Comparison of Different Mathematical Models for an Inhibitory Cluster of Neurons

V. W. Noonburg

November 1, 2021

This paper will consider possible mathematical models for an n-cell cluster of inhibitory neurons. It is assumed that at time $t = 0$ each cell in the cluster receives an initial burst of activity $x_i(0)$. Over a short period of time $0 \leq t \leq T$ the activity $x_i(t)$ in the ith cell is assumed to grow logistically, and is simultaneously damped by the activity in each of the other $n-1$ connected cells. It will be assumed that the activity in the ith neuron of the cluster satisfies the differential equation

$$x_i'(t) = F_i(t, \vec{x}) = x_i(t)\left(1 - c_i x_i(t) - \sum_{k=1..n, k\neq i} A_{ik} x_k(t)\right), \ 1 \leq i \leq n. \qquad (1)$$

(Note: when these equations are used to model the growth of interacting populations the constant $1/c_i$ is called the carrying capacity of the ith population and refers to the maximum number of individuals in that population that the environment can sustain).

In the above equation the constant A_{ik} *determines the negative effect that the current activity in cell k has on the activity in cell i.* If the A_{ik} are positive constants this is just the Lotka-Volterra system for n competing species. Much research has been done on this system (see Hirsch, [2]), and it is known to have several different types of asymptotic behavior. In Section 1 we will show that if the interaction coefficients A_{ij} are all positive constants, and a relatively simple condition is put on the $n \times n$ coefficient matrix

$$\mathbf{M} = \begin{pmatrix} c_1 & A_{12} & A_{13} & \cdots & A_{1n} \\ A_{21} & c_2 & A_{23} & \cdots & A_{2n} \\ & & \vdots & & \\ A_{n1} & A_{n2} & A_{n3} & \cdots & c_n \end{pmatrix}, \qquad (2)$$

there will be a single asymptotically stable equilibrium point in the positive cone $\Re^n_+$ of $\Re^n$, and all trajectories that start in the interior of $\Re^n_+$ will tend to that equilibrium point as $t \to \infty$.

Since a cluster of neurons that produces the same response to every input would not be very useful as a pattern recognition device, this paper will explore some simple changes in the system that cause it to produce a much more interesting and useful classification of its inputs.

1 The Model with Constant Interaction Coefficients

In this section we will examine closely the solution of the system (1) with constant interaction coefficients A_{ik}.

An **equilibrium**, or critical point, for the system (1) is a vector $\bar{x} = (\bar{x}_1, \bar{x}_2, \cdots, \bar{x}_n)$ where each derivative $F_i(t, \bar{x}) = 0$; that is, it is a state of the system at which no further change in any of the activity levels can occur. If none of the $\bar{x}_i$ are equal to zero at an equilibrium, this requires that

$$c_i \bar{x}_i + \sum_{k=1..n, k \neq i} A_{ik} \bar{x}_k = 1, \; 1 \leq i \leq n. \tag{3}$$

Using the matrix $\mathbf{M}$ defined in (2) above, this means that for $\bar{x}$ to be an equilibrium in the interior of $\Re^n_+$ it must satisfy the condition

$$\mathbf{M}\bar{x} = \begin{pmatrix} 1 \\ 1 \\ \vdots \\ 1 \end{pmatrix}.$$

If the matrix $\mathbf{M}$ is invertible this means there can exist at most one equilibrium point, and if this is a point in the interior of $\Re^n_+$ then its stability can be determined by the eigenvalues of the Jacobian matrix $\vec{\nabla} F = \left(\frac{\partial F_i}{\partial x_j} \right)_{x=\bar{x}}$ where F_i are the functions defined in (1). Differentiating the system equations (1) we see that $\vec{\nabla} F$ has the form

$$\begin{pmatrix} 1 - 2c_1\bar{x}_1 - \sum_{k\neq 1} A_{1k}\bar{x}_k & -A_{12}\bar{x}_1 & \cdots & -A_{1n}\bar{x}_1 \\ -A_{21}\bar{x}_2 & 1 - 2c_2\bar{x}_2 - \sum_{k\neq 2} A_{2k}\bar{x}_k & \cdots & -A_{2n}\bar{x}_2 \\ \vdots & & & \\ -A_{n1}\bar{x}_n & -A_{n2}\bar{x}_n & \cdots & 1 - 2c_n\bar{x}_n - \sum_{k\neq n} A_{nk}\bar{x}_k \end{pmatrix}. \tag{4}$$

