A Wilson-Cowan System with Delay

Consider the differential-delay system

$$\begin{aligned} x'(t) &= -x(t) + S(ax(t-\tau) - by(t-\tau) - \theta_x) \\ y'(t) &= -y(t) + S(cx(t-\tau) - dy(t-\tau) - \theta_y) \end{aligned} \qquad (1)$$

where S is the function $S(z) = \frac{1}{1+e^{-z}}$. If the delay τ is zero, this is a simple version of the Wilson-Cowan system which models the interaction between two groups of nerve cells in the brain. The function $x(t)$ represents the percent of cells active at time t in the population E of excitatory cells, and $y(t)$ represents the percent of cells active in the inhibitory population I. The terms θ_x and θ_y are external inputs to the cells in E and I, respectively. The system (1) with $\tau > 0$ models two interacting populations of cells where the feedback from cells is delayed by a constant time $\tau > 0$.

For the non-delayed system, with $\tau = 0$, it is clear that any constant solution $x(t) \equiv \bar{x}, y(t) \equiv \bar{y}$ must satisfy the two equations

$$\begin{aligned} \bar{x} &= S(a\bar{x} - b\bar{y} - \theta_x) \\ \bar{y} &= S(c\bar{x} - d\bar{y} - \theta_y). \end{aligned}$$

Note that the same points $(\bar{x}, \bar{y})$ are also the **equilibrium solutions** of (1) for any delay τ, since if $x(t)$ is a constant, then $x(t-\tau) \equiv x(t)$ for any value of τ, and similarly for $y(t)$.

In the case of the non-delayed system with $\tau = 0$, determining the *stability* of a constant solution $(\bar{x}, \bar{y})$ involves linearizing the system around $(\bar{x}, \bar{y})$, and then writing the linearized system in matrix form as $X'(t) \approx AX(t)$. The solutions of this linear system can be written as a linear combination of $e^{\lambda t}\vec{v}$ where $(\lambda, \vec{v})$ range over the eigenpairs of the matrix A, and the solution $(\bar{x}, \bar{y})$ can be shown to be *asymptotically stable* if, and only if, all of the eigenvalues λ of A have negative real part. The same sort of analysis can be applied to the delayed system (1).

Let $(\bar{x}, \bar{y})$ be any equilibrium solution of (1), and write

$$\begin{aligned} x(t) &= \bar{x} + u(t) \\ y(t) &= \bar{y} + v(t) \end{aligned}$$

where the functions u and v are assumed to be small. We want to know if this perturbed solution will tend to the point $(\bar{x}, \bar{y})$ as $t \to \infty$. This will happen if, and only if, both $u(t)$ and $v(t)$ tend to zero as $t \to \infty$. To obtain equations for u and v, substitute the assumed functions $x(t) = \bar{x} + u(t)$ and $y(t) = \bar{y} + v(t)$ into (1). Since $\bar{x}$ and $\bar{y}$ are constants, it is clear that $u'(t) \equiv x'(t)$ and $v'(t) \equiv y'(t)$.

Consider the first equation in the system (1):

$$x'(t) \equiv u'(t) = -(\bar{x} + u(t)) + S(a(\bar{x} + u(t-\tau)) - b(\bar{y} + v(t-\tau)) - \theta_x).$$

Let the argument of the function S be written as $z + \Delta z$, where $z = a\bar{x} - b\bar{y} - \theta_x$ is a constant, and $\Delta z = au(t-\tau) - bv(t-\tau)$ is a *small* perturbation term. Then the equation becomes

$$u'(t) = -\bar{x} - u(t) + S(z + \Delta z).$$

Since S is an analytic function with derivative $S'(z) = S(z)(1 - S(z))$, we can use its Taylor series to write

$$S(z + \Delta z) = S(z) + S'(z)\Delta z + O((\Delta z)^2)$$

where the term $O((\Delta z)^2)$ contains all of the nonlinear terms in $u(t-\tau)$ and $v(t-\tau)$. Then

