

1. I have put a copy of an ODE file for the HH model on the web. If you want to use MatLab for this, exercise, this is fine - the equations should be easy to read. With the parameters as in the file (I0=10), integrate the equations for a while. You should get an oscillation with a period of about 14.65 msec. We will compute the adjoint for the HH equation and then compute the coupling interaction for excitatory and inhibitory coupling and also manipulate the time course of the synapse. The coupling of two neurons is through the voltage:

$$C \frac{dV_1}{dt} = \dots + \epsilon s_2 (V_{syn} - V)$$

so that the interaction function,  $H(\phi)$  is defined as

$$H(\phi) = \frac{1}{CT} \int_0^T V^*(t) s(t + \phi) (V_{syn} - V(t)) dt.$$

where  $V^*(t)$  is the voltage component of the adjoint. The synapse satisfies

$$\frac{ds}{dt} = a(V(t))(1 - V(t)) - s(t)/\tau_{syn}$$

The equations for  $s$  are also in the ODE file. Here is how to compute  $H(\phi)$ .

- (a) Compute one period of the oscillation. (In this case, this includes the 4 variables for the HH plus the synapse)
- (b) Find the peak of the action potential and use this as the starting condition to compute one cycle. (In XPP, use the Data Browser to find where  $V=1000$  - it will get to the max. Then click on Get in the Data Browser. Then integrate one more time.)
- (c) Find the adjoint. In matLab, Izhikevich provides code <http://www.izhikevich.org/publications/dsn.pdf> on page 493 to find the adjoint for a two-dimensional model. I guess it can be extended. In XPP, click on Numerics Averaging New Adjoint. Then Exit the numerics and click on XvsT to plot  $V^*(t)$ . It should be negative up to about  $t = 10$  and then positive the rest of the way.
- (d) Once you have  $V^*(t)$ , then you can compute the integral above for  $H(\phi)$  by using a shifted version of the stored values of the synapse and the values of the voltage. In XPP click on Numerics Averaging Make H. The column labeled "V" has  $H$  and the column labeled "M" has the odd part. Note that zeros of the odd part correspond to phase-locked solutions for mutual coupling. Neither synchrony nor anti-phase are stable since  $H'_{odd}(\phi) < 0$ .
- (e) Change  $V_{syn}$  to  $-80$  (inhibition) and repeat the calculation of  $H$ . You don't have to solve the adjoint again, it is the same. Report your results

- (f) Now change  $\tau_{syn}$  from 20 to 5. Integrate again a few times, compute the adjoint, and plot the odd part of the  $H$  function for excitatory  $V_{syn} = 0$  and inhibitory  $V_{syn} = -80$  coupling. Note that in the former, synchrony is stable and in the latter anti-phase is stable.
- On page 210 of the PDF chapter 8 of my book, I describe a 4 oscillator central pattern generator (CPG). Do exercise 24 on page 235.
  - Implement a 4 oscillator model using the HH equations with the same symmetries as in equation 46. (I have included code for you). There are several parameters to manipulate in this model; specifically whether coupling is excitatory or inhibitory ( $V_{syn}$ ), the time constant of the synapse ( $\tau_{syn}$ ) the overall strength of coupling  $gg$ , and the coupling between diagonals, left-right, and front-back. Try to get your CPG to generate a pronk, trot, walk, bound. The correct relations are given in the table.
  - Consider a ring of  $N$  oscillators

$$\theta'_i(t) = 1 + a[H(\theta_{i-1} - \theta_i) + H(\theta_{i+1} - \theta_i)] + b[H(\theta_{i+2} - \theta_i) + H(\theta_{i-2} - \theta_i)]$$

where  $i = 0, \dots, N - 1$  and we take modulo  $N$  for the indices. Thus,  $\theta_{-2} = \theta_{N-2}$  for example.

- (a) Show that there is a family of phase-locked solutions of the form

$$\theta_i = \Omega_m t + 2\pi im/N$$

and give an explicit formula for  $\Omega_m$ . Note that when  $m = 0$ , the solution is synchronous and when  $m = 1$ , this is a traveling wave with one cycle.

- (b) Determine conditions such that the synchronous solution is stable. (You will get a circulant stability matrix, for which you can write explicit eigenvalues). Determine conditions for which the  $m = 1$  wave is stable. Are there conditions such that synchrony is unstable but the wave is stable?

- Do exercise 28 page 236. As the exercise is somewhat mysteriously written, here are the equations:

$$\theta'_{i,j} = 1 + \sum_{k,l} \sin(\theta_{k,l} - \theta_{i,j})$$

where  $(k, l)$  are the nearest neighbors of  $(i, j)$ . Note that for example,  $(1,1)$  connects only to  $(1,2)$  and  $(2,1)$ , while  $(2,3)$  connects to  $(1,3), (3,3), (2,4)$ , and  $(2,2)$ . The phase locked solution will be  $\theta_{i,j} = t + \phi_{i,j}$ . The values of  $\phi_{i,j}$  are given in the diagram with one unknown  $\xi$  which you should be able to find using trig.

6. Holmes and Cohen (and Ermentrout and Kopell) consider the following model chain of  $N + 1$  oscillators

$$\begin{aligned}\theta'_1 &= 1 + \sin(\theta_2 - \theta_1) \\ \theta'_j &= 1 + c(j - 1) + \sin(\theta_{j+1} - \theta_j) + \sin(\theta_{j-1} - \theta_j), \quad j = 2, \dots, N + 1 \\ \theta'_{N+1} &= 1 + cN + \sin(\theta_N - \theta_{N+1}).\end{aligned}$$

The parameter  $c$  is a gradient in natural frequencies.

- (a) Let  $\phi_j = \theta_{j+1} - \theta_j$ , for  $j = 1, \dots, N$ . These are the phase-lags between successive oscillators. Write down the ODEs that these solve exploiting the fact that  $\sin(-x) = -\sin(x)$ .
- (b) Equilibrium points of this system are phase locked solutions. Show that they satisfy

$$\begin{aligned}0 &= c - 2 \sin \phi_1 + \sin \phi_2 \\ 0 &= c - 2 \sin \phi_j + \sin \phi_{j+1} + \sin \phi_{j-1} \\ 0 &= c - 2 \sin \phi_N + \sin \phi_{N-1}\end{aligned}$$

Let  $z_j = \sin \phi_j$ . Then the equilibria satisfy

$$c \begin{pmatrix} 1 \\ 1 \\ \vdots \\ 1 \end{pmatrix} = \begin{pmatrix} 2 & -1 & 0 & \dots & 0 & 0 \\ -1 & 2 & 1 & 0 & \dots & 0 \\ 0 & \vdots & \vdots & \vdots & \vdots & 0 \\ 0 & \dots & 0 & 0 & -1 & 2 \end{pmatrix} \begin{pmatrix} z_1 \\ z_2 \\ \vdots \\ z_N \end{pmatrix}$$

Invert this matrix to solve for  $z_1, \dots, z_N$ . It might help to get MatLab or Maple to do a few values of  $N$  for you until you see a pattern!

- (c) Given that  $\sin \phi_j = z_j$  find the range of  $c$  for which you can expect there is phase-locked solution. Show that if there is 1 phase-locked solution, then there is actually  $2^N$  locked solutions. You can use the general stability theorem on page 205 to show that the one corresponding to inverse sine that tends to 0 as  $c \rightarrow 0$  is stable. In fact, the others are all unstable.