At the critical point $\bar{x}$ equation (3) can be used to simplify the diagonal elements of $\vec{\nabla}F$ to $-c_j\bar{x}_j$ so that the Jacobian matrix becomes

$$\vec{\nabla}F = \begin{pmatrix} -c_1\bar{x}_1 & -A_{12}\bar{x}_1 & \cdots & -A_{1n}\bar{x}_1 \\ -A_{21}\bar{x}_2 & -c_2\bar{x}_2 & \cdots & -A_{2n}\bar{x}_2 \\ \vdots & & & \\ -A_{n1}\bar{x}_n & -A_{n2}\bar{x}_n & \cdots & -c_n\bar{x}_n \end{pmatrix} \tag{5}$$

$$= - \begin{pmatrix} \bar{x}_1 & 0 & \cdots & 0 \\ 0 & \bar{x}_2 & \cdots & 0 \\ \vdots & & & \\ 0 & 0 & \cdots & \bar{x}_n \end{pmatrix} \cdot \mathbf{M}.$$

Example 1 *: Consider a* 5*-cell cluster with all of the* c_i *equal to* 0.25*. Using randomly generated small values for the weights, the coefficient matrix we will use is:*

$$\mathbf{M} = \begin{pmatrix} 0.25 & 0.02 & 0.06 & 0.01 & 0.04 \\ 0.05 & 0.25 & 0.06 & 0.02 & 0.01 \\ 0.04 & 0.02 & 0.25 & 0.05 & 0.07 \\ 0.07 & 0.08 & 0.02 & 0.25 & 0.05 \\ 0.04 & 0.01 & 0.07 & 0.08 & 0.25 \end{pmatrix} \cdot .$$

The equilibrium solution is

$$\bar{x} = \mathbf{M}^{-1} \begin{pmatrix} 1 \\ 1 \\ 1 \\ 1 \\ 1 \end{pmatrix} \approx \begin{pmatrix} 2.793641 \\ 2.644354 \\ 2.370383 \\ 1.736378 \\ 2.227895 \end{pmatrix},$$

and the eigenvalues of the Jacobian matrix $\vec{\nabla}F$ *can be found using Maple. The five eigenvalues are* $-1, -0.34223, -0.57562,$ *and* $-0.51266 \pm 0.04657\mathbf{i}$*, implying that the equilibrium* $\bar{x}$ *is a spiral attractor.*

The two graphs below show numerical solutions of the system for $0 \le t \le 13$ for two different initial vectors $\vec{x}(0)$. Notice that by time $t = 13$ the activity in each of the neurons has nearly reached its equilibrium value; that is, $x_i(13) \approx \bar{x}_i$. The activity levels at time $t = 13$ are totally independent of the initial activity received by the cluster even though the value of $x_1(0)$ is changed from a very small value to a significantly large value. Since the output activity of a neuron cluster with this type of behavior would be of no use in discriminating between different patterns of input activity Section 2 will explore the behavior of a slightly more complex and useful network.

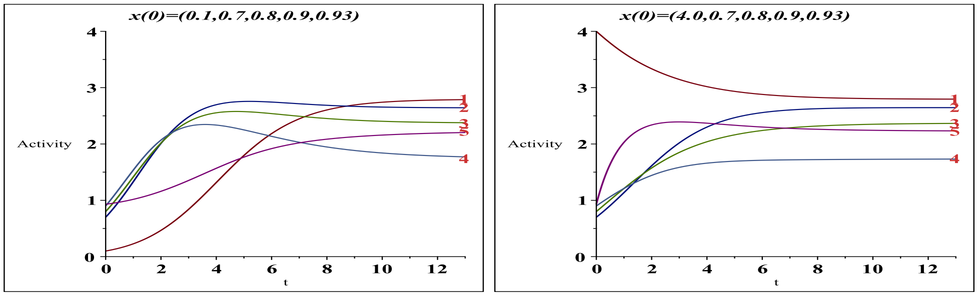

Figure 1: Trajectories of the 5-dimensional system with different initial conditions.