$$\begin{aligned} S(a(\bar{x}+u(t-\tau)) - b(\bar{y}+v(t-\tau)) - \theta_x) &= S((a\bar{x} - b\bar{y} - \theta_x) + (au(t-\tau) - bv(t-\tau))) \\ = S(a\bar{x} - b\bar{y} - \theta_x) &+ S'(a\bar{x} - b\bar{y} - \theta_x)(au(t-\tau) - bv(t-\tau)) + O((\Delta z)^2) \\ &= \bar{x} + \bar{x}(1-\bar{x})(au(t-\tau) - bv(t-\tau)) + O((\Delta z)^2). \end{aligned}$$

Putting this back into the equation for $u'(t)$, and dropping the nonlinear terms, we have

$$u'(t) \approx -u(t) + \bar{x}(1-\bar{x})(au(t-\tau) - bv(t-\tau)).$$

Similarly, the equation for $v'(t)$, when linearized, becomes

$$v'(t) \approx -v(t) + \bar{y}(1-\bar{y})(cu(t-\tau) - dv(t-\tau));$$

and the linearized system (1) can be written in matrix form as

$$\begin{pmatrix} u(t) \\ v(t) \end{pmatrix}' = -\begin{pmatrix} u(t) \\ v(t) \end{pmatrix} + M \begin{pmatrix} u(t-\tau) \\ v(t-\tau) \end{pmatrix}, \qquad (2)$$

where the matrix $M = \begin{pmatrix} a\bar{x}(1-\bar{x}) & -b\bar{x}(1-\bar{x}) \\ c\bar{y}(1-\bar{y}) & -d\bar{y}(1-\bar{y}) \end{pmatrix}$.

It is known that, in a *small* neighborhood of an equilibrium $(\bar{x}, \bar{y})$, solutions of (1) will behave very much like solutions of the linearized system (2), and solutions of the linear system can be assumed to have the form

$$\begin{aligned} u(t) &= \bar{u}e^{st} \\ v(t) &= \bar{v}e^{st}. \end{aligned} \qquad (3)$$

Substituting the functions (3) into (2), we have

$$\begin{pmatrix} u(t) \\ v(t) \end{pmatrix}' = \frac{d}{dt}\left(e^{st}\begin{pmatrix} \bar{u} \\ \bar{v} \end{pmatrix}\right) = se^{st}\begin{pmatrix} \bar{u} \\ \bar{v} \end{pmatrix};$$

and the linearized system (2) has the form

$$se^{st}\begin{pmatrix}\bar{u}\\ \bar{v}\end{pmatrix}+e^{st}\begin{pmatrix}\bar{u}\\ \bar{v}\end{pmatrix}-Me^{st}e^{-s\tau}\begin{pmatrix}\bar{u}\\ \bar{v}\end{pmatrix}\equiv\begin{pmatrix}0\\ 0\end{pmatrix}.$$

Dividing by e^{st},

$$(sI+I-e^{-s\tau}M)\begin{pmatrix}\bar{u}\\ \bar{v}\end{pmatrix}=\begin{pmatrix}0\\ 0\end{pmatrix},$$

and this matrix equation can have *non-zero solutions* if, and only if, the determinant of the matrix $(s+1)I-e^{-s\tau}M$ is zero; that is, we need to find all solutions of the equation

$$det\begin{pmatrix} s+1-e^{-s\tau}a\bar{x}(1-\bar{x}) & e^{-s\tau}b\bar{x}(1-\bar{x})\\ -e^{-s\tau}c\bar{y}(1-\bar{y}) & s+1+e^{-s\tau}d\bar{y}(1-\bar{y})\end{pmatrix}$$

$$=(s+1)^2+(d\bar{y}(1-\bar{y})-a\bar{x}(1-\bar{x}))(s+1)e^{-s\tau}-((ad-bc)\bar{x}\bar{y}(1-\bar{x})(1-\bar{y}))e^{-2s\tau}=0.$$

