

Bifurcation from a Stable Equilibrium in the Genome

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Abstract

This work explores a genome network and introduces the concepts of core and layering within the network. Based on this structure, a dynamical system for gene expression levels is developed. The system exhibits two main bifurcations arising from a stable equilibrium. Preliminary results toward understanding these bifurcations in n -dimensions are also presented. This work contributes to a deeper understanding of genome dynamics and controllability.

Key Words: Bifurcation, Hopf-Bifurcation, Pitchfork Bifurcation, Gene Network, Genome.

AMS Classification: 34C23, 34C37, 34D05, 34A34.

1 Introduction

Development of a single cell into a multicellular organism involves a remarkable of gene expression, molecular signaling and environment. Emergence of specific cell types depends on selective use of genes, This phenomenon known as gene regulation, at critical times during development. Our goal is to build a mathematical foundation for gene regulation and its dynamics. Gene regulation dynamics traditionally takes the form:

$$\frac{dx}{dt} = F(x) \quad (1.1)$$

Bifurcation theory, especially the pitchfork, will help in gene regulation. Two and three gene networks will be given where the pitch fork and Hopf bifurcations are exhibited,

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starting from Hill functions , the points of bifurcation even when distinct degradation rates of proteins are allowed.

2 The Network and Associated Dynamics

The configuration space is the set of n non negative real numbers , representing gene expression levels of the n genes . This configuration space is $(\mathbb{R}^+)^n$ with its element $x = (x_1, \dots, \dots, \dots, x_n)$

$$X = \prod_{i=1}^n [0, k_i] \quad (2.1)$$

Where x_i represents the concentration of a protein and k_i is its maximum value . The dynamics are described by an ordinary differential equation of the form .

$$\frac{dx_i(t)}{dt} = F_i(x_1(t), \dots, \dots, \dots, x_n(t)), i = 1, 2, \dots, n \quad (2.2)$$

We will construct a network for the genome that end define an oriented graph and label the nodes of graph to obtain the network.

2.1.1 THE GRAPH

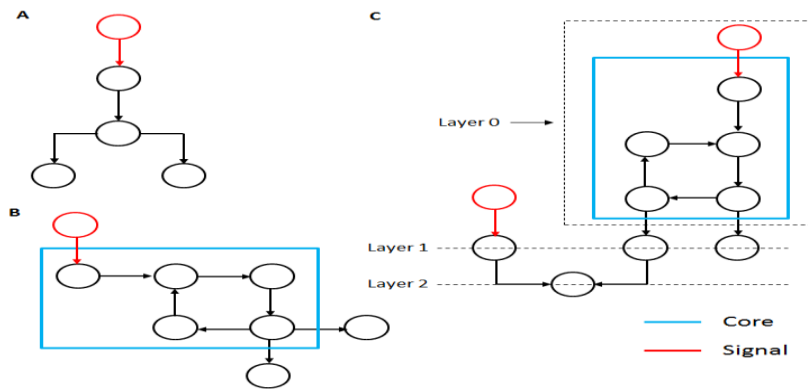
The nodes are two types.

- i) The Genes $g \in G$
- ii) The inputs I to be interpreted as signals.

There is also a special subset T of G called transcription factors.

The oriented edges of a graph, $E(i, j)$ from a node i to node j . The first type of edge satisfies $i \in I$ and $j \in T$. The second type satisfies $i \in T$ and $j \in G$ and is interpreted as i has some control over j , as when the protein generated by gene i is a transcription factor and bind the promoter of gene j .

A predecessor of node j is a node i such that $E(i, j)$ is a edge and assume that each node $i \in I$ has no predecessor and other nodes have atleast one predecessor and assume that the graph is connected. The nodes which belong to some cycle of the graph and nodes with a path leading to a cycle.



2.1.2 The Network

The graph to a “network” by attaching some label to each node then consider a node whose level is y together with a single predecessor in G level is denoted by $x \in [0, k]$. Let $H: [0, k] \rightarrow \mathbb{R}$ be given as well as a positive real number b . H is a map from concentration x to rate of change of y . Assume H is smooth, non-negative and bounded by bk . Here is the Hill type equation,

$$\frac{dy}{dt} = H(x(t) - by(t)) \quad (2.3)$$

With the last term representing the degradation of the node that expresses y with (H, b) then the predecessor is an input node or $x(t)$ is a signal. The preceding Hill type function to the case of a node g with more than one predecessor.

Define p_g to be the set of predecessors of $g \in G$ and let $w_g = \prod_{i \in p_g} X_i$ where $X_i = [0, k_i]$ is the space of expression of gene. The Hill type function is a now a map.

$$H_g: W_g \rightarrow \mathbb{R}$$

$$\frac{dy}{dt} = H_g(x(t)) - (by(t)) \quad (2.4)$$

For each gene, the node g with (H_g, b) . we have completed the description of the network attached to the genome.