2 The Model with Time-varying Weights

In this section it will be shown that a simple change in the model will enable it to produce much more interesting information about its input. It will be assumed that the neurons in the inhibitory cluster have a certain kind of plasticity so that the weights A_{ik} vary over time. In particular we will assume that the magnitude of the negative effect A_{ik} of neuron k on neuron i increases with increased **simultaneous activity** in neurons i and k. This can be thought of as a type of short-term "learning" or adaptation (see [3, 5, 6] for more information). It is easily modelled by making A_{ik} a function of t which averages the product of the activity levels $x_i(t)x_k(t)$ over an interval of time from $t = 0$ to the present. This will be done by writing

$$A_{ik}(t) = \int_0^t w(s,t)x_i(s)x_k(s)ds$$

where the function w is a weighting function over the time interval $(0, t)$. A simple choice for w is the exponential function

$$w(s,t) = \frac{1}{T}e^{\frac{s-t}{T}}$$

which weighs the recent past more heavily and uses a parameter T to alter the extent of the interval over which most of the average is computed.

Writing

$$A_{ik}(t) = \int_0^t \frac{1}{T}e^{\frac{s-t}{T}}x_i(s)x_k(s)ds,$$

and using the Leibnitz integral rule for differentiating the integral

$$\frac{d}{dt}\left(\int_0^{b(t)} F(s,t)ds\right) = F(b(t),t)\frac{db}{dt} + \int_0^{b(t)} \frac{\partial}{\partial t}F(s,t)ds$$

results in a simple differential equation for $A_{ik}(t)$ of the form

$$A'_{ik}(t) = \frac{1}{T}x_i(t)x_k(t) - \frac{1}{T}\int_0^t \frac{1}{T}e^{\frac{s-t}{T}}x_i(s)x_k(s)ds = \frac{1}{T}\left[x_i(t)x_k(t) - A_{ik}(t)\right]. \quad (6)$$

This leads to the following system of n^2 ordinary differential equations:

$$x'_i(t) = x_i(t)\left(1 - c_i x_i(t) - \sum_{k=1..n,k\neq i} A_{ik}(t)x_k(t)\right),\ 1 \leq i \leq n.$$
$$A'_{ik}(t) = \frac{1}{T}\left[x_i(t)\cdot x_k(t) - A_{ik}(t)\right], i = 1..n, k = 1..n, k \neq i. \quad (7)$$

Since $x_i(t)$ represents the level of activity in a neuron, critical points $\bar{x} = (\bar{x_1}, \bar{x_2}, \cdots, \bar{x_n})$ of (7) will be assumed to be vectors in $\Re^n_+$; that is, with all components greater than or equal to zero. Note that a critical point is completely determined by the values of the $\bar{x}_i$ since requiring A'_{ik} to be zero means that at any critical point $\bar{x}$ the value of $\bar{A}_{ik}$ must be equal to the product $\bar{x}_i \cdot \bar{x}_k$. When we consider the stability of the critical points it will be shown that if any component $\bar{x}_i$ is zero, the critical point is not an asymptotically stable equilibrium; therefore, we can assume that the critical points of interest are those for which all components $\bar{x}_i > 0$. This also implies that any trajectory of (7) that starts in $\Re^n_+$ will remain there. We are also going to assume that the neurons in the cluster all have similar physical properties, and use this to assume that all of the constants c_i have the same value c.

To determine the stability of a critical point of (7) we will write it as an n^2 dimensional vector $\vec{Y}$ with components in the order

$$\vec{Y} = (\bar{x}_1, \bar{x}_2, \cdots, \bar{x}_n, \bar{A}_{12}, \bar{A}_{13}, \cdots, \bar{A}_{1n}, \bar{A}_{21}, \bar{A}_{23}, \cdots, \bar{A}_{2n}, \cdots, \bar{A}_{n1}, \bar{A}_{n2}, \cdots, \bar{A}_{n,n-1}).$$

To be a critical point, each component $\bar{Y}_i$ must satisfy $\frac{d\bar{Y}_i}{dt} = 0$; therefore, $\bar{x}_i$ is a solution of the equation

$$1 - c\bar{x}_i - \sum_{k=1..n,k\neq i} \bar{A}_{ik}\bar{x}_k = 0$$

and $\bar{A}_{ik} = \bar{x}_i\bar{x}_k$. Defining $B = \sum_{k=1..n}(\bar{x}_k)^2$ and using $\bar{A}_{ik} = \bar{x}_i\bar{x}_k$ implies that

$$1 - c\bar{x}_i - \bar{x}_i(B - (\bar{x}_i)^2) \equiv \bar{x}_i^3 - (B + c)\bar{x}_i + 1 = 0.$$