If this last equation is multiplied by the positive quantity $e^{2s\tau}$ it becomes a simple quadratic equation in $\rho=e^{s\tau}(s+1)$:

$$\rho^2+(d\bar{y}(1-\bar{y})-a\bar{x}(1-\bar{x}))\rho-(ad-bc)\bar{x}\bar{y}(1-\bar{x})(1-\bar{y})=0. \tag{4}$$

Then if $\rho=r_1$ and $\rho=r_2$ are the two roots of this quadratic equation, it will be the case that the equilibrium solution $(\bar{x},\bar{y})$ is stable if, and only if, all complex roots s of the two equations

$$(s+1)e^{s\tau}=r_i,\ \ i=1,2 \tag{5}$$

have real parts less than zero.

The following theorem (see [2]) addresses this problem. The proof of the theorem requires some messy analysis in complex variables, but should be readable by anyone who has had at least one introductory course covering complex variables. For a very readable book covering differential-delay equations see [1].

Theorem 1 *If $a>0$, the roots of the equation*

$$se^s+ae^s+(u+v\imath)=0$$

all satisfy $\Re(s)<0$ if, and only if, $u+v\imath$ is in the bounded convex region, symmetric about the u-axis, where

$u^2+v^2<a^2+y_{-1}^2$ if $u+v\imath$ is in the first or fourth quadrant

$u^2+v^2<a^2+y_0^2$ if $u+v\imath$ is in the second or third quadrant.

Both y_{-1} and y_0 are roots of the transcendental equation $y_i\tan(y_i+\alpha)=a$, with $0<y_0<\frac{\pi}{2}-\alpha$, and $-\frac{\pi}{2}-\alpha<y_{-1}<-\alpha$, where $\alpha=\arctan\left|\frac{u}{v}\right|,\ \ 0\le\alpha\le\frac{\pi}{2}$.

Note: If a root $u + v\imath$ of the polynomial is real, that is $v = 0$, then $\alpha = \arctan|\frac{u}{v}| = \arctan|\infty| = \frac{\pi}{2}$. This implies that $y_0 = 0$ and $y_{-1}\tan(y_{-1}+\frac{\pi}{2}) = a$ with $-\pi < y_{-1} < -\frac{\pi}{2}$.

Notice that if we multiply (5) by the positive time delay τ, and let $z = s\tau$ then we will need to show that the roots of

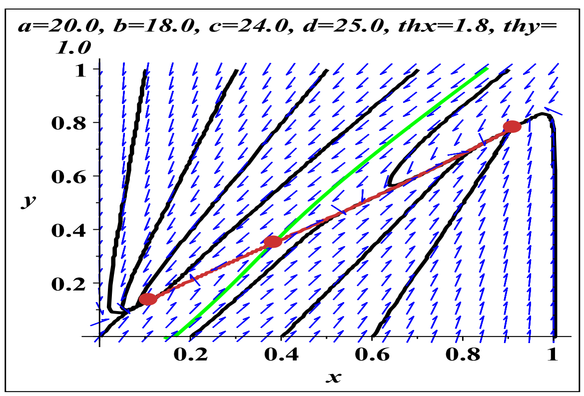
$$ze^z + \tau e^z - \tau r_i = 0$$

all have negative real parts, so that the Theorem applies directly to our problem.

Example: Consider the delayed Wilson-Cowan system

$$\begin{aligned} x'(t) &= -x(t) + S(20x(t-\tau) - 18y(t-\tau) - 1.8) \\ y'(t) &= -y(t) + S(24x(t-\tau) - 25y(t-\tau) - 1.0). \end{aligned} \qquad (6)$$

The figure below shows a phase plane for this system, with $\tau = 0$.



Exercise 1. Show that (6) has exactly three critical points $(\bar{x}, \bar{y})$ at $P_1 \approx (0.108407, 0.137514)$, $P_2 \approx (0.383516, 0.352498)$ and $P_3 \approx (0.910481, 0.782783)$.