2.1.3 Network and The Dynamics

The network described by our graph and the nodes just labeled determines the dynamics of the genome equation is, $\frac{dy}{dt} = H_g(x(t)) - by(t)$

To define the $F_i \frac{dx}{dt} = F(x)$ where F_i depends then only on predecessors of gene i . We identify gene g with gene i above and below.

2.1.4 Basic Definitions and Boundary Conditions

At a boundary point of, if $y_i = k_i$, some i then $\frac{dy_i}{dt} > 0$ is a condition which is not compatible with our interpretation of the biology. one cannot increase the concentration if one is already at the maximum. such a point, $H_g < bk_g$ implies by equation 2.4 $\frac{dy_i}{dt} < 0$ for each gene g .

Function $H_g(x)$ in 2.3 is bounded by bk_g as a function of x with,

$$H_g(x) > 0 \text{ for } x \in W_g \tag{2.5}$$

2.5 is important for a boundary point of x satisfying $x_i = 0$ for some i , then $\frac{dy_i}{dt} > 0$

2.1.5 Special Hill Functions

Differential equations for gene involve the Hill functions defined by ,

$$H(x) = \frac{\beta x^p}{(k_1)^p + x^p} \text{ or } G(x) = \frac{\gamma}{1 + (\frac{x}{k_2})^q} \tag{2.6}$$

Where x is concentration of a transcription factor in a cell and H represents activation and G represents repression. The p and q consider as a function of a bifurcation parameter.

In general, i is gene with single predecessor,

$$F_i(x_i) = H(x_j) - a_i x_i \quad (\text{or})$$

$$F_i(x_i) = G(x_j) - a_i x_i$$

in equation 2.2 and equation 2.6.

For all $H(x_i) = \frac{\beta_i x_i^p}{(k_{1i})^p + x_i^p}$ and similarly for $G(x_i)$

For both activation and repression at $p_i = q_i = 0$, $i = 1, 2, \dots, n$ equilibrium equations to $x_i = \frac{\beta_i}{2a_i}$. The equilibrium is globally stable the eigen values of Jacobian matrix at the equilibrium are negative ($-a_i, i = 1, 2, \dots, n$).

The equation is

$$J = \begin{pmatrix} \frac{\partial F_1}{\partial x_1} & \dots & \dots & \frac{\partial F_1}{\partial x_n} \\ \vdots & \frac{\partial F_i}{\partial x_i} & & \vdots \\ \frac{\partial F_n}{\partial x_1} & \dots & \dots & \frac{\partial F_n}{\partial x_n} \end{pmatrix}$$

Where $F = (F_1, \dots, F_n)$

The equilibrium $(x)_i = \left(\frac{\beta_i}{2a_i}\right)$ is a starting point of a path $x(\mu)$ of equilibrium parameterized by a bifurcation parameter $\mu < \mu_0$

The equilibrium in 2.4 is feasible provided

$$\left(\frac{\beta_i}{2a_i}\right) < k_i \quad (2.7)$$

This will be true if k_i is big enough.

3 Induced Equilibrium

Consider an equilibrium x in core dynamics of the network in the form, $x_i(t) = c_i$, a constant for each i belonging to the core.

Let gene g be in the first layer in the core 2.4, H_g at the equilibrium in W_g where c_g is constant. for any $y(t)$ for gene g , $\frac{dy}{dt} = 0$ if and only if $g(t) = \frac{c_g}{b}$

$$\text{Define } y(t) = \frac{c_g}{b}$$

For any g in the first layer and do the same for whole genome. If x is a stable 2.4, since the derivative is $-b$. An equilibrium solution in the core induces a natural equilibrium in the set of all layers generate by the core in the whole genome. The induced equilibrium is stable if the core equilibrium is stable.

4 First Bifurcation From a Stable Equilibrium

This is a family F_μ with bifurcation parameter $\mu \in (-e, e)$ describing a dynamic,

$$\frac{dx}{dt} = F_\mu(x)$$

x belongs to a domain X of \mathbb{R}^n and $F_0(x) = F(x)$.

The dynamics of F_μ is that of a stable equilibrium (μ) , basin B_μ for $\mu < \mu_0$, $\mu_0 = 0$ and bifurcation at $\mu = 0$. $J_\mu = J(x(\mu))$ as in 2.7 there is a neighbourhood N of x_0 , such that N is contained in B_μ for all $\mu < 0$ even at $\mu = 0$, x_0 is a sink in the sense that $x(t) \rightarrow x_0$. If the initial point belongs to N for the dynamics of F_μ , $\mu = 0$ with basin B_{μ_0} , the eigen values of J_μ at the stable equilibrium and the bifurcation value μ all have negative real part, either real or complex conjugate pairs. At the bifurcation, one has either a single real eigen value becoming zero and then positive with the pitchfork, or a complex conjugate pairs of distinct

eigen values with real parts at zero to become positive after the bifurcation and then the Hopf oscillation. A pitchfork bifurcation converts a stable equilibrium into two stable equilibria. The Hopf bifurcation converts a stable equilibrium into a stable periodic solution.