For any dimension $n \geq 2$ there is a unique critical point $\bar{x}$ with all of the $\bar{x}_i$ equal. The value r of each $\bar{x}_i$ is found by setting $1 - cr - \sum_{k \neq i} r^2 r = 1 - cr - (n-1)r^3 = 0$. Using a standard formula for the solution of a cubic, it can be shown that this cubic has a single positive solution

$$r = \left(\frac{1}{n-1}\left(\frac{1}{2} + \sqrt{\frac{1}{4} + \frac{c^3}{27(n-1)}}\right)\right)^{\frac{1}{3}} + \left(\frac{1}{n-1}\left(\frac{1}{2} - \sqrt{\frac{1}{4} + \frac{c^3}{27(n-1)}}\right)\right)^{\frac{1}{3}}.$$

For any integer $n > 2$ we can assume that $(r, r, \cdots, r)$ is a critical point of the system (7).

To find any other critical points we use the fact that each component $\bar{x}_i$ must be a root of the same cubic $z^3 - \alpha z + 1$ where $\alpha = c + \sum_{i=1}^{n} \bar{x}_i^2$. For any $\alpha > \sqrt{3/4^{\frac{1}{3}}} \approx 1.89$ the cubic $z^3 - \alpha z + 1$ has two unequal positive roots $b > s$. Letting the third root be q, and factoring,

$$z^3 - \alpha z + 1 \equiv (z-b)(z-s)(z-q) = z^3 - (b+s+q)z^2 + (bs+bq+sq)z - bsq.$$

Equating coefficients of z^2 implies $q = -(b+s)$ and from the coefficients of z,

$$\alpha = -(bs+bq+sq) = -(bs-(b+s)^2) = b^2 + bs + s^2. \tag{8}$$

If $n \geq 3$ and the critical point has two or more components equal to the larger root b then

$$\alpha = c + \sum_{i=1}^{n} \bar{x}_i^2 > b^2 + b^2 + s^2 > b^2 + bs + s^2$$

which contradicts (8). This means that every critical point $\bar{x}$ other than $(r, r, ..., r)$ must be a vector containing **exactly** one component equal to b and all of the other components equal to s, where $b > s$ are the two positive roots of $z^3 - \alpha z + 1$ with $\alpha = c + \sum_{k=1}^{n} \bar{x}_i^2$.

We need to find all vectors that satisfy the two conditions:

1. $b > s$ are the two positive roots of $z^3 - Gz + 1$, and simultaneously
2. $G = b^2 + (n-1)s^2 + c$.

It was shown in an earlier paper [6] that in order for any critical points other than $(r, r, \cdots, r)$ to exist the value of c must be less than a certain value $c^*(n)$ which depends on the dimension n. The bifurcation value $c^*(n)$ is given by

$$c^*(n) = \frac{1}{2}\left(\left[(2n-3)^2(32n(n-3)+63)^2 + 108(n-1)(n-2)\right]^{\frac{1}{2}} - (2n-3)(32n(n-3)+63)\right)^{\frac{1}{3}}.$$

Some representative values are shown in the table below:

n	$c^*(n)$
3	0.4147
4	0.3487
5	0.3115
10	0.2315
20	0.1786

Example 2 : *As an example, let* $n = 5$ *and* $c = 0.25 < c^*(5)$. *To find all critical points with exactly one* $\bar{x}_i = b$ *we need to graph the function* $F(G) = G - (b(G)^2 + 4s(G)^2 + c)$, *where* $b(G) > s(G)$ *are the two positive roots of* $z^3 - Gz + 1 = 0$, *and locate any zeros of* $F(G)$. *At each zero of* $F(G)$, *the values of the two positive roots* $b(G)$ *and* $s(G)$ *will give us* 5 *critical points* $(b, s, s, s, s), (s, b, s, s, s), \cdots, (s, s, s, s, b)$.

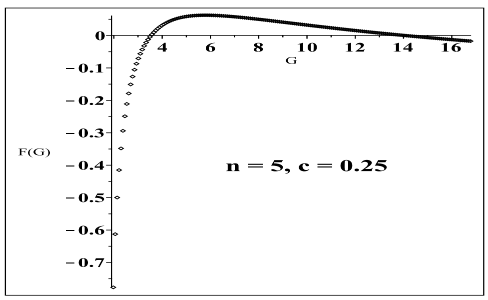

Figure 2: Finding zeros of the function $F(G) = G - (b^2 + 4s^2 + c)$

For $n = 5$ *and* $c = 0.25$ *a graph of* $F(G)$ *is shown in Fig.(2). The graph shows two zero crossings at* $G_1 \approx 3.577574$ *and* $G_2 \approx 13.921975$. *In the next seciton we will be able to show that the vectors with* $b_1 \approx 1.732122$ *and* $s_1 \approx 0.286062$ *computed at* G_1 *are all unstable and the vectors using* $b_2 \approx 3.694770$ *and* $s_2 \approx 0.071956$ *are stable equilibria.*