Exercise 2. Show that when $\tau = 0$, the point P_1 is a sink, P_2 is a saddle point, and P_3 is a sink. The green and red trajectories in the figure are the stable and unstable manifolds of the saddle point. Note that any trajectory that starts to the left of the stable manifold ends up at $P_!$, and those starting on the right end up at P_3.

Exercise 3. Use Theorem 1 to show that P_1 becomes unstable for τ between 1.94 and 1.95.

Exercise 4. Use Theorem 1 to show that P_3 becomes unstable for τ between 0.69 and 0.70. (A solution of Exercise 4 is given at the end of this paper.)

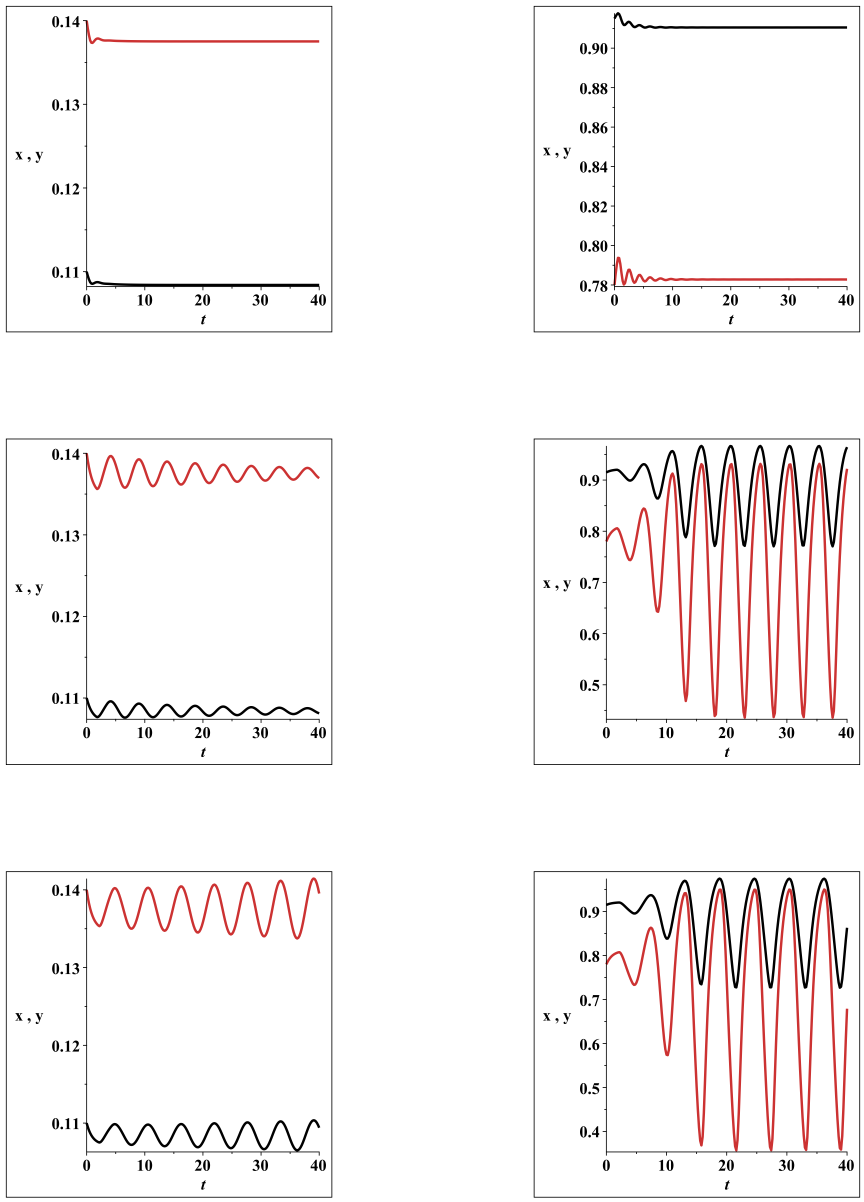
Numerical routines for solving differential-delay equations have recently been developed, and are now available in Maple and other computer algebra systems. Information concerning the use of these routines in Maple can be found on the **dsolve**[**numeric**][**delay**] help page. To see how the behavior of trajectories of (6) changes around the critical points we used the following Maple routines:

