as exercises anyway). Unmarked problems are required for everybody.

1. There are two short papers to read this time. The first paper (in file halfcenter.pdf) is a general discussion of "half-center" oscillators which are very important in rhythmogenesis. This paper discusses the neurophysiology of such oscillators. Discuss how the models we have discussed in class can describe the described behavior. Which of the models we have discussed would best describe the systems described in this paper?

   The second paper (in bressloff.pdf) provides an analysis of a ring of integrate-and-fire neurons using group theoretic methods. We have discussed much of this paper in class, so you should be able to follow it, despite its terseness. Think about the drawbacks to the methods discussed here (think of this as a model system that is used to illustrate a method, and not a model of particular neural circuit).

2. (*) Work out the self-consistency argument that leads to equation (2) in the paper by Bressloff and Coombs. Show that in the case of 2 oscillators, which are either in phase or 1/2 period out of phase, this is a simple equation. What equation do you get for the period of a traveling wave solution in a ring of N oscillators (this is the solution where each oscillator is $1/N$ out of phase with the adjacent ones).

3. Consider a network of N oscillators, and assume that we can reduce the equation for the phases to the following

$$\theta_i' = \omega + h(\theta_{i-1} - 2\theta_i + \theta_{i+1}), \qquad i = 1, \ldots, N$$

   where the index i is taken modulo N (in other words, the cell indexed by 0 is cell N, and the cell indexed by $N+1$ is cell 1). As in class, we define the phase difference $\Delta_i = \theta_i - \theta_{i-1}$ (the index is again taken modulo N).

   (a) Check that this system has $D_N \times S^1$ symmetry. In the case of 4 cells find all symmetries that are given in the table that was explained in class (the table contains all the symmetric solutions for this case). Pick two of these solutions and check directly that they are in fact solution by replacing them in the equation.

   (b) In the case of two oscillators we have

$$\theta_1' = \omega + h(\theta_2 - \theta_1) \qquad \theta_2 = \omega + h(\theta_1 - \theta_2).$$

   In this case the action of the group consists of switching the two cells. There are two symmetric solutions $\Delta = 0$ and $\Delta = \frac{1}{2}$ (I have used the convention that the phase is defined on [0,1]).

Show that if $\Delta_0 \neq 0, \frac{1}{2}$ is a stable fixed point for the phase difference, then so is $-\Delta_0$ (find the equation for the phase difference in show that these are both *stable* fixed points).

(c) Can the fixed point $\Delta = 0$ disappear in a saddle-node bifurcation? What other bifurcation can you expect in this case (hint: it has the same name as a tool that is used to handle hay).

Suppose $h(x) = \sin(2\Pi x^2)$ for $x \in [0, 1]$. Plot this function and show that at a certain value for the parameter a, the system indeed undergoes the bifurcation discussed above. Simulate this system using XPP and observe how this bifurcation occurs. Look in the manual or tutorial online to find out how to define periodic variables. Would you see something different for $h(x) = \sin(2\Pi x)$? Why is this case atypical?

(d) Explore the ring of 4 oscillators with the interaction defined by the same function. Can you detect any interesting bifurcations?

4. Consider the problem of identical pulse coupled oscillators we considered in class. We have defined the return map for two oscillators by $R(\phi) = h(h(\phi))$ where $h(\phi) = g(\epsilon + f(1 - \phi))$ (see the class notes for the definitions of the various variables and constants. As I mentioned in class, R can not be defined on the entire interval $[0, 1]$. What is the domain of definition of the function R?

   Assume that $f(\phi) = 1/b \ln(1 + [e^b - 1]\phi)$, where b is a constant. Compute g, h, and R (the last two should be relatively simple). Plot f for different values of the parameter b. Can you think of a biophysical interpretation of this parameter, if this was to model the subthreshold behavior of a neuron? How does changing ϵ and b affect how fast the two systems will take to synchronize?

   Simulate this system using XPP (see the scanned pages on how to simulate this type of system), and check whether your explanation about the speed at which things synchronize is justified.

   (*) As was mentioned in class, the argument I presented in class can be used to show that for most initial conditions (in a sense to be made precise below), N oscillators in an all to all coupled network of pulse coupled integrate and fire neurons will synchronize. The following is a first step in this proof.

   First the "strobing" map that was defined in the case of two oscillators needs to be extended to the more general case. We need to allow for the fact that a synchronous group of oscillators has formed. Since the behavior of oscillators in this group is identical, it is sufficient to track only one phase. However, when the group fires, the value of x for all other oscillators in the network is increased by $k\epsilon$, where k is the number of oscillators in this group. To deal with this problem it is sufficient to work under the assumption that the internal behavior of all oscillators is identical, but that the coupling strength between the is nonidentical.

   To define the new strobing map, notice that if we number the oscillators in the network after their phases ($0 < \phi_1 < \phi_2 < \ldots < \phi_n < 1$), then an oscillator with a lower number cannot overtake an oscillator with a higher number (Why?). Therefore the strobing map can be defined on the space

$$S = \{\phi = (\phi_1, \ldots, \phi_n) s.t 0 < \phi_1 < \phi_2 < \ldots < \phi_n < 1\},$$

with the exception of a small subset (to be defined below). To define the strobing map first define the map $\sigma(\phi)$ which advances all oscillator up to the next firing (which occurs at $1 - \phi_n$). We suppose that all oscillators fire with different strengths (it is not important to assume that they are multiples of ϵ). If oscillator ϕ_n fires with strength ϵ_n at this time, then, we can also define the map τ_{ϵ_n} which updates the phase of each oscillator. The equivalent of the map h above is now the map $h_n(\phi) = \tau_{\epsilon_n}(\sigma(\phi))$.

What space is this map defined on? Remember that it is possible that $f(\phi_i) + \epsilon_n \geq 1$, which means that oscillator i will fire synchronously with oscillator n from here on. Thus the oscillator i would get *absorbed* into the cluster n, and this event is called an absorption.

Using this definition, define the subset $A \subset S$ of oscillators that never get absorbed. Let R be the return map, which is obtained by composing h_i for all oscillators firing in succession (this is the equivalent of the R map defined previously, except that there will now be n h maps in the definition. Note that $R(A) \subset A$, and that R is one-to-one on the domain on which it is defined.

The following argument shows that A is small by showing that the determinant of the Jacobian of R, the return map, has absolute value greater than one (technically this would show that the set of A has measure zero, which means approximately that it cannot contain any open sets. You can convince yourself that if you define an expanding map on a closed set and iterate it many times, then most of the points in the set will eventually leak out of the sides, and what remains is very small).

To compute $\det(DR)$, express it as a product of the h's and show $\det(DR) = \Pi_{i=1}^{n} \det(D\tau_i) \det(D\sigma)$. Show that $\det(D\sigma) = \pm 1$, and that $\det(D\tau_i)$ is a diagonal matrix. Use the chain rule, and the definition of g to express $\det(D\tau_i)$ as a product of fractions involving g and f. Finally use the assumptions we made on f to show that $\det(D\tau_i) > 1$ if $\epsilon_i > 0$.

If you get stuck at some point you can consult the paper by Mirollo and Strogatz which can be found in JSTOR:

Renato E. Mirollo; Steven H. Strogatz, "Synchronization of Pulse-Coupled Biological Oscillators", *SIAM Journal on Applied Mathematics*, Vol. 50, No. 6. (Dec., 1990), pp. 1645-1662.

5. Problem 2 on this list:

   `http://www.math.pitt.edu/~bard/bardware/classes/compneuro/hw5.html`