3 Stability of the Critical Points in an Adaptive System

Once all of the critical points for a given n and c are determined their stability can be tested by finding the eigenvalues of the Jacobian matrix $\vec{\nabla} F = \left(\frac{\partial Y_i'}{\partial Y_j}\right)$. As noted previously, the n^2 variables in the system (6) will be listed in the order

$$\vec{Y} = (x_1, x_2, \cdots, x_n, A_{12}, A_{13}, \cdots, A_{1n}, A_{21}, A_{23}, \cdots, A_{2n}, \cdots, A_{n1}, A_{n2}, \cdots, A_{n,n-1}).$$

This means that $\vec{\nabla} F$ will be an $n^2 \times n^2$ matrix with $i,j-$element equal to $\frac{\partial Y_i'}{\partial Y_j}$. The Jacobian matrix can be partitioned as shown below.

The $n \times n$ submatrix Z contains the elements $Z(i,j) = \frac{\partial x_i'}{\partial x_j}$. It is exactly the same as the matrix $\vec{\nabla} F$ for the constant weight system (see equation (4) in Section 1). The $(n^2-n)\times(n^2-n)$ matrix D is diagonal with $\frac{\partial A_{ij}'}{\partial A_{ij}} = -\frac{1}{T}$ on the diagonal and zeros elsewhere. The B and C matrices are more difficult to define but beginning with an $n^2 \times n^2$ matrix of zeros, the following four loops will create the Jacobian.

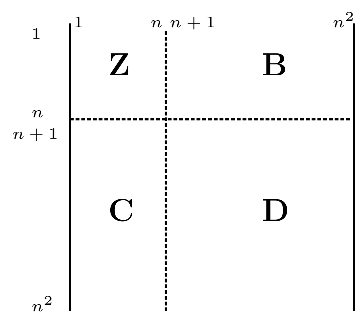

Figure 3: Form of the $n^2 \times n^2$ Jacobian matrix.

```
Generate the Z submatrix
  for i from 1 to n do for j from 1 to n do
    if i = j then F[i, j] := 1-x[i]*(2*c + sum{x[m]^2,m=1..n)}-x[i]^2)
    else F[i,j] := -x[i]^2*x[j] fi; od; od:
Generate the B submatrix
  for i from 1 to n do k := n+1+(i-1)*(n-1); for j from 1 to n do
    if j <> i then F[i, k] := -x[i]*x[j]; k := k+1 fi; od; od:
Generate the C submatrix
  for i from 1 to n do k := n+1+(i-1)*(n-1); for j from 1 to n do
    if j <> i then F[k, j] := x[i]/T; F[k, i] := x[j]/T; k := k+1 fi; od; od:
Generate the D submatrix
  for i from n+1 to n^2 do for j from n+1 to n^2 do
    if j = i then F[i, j] := -1.0/T else F[i, j] := 0 fi; od; od:
```

It can now be seen that if any $\bar{x}_i$ in a given critical point is equal to zero then the *ith* row of $\vec{\nabla} F$ contains a diagonal element equal to one, and all of the other elements in the row are zero; therefore, one is an eigenvalue of $\vec{\nabla} F$ and the critical point is not stable.

In a previous paper [6] the determinant of the matrix $\vec{\nabla} F - \lambda I$ was analyzed algebraically. It was shown there that the critical point $(r, r, \cdots, r)$ is stable iff either $r^2 \le c$ or $r^2 > c$ and $T < \frac{1.0}{r(r^2-c)}$. This means that if the maximum activity level $1.0/c$ is too large then the adaptation time T must be restricted in order for any solutions to tend asymptotically to $(r, r, ..., r)$. In this paper the adaptation is assumed to be taking place over a short time period between when the input to the neurons occurs and the time of measuring their output.