- To define the system (enter desired values for $x(0)$ and $y(0)$):
```
ddesys:={diff(x(t),t)=-x(t)+1.0/(1.0+exp(1.8+18*y(t-tau)-20*x(t-tau))),
   diff(y(t),t)=-y(t)+1.0/(1.0+exp(1.0+25*y(t-tau)-24*x(t-tau))),x(0)=..,y(0)=..):
```
- To solve the system (enter desired value for the delay tau):
```
dsn:=dsolve(eval(ddesys,tau=...),numeric);
```
- To plot the solution $x(t)$ from $t = 0$ to $t = 40$:
```
Px:=plots[odeplot](dsn,0..40,labels=[t,x]);
```
- To plot the solution $y(t)$ from $t = 0$ to $t = 40$:
```
Py:=plots[odeplot](dsn,[[t,y(t),color=green]],0..40,labels=[t,y]);
```
- To plot an (x, y) phase plot in the unit square, with t ranging from 0 to 40:
```
Pxy:=plots[odeplot](dsn,[[x(t),y(t)]],0..40,x=0..1,y=0..1,labels=[x,y]);
```

Using these instructions, trajectories of $x(t)$ and $y(t)$ near the two critical points P_1 and P_3 were calculated, and plotted for three different values of the delay τ. In the six figures below, the graph on the left shows a solution starting near the critical point P_1 and the graph on the right uses initial conditions near P_3. The values of τ increase from top to bottom, using the three values $\tau = 0.5, 1.7$, and 2.1. In the graphs on the left the initial conditions are $x(0) = 0.11, y(0) = 0.14$ and on the right the initial conditions are $x(0) = 0.915, y(0) = 0.78$. In all six cases, the resulting trajectory either approaches or spirals around the nearest critical point. It looks like limit cycles occur at both of the points P_1 and P_3 when they become unstable with increasing delay. The critical point P_2 is an unstable saddle point when $\tau = 0$, and you can use Theorem 1 to show that it will remain unstable for any positive delay τ. This means that when $\tau \geq 1.95$ the system has *no* stable attractors. The following lines of Maple code were used to generate the *top* graph on the *left*.

```
with(plots);
ddesys := {diff(x(t), t) = -x(t)+1.0/(1.0+exp(1.8+18*y(t-tau)-20.0*x(t-tau))),
 diff(y(t),t)=-y(t)+1.0/(1.0+exp(1+25*y(t-tau)-24*x(t-tau))),x(0)=.11,y(0)=.14};
dsn := dsolve(eval(ddesys, tau=0.5), numeric);
Px := plots[odeplot](dsn,0..40,color = black,thickness=3,labels=[t,"x , y"]);
Py := plots[odeplot](dsn, [[t, y(t), color = orange, thickness = 3]], 0..40);
display(Px,Py);
```

$x(0) = 0.11, y(0) = 0.14$ $\qquad\qquad$ $x(0) = 0.92, y(0) = 0.78$



$\tau = 0.5$

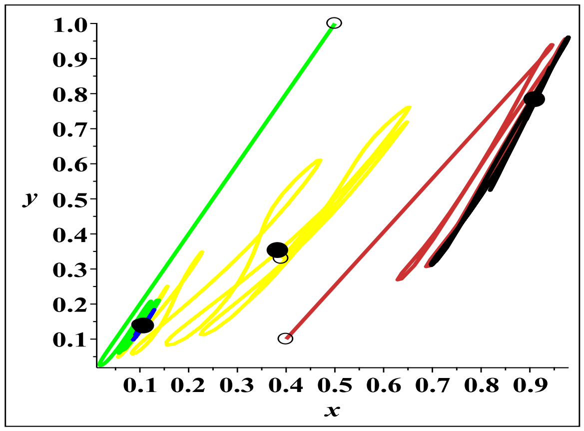
$\tau = 1.7$

$\tau = 2.1$

In the figure below some trajectories are shown plotted in the (x, y) plane, with the value of $\tau = 2.4$. Notice that trajectories can intersect in the phase plane. There is no uniqueness theorem for a differential equation with delay. The numerical routines used here assume the value of the functions x and y on the initial interval $-\tau < t < 0$ is equal to the constant value $x(0)$, or $y(0)$, respectively. Even with this assumption there can be infinitely many solution curves passing through a given point.

Exercise 5. With $\tau = 2.4$, see how close to P_1 a trajectory can start and still wind up oscillating around P_3. Use the phase plane for $\tau = 0$ to help you decide where to start.

Some trajectories in the phase space of (1) with $\tau = 2.4$



Solution of Exercise 4

At the critical point $P_3 = (0.910481, 0.782783)$ the quadratic (4) is

$$\rho^2 + 2.620737\rho - 0.942386,$$

and its two roots are $r_1 = -2.941153$ and $r_2 = 0.320413$. Check it!

For the point P_3 to be stable, we need to determine for what values of $\tau > 0$ all roots of $ze^z + \tau e^z - \tau r_i$ have negative real parts for both $r_i = r_1$ and r_2. Using the notation in Theorem 1, this is equivalent to asking for what values of τ do all of the roots of

$$ze^z + ae^z + (u + v\imath)$$

have negative real parts, where $a \equiv \tau$ and $u + v\imath \equiv -\tau r_i$.

Consider first the root $r_i = r_1$, so $u + v\imath \equiv (2.941153)\tau + 0\imath$, which is a positive real number, hence in the positive half plane. This means we must use Theroem 1 with $Y = y_{-1}, \alpha = arctan|\frac{u}{v}| = arctan(\infty) = \frac{\pi}{2}$. According to the theorem, the value of Y must satisfy $Y \tan(Y + \frac{\pi}{2}) = a \equiv \tau$. We can write a simple one line Maple program to produce a table with columns $(\tau, Y, u^2 = (\tau r_1)^2, \tau^2 + Y^2)$. Print this Table for increasing values of τ until the entry in column 3 becomes larger than the entry in column 4. If this is done with small increments in τ, it will locate the value of τ where P_3 becomes unstable. Check that it happens between $\tau = 0.693$ and 0.694.

For the other root r_2, $u + v\imath = (-0.320413)\tau$, and we need to use Theorem 1 with $Y = y_0$. For stability we must have

$$u^2 + v^2 < a^2 + Y^2.$$

Since $u = -\tau r_2 = (-0.320413)\tau$, $v = 0$, $a = \tau$, and $Y = y_0 = 0$, this condition becomes $0.10266\tau^2 < \tau^2$, and it is satisfied for any positive value of τ. Therefore the point P_3 is stable if $\tau \leq 0.693$ and unstable if $\tau \geq 0.694$. Remember that the conditions must be satisfied for both of the roots r_1 and r_2.

Exercise 3 can be solved in a similar manner.

Exercise 5. Read as much as you can in [3] and see if you can prove that Hopf bifurcations occur at the critical points P_1 abd P_3 when they lose stability. This is not a simple problem.

References

[1] Richard Bellman and Kenneth L. Cooke. *Differential-Difference Equations*, Academic Press, New York 1963.

[2] V. W. Noonburg. *Roots of a transcendental equation associated with a system of differential-difference equations*, SIAM J. Appl. Math, **17**, 1969.

[3] For a more recent (2011) article, by Richard Rand, see:

`pi.math.cornell.edu/~rand/randpdf/DDE-chapter3.pdf`

on the web. It describes periodic motions in differential-delay equations that are created in Hopf bifurcations.