School of Mathematical Sciences

G14TNS Theoretical Neuroscience

Problem sheet 8

1. Consider the *delayed* two neuron system

$$\dot{x}_i(t) = -x_i(t) + \sum_{j=1}^{2} W_{ij} \tanh(\beta x_j(t-\tau))$$

for $i = 1, 2$. Linearisation about the fixed point at the origin gives the linear delay-differential equation

$$\dot{x}_i(t) = -x_i(t) + \beta \sum_{j=1}^{2} W_{ij} x_j(t-\tau))$$

with solutions of the form $x_i(t) = \nu_i e^{\lambda t}$.

(a) Show that if $\mathbf{W}$ is symmetric and $\mathbf{v} = (\nu_1, \nu_2)$ is one of the eigenvectors of $\mathbf{W}$ with corresponding (real) eigenvalue ν, then λ satisfies the characteristic equation

$$\lambda + 1 = \beta \nu e^{-\lambda\tau}$$

(b) Substitute $\lambda = \imath\omega$ into the characteristic equation and equate real and imaginary parts to derive the pair of equations

$$\omega = -\tan\omega\tau, \qquad \beta|\nu| = \sqrt{1+\omega^2}$$

(c) Show that a static bifurcation ($\omega = 0$) occurs at the critical point

$$\beta_c \nu_+ = 1$$

where ν_+ is the smallest positive eigenvalue.

(d) Using a graphical argument establish that the smallest non-zero positive solution ω_c of the transcendental equation $\omega = -\tan\omega\tau$ lies in the range $\pi/2 \leq \omega_c\tau \leq \pi$. Hence show that the fixed point can destabilise via a Hopf bifurcation at the critical point

$$\beta_c \nu_- = -\sqrt{1+\omega_c^2}$$

Also show that

i.

$$\beta_c \nu_- \approx -\frac{\pi}{2\tau} \text{ when } \tau \ll 1$$

ii.

$$\beta_c \nu_- \approx -\sqrt{1+\left(\frac{\pi}{\tau}\right)^2} \text{ when } \tau \gg 1$$

(e) From parts (c) and (d) write down the condition for a Hopf bifurcation to *win* over a static bifurcation.

2. Consider the functional-differential equation

$$\frac{du}{dt} = r\left[-u + \left(1 - \int_{t-1}^{t} u(s)ds\right) f(u)\right]$$

which Wilson and Cowan introduced as a model of the fraction of firing neurons, u, within some population with self-feedback. Here $f : \mathbb{R} \to [0, 1]$ is a smooth monotonically increasing firing rate function and r is the absolute refractory period of the neurons.

   (a) Show that there is at least one fixed point $\overline{u}\ in (0, 1/2)$.

   (b) Show that the linearised equations of motion are

$$\frac{dy}{dt} = r\left(-Ay - b\int_{t-1}^{t} y(s)ds\right)$$

   with $A = 1 - (1 - \overline{u})f'(\overline{u}) < 1$ and $b = f(\overline{u}) \in (0, 1)$.

   (c) Show that solutions of the form $y(t) = e^{\lambda t}$ yield the characteristc equation

$$\lambda + Ar + br\frac{1 - e^{-\lambda}}{\lambda} = 0$$

   (d) Assume $-b < A < bM$ where $M = -sin(\xi)/\xi$ with ξ the smallest root of $\tan(\xi) = \xi$ greater than π. Then show that the fixed point becomes unstable at

$$r = \frac{1}{b}\frac{\omega_c^2}{1 - \cos\omega_c}, \qquad \frac{A}{b} = -\frac{\sin\omega_c}{\omega_c},$$

   (e) By introducing $\epsilon = 1/r$ and

$$z(t) = \int_{t-1}^{t} u(s)ds$$

   show that the model is equivalent to the two-dimensional delay-differential equation

$$\epsilon\frac{du}{dt} = -u + (1 - z)f(u), \qquad \frac{dz}{dt} = u(t) - u(t - 1)$$

   (f) Consider the limit $\epsilon \to 0$ and and describe how to construct a singular periodic orbit when $f(u)$ has a sigmoidal shape.

   (g) Show that the period, T, of such a singular orbit must satisfy $T < 2$.

   (h) Use the following XPP ODE file to simulate this model and to plot the slow manifold

```
par a=8.0,theta=-0.333,r=300
f(x)=1.0/(1+exp(-a*(x+theta)))

u(0)=0.2
z(0)=0.1

u'=r*(-u+(1-z)*f(u))
z'=u-delay(u,1.0)

@ delay=1,method=stiff,dt=0.001,transient=18,total=20,
@ xp=u,yp=z,xlo=0,ylo=0,xhi=1,yhi=0.5

done
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