5. Hopf Bifurcation Setting

Let $x(\mu)$ be a stable equilibrium for μ for all $\mu < \mu_0$. suppose that the equilibrium does not “leave it’s basin” in the sense there is a neighbourhood N of x_0 , such that N is contained in B_μ for all $\mu < \mu_0$.

Suppose that all eigenvalues of Jacobian, J at $x(\mu_0)$ have negative real parts except one conjugate purely imaginary pair $\pm ib$ and two eigen values cross the imaginary axis when $\mu > \mu_0$. Then the dynamics undergoes a bifurcation at (x_0, μ_0) resulting in a stable periodic solution. This is called a Hopf bifurcation.

The periodic solutions are in two ways:

- 1) $\frac{d(Re \lambda(\mu))}{d\mu} |_{\mu = \mu_0} \neq 0$
- 2) A certain third derivative is not zero.

5.1 Pitchfork Bifurcation

A normal form of the pitchfork bifurcation is,

$$\frac{dx}{dt} = \mu x - x^3, x \in \mathbb{R}', \mu \in \mathbb{R}'$$

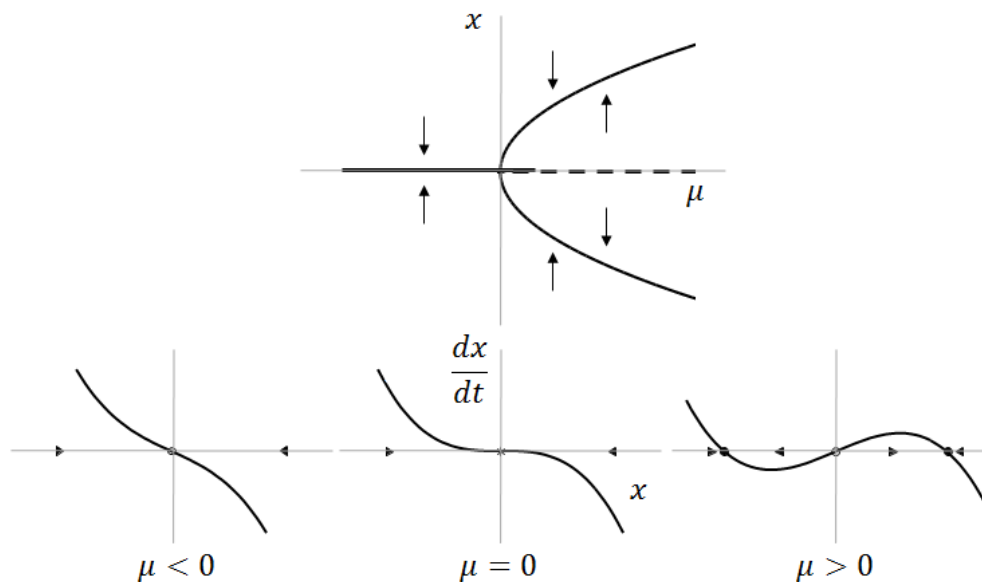


Figure : pitchfork bifurcation (super critical) for $\frac{dx}{dt} = \mu x - x^3$

Top : The vertical axis is $x(\mu)$, the equilibria solid line represent stable , dotted line is unstable **Bottom :** These cases of μ , for all $\mu < 0$ there is a single stable fixed point at $x = 0$

when $\mu = 0$ there is a single fixed point at $x = 0$. For $\mu > 0$, $x = 0$ is unstable, and there are two stable fixed points at $x = \pm\sqrt{\mu}$. This system has an equilibrium $x_0 = 0$ for all μ . The equilibrium is stable for $\mu < 0$ and unstable for $\mu > 0$.

For $\mu > 0$ there are two extra equilibria from origin (namely $x_{1,2} = \pm\sqrt{\mu}$) are stable. This bifurcation is called a pitchfork bifurcation. In an n -dimensional system we write in addition,

$$\frac{dx_i}{dt} = -x_i, i = 2, \dots, n$$

5.2 Hopf Bifurcation

Example of a Hopf bifurcation is,

$$\frac{dx}{dt} = y - f_\mu(x)$$

$$\frac{dy}{dt} = -x$$

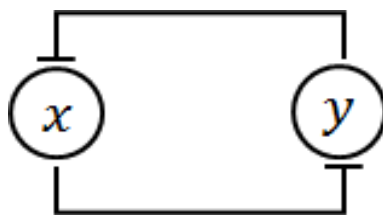
$f_\mu(x) = x^3 - \mu x$ and μ lies in the interval $[-1, 1]$. The only equilibrium in this system is $x_0 = 0, y_0 = 0$.

The Jacobian matrix J at the equilibrium is,

$$J = \begin{pmatrix} \mu & 1 \\ 1 & 0 \end{pmatrix} \text{ and the eigen values are } \lambda_{\pm} = \frac{1}{2}(\mu \pm \sqrt{\mu^2 - 4}).$$

Thus, the equilibrium is stable