4 Interesting Properties of the Adaptive Model

The ability of the neuron cluster to adapt over time has a very profound effect on its output. Consider a cluster with $n = 5$ and $c = 0.25 < c^*(5)$. The value $T = 15$ will be chosen arbitrarily. The values $b_2 \approx 3.694770$ and $s_2 \approx 0.071956$ were found in Example 2. The positive root r of the cubic $r^3 + \frac{c}{n-1} r - \frac{1}{n-1}$ is 0.5969216. We now know there are eleven critical points

$$(r, r, ...r), (b_2, s_2, s_2, s_2, s_2), \cdots, (s_2, s_2, s_2, s_2, b_2), (b_1, s_1, s_1, s_1, s_1), \cdots, (s_1, s_1, s_1, s_1, b_1),$$

and the Jacobian can be used to show that the first 6 of these are stable attractors. Note that $(r, r, \cdots, r)$ is stable since $T = 15.0 < \frac{1}{r(r^2-c)} \approx 15.76$.

What can we expect to happen for a given initial vector $\vec{x}(0)$?. After computing several solutions it became apparent that if one of the inputs $x_i(0)$ is much larger than all of the others the solution will tend to the critical point with b_2 in the *ith* position. This does not seem very exciting, but it also appears that if $x_i(0)$ is **much smaller** than the other inputs the system also converges to the critical point with b_2 in the *ith* position. This is a highly nonlinear type of response. The cluster detects the input that is *most unlike* the others. If there is very little difference in the $x_i(0)$, the system converges to the equilibrium $(r, r, \cdots, r)$. This could be a useful mechanism for detecting anomalies in the input under both light and dark conditions, for example.

Example 3 *Figure 4 below shows six different solutions of the* 5*-cell system with* $c = 0.25$ *and* $T = 15$. *The initial values* $\vec{x}(0) = (x_1(0), 0.7, 0.8, 0.9, 0.93)$ *are equal except for the value of* $x_1(0)$ *which varies from* 0.1 *in the top left graph to* 4.0 *on the bottom right.*

The dashed horizontal lines denote the values of $s \ll r \ll b$. *It would be very easy to set a threshold on the output of each neuron to detect which, if any, of the neurons received a most unusual input. In each of the* 6 *solutions the initial weights were all set equal to a very small value. Because of the symmetry it is clear that the same result would occur if any of the five neurons had been given the unusual value at* $t = 0$.

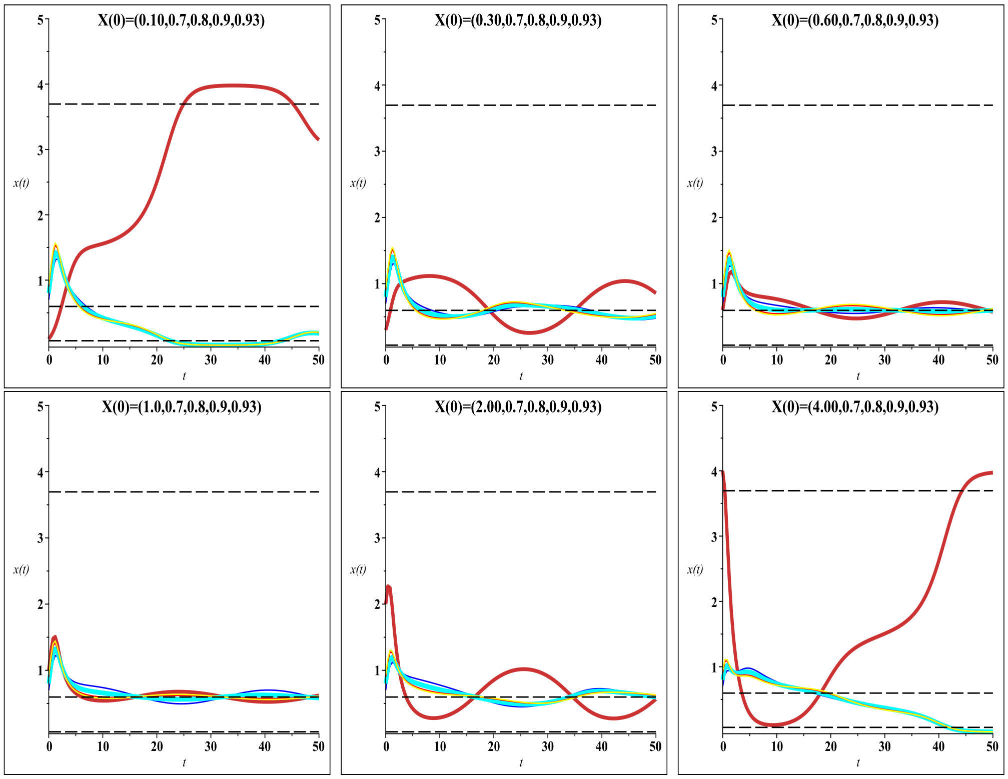

Figure 4: Increasing values of $x_1(0)$

It would be very interesting to see if a mathematical explanation could be found to explain this type of behavior.

A simulation was also run to see what happens when $T > \frac{1}{r(r^2-c)}$, so that the critical point (r, r, r, r, r) becomes unstable. With nearly equal initial values in $x(0)$, the result is shown in Figure 5.

It appears that when $T = 16$ there is a limit cycle around the critical point (r, r, r, r, r).

The eigenvalues of the three cases $T = 15, 15.75747, 16$ were calculated, and it was seen that in each case seventeen of the eigenvalues were real and negative, and there were fours sets of complex roots. The real part of these complex roots were all equal to -0.0016 at $T = 15$, equal to zero at $T = 15.75747$, and equal to 0.00004809 at $T = 16.0$. The graph in Figure 5 suggests that a Hopf bifurcation occurs when T passes through the value $\frac{1}{r(r^2-c)}$. It might also be of interest to study stability of the other equilibrium points.

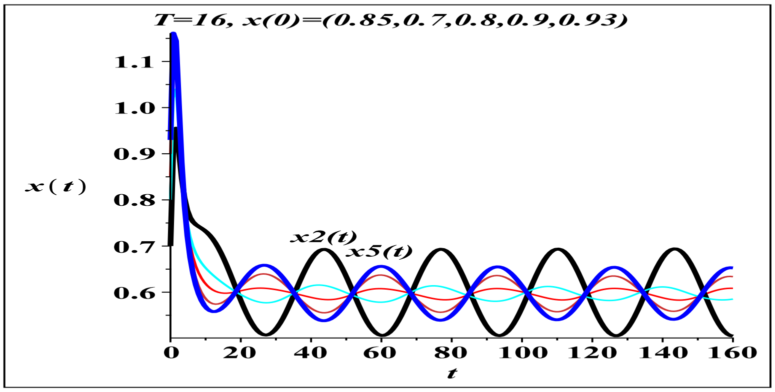

Figure 5: The solution with $T = 16$ and initial values $X(0) = (0.85, 0.7, 0.8, 0.9, 0.93)$

5 Introduction of a Time-delay into the Adaptive System

Another interesting question is " how would a delay in the feedback between neurons affect the behavior of the adaptive system?" On the next page solutions of the differential-delay system

$$x_i'(t) = x_i(t)\left(1 - c_i x_i(t) - \sum_{k=1..n,k\neq i} A_{ik}(t)x_k(t-\tau)\right),\ 1 \le i \le n.$$
$$A_{ik}'(t) = \frac{1}{T}\left(x_i(t)\cdot x_k(t-\tau) - A_{ik}(t)\right), i = 1..n, k = 1..n, k \neq i. \qquad (9)$$

are shown.

$\tau = \mathbf{0.1}$ $\qquad\qquad$ $\tau = \mathbf{0.2}$ $\qquad\qquad$ $\tau = \mathbf{0.5}$

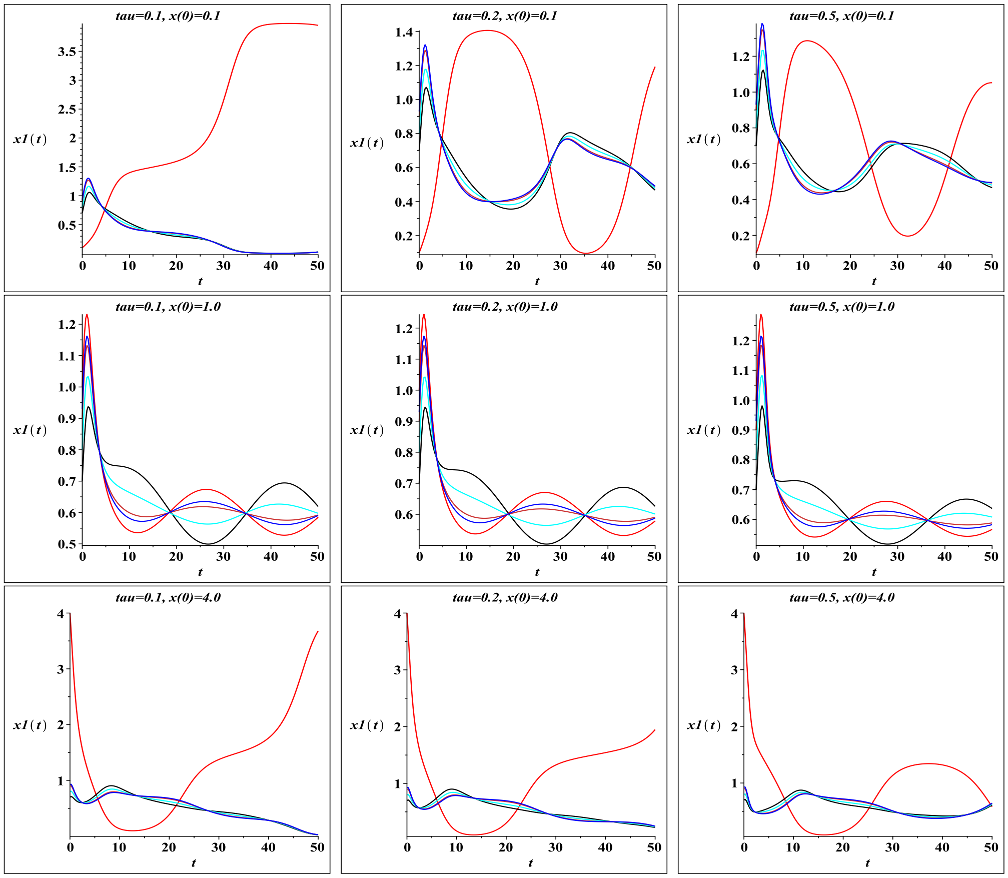

Figure 6: Solutions of the delay system with $x_1(0) = 0.1, 1.0, 4.0$ and delays $\tau = 0.1, 0.2, 0.5$.

The parameters $n = 5$, $c = 0.25$ and $T = 15.0$ are the same as in the previous example, but a delay τ is assumed to occur in the feedback between any two neurons. For three of the initial conditions the resulting solutions with $\tau = 0.1, 0.2$, and 0.5 are shown. It appears that the interesting nonlinear behavior is not affected for the small value of τ, but may disappear for larger delays, possibly due to instability of the critical points $(b, s, \cdots, s)$. This could definitely be studied using known results on stability of critical points of a differential-delay system. For more information on this topic, see [1, 4].

Some questions for further study:

1. What equilibrium point will the adaptive system approach if exactly 2 of the 5 initial inputs $x_i(0)$ are much larger than the other 3? For example let $\vec{x}(0) = (4.0, 1.0, 4.0, 1.0, 1.0)$. Elaborate on this point using values of $n > 5$.

2. Run the adaptive model on a **large set** of inputs $\vec{x}(0)$. Choose a threshold value θ and an end time T. Assign value k to $\vec{x}(T)$ if the output is $(s, ..., b, ..s)$ with b in position k, and $k = 0$ if the output is $(r, r, ..., r)$. Try to give a meaningful statistical description of the result.

3. How is the **stability** of the critical points affected by a delay in the system?

4. Note that the system of equations considered in this paper was originally derived to model the behavior of a set of competing species in a particular ecosystem. The type of adaptation described in Section 2 could represent a population's increased ability to prey on another species due to its increased level of interaction with that species. Speculate about what the results imply on the ability of a population with very few members to become the dominant species over time.

5. Come up with a question of your own about the behavior of an inhibitory cluster. Try to answer it.

References

[1] R. Bellman, K. L. Cooke. Differential-Difference Equations, Academic Press, New York 1963.

[2] M. Hirsch, *On Existence and Uniqueness of the Carrying Simplex for Competitive Dynamical Systems, J. Biol. Dyn. 2, No. 2, pp. 169-179, 2008.*

[3] D. Lacitignola, C. Tebaldi. *Effects of ecological differentiation on Lotka-Volterra systems for species with behavioral adaptation and variable growth rates, Math. Biosciences, Vol. 194, Issue 1, pp. 95-123, 2005.*

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

[5] V. W. Noonburg, *Effects of behavioral adaptation on a predator-prey model. J. Math. Biology, pp. 239-247, 1982.*

[6] V. W. Noonburg. *A Neural Network Modeled by an Adaptive Lotka-Volterra System, SIAM J. Appl. Math, 49, pp.1779-1792, 1989.*

For a more recent (2011) article on Hopf bifurcations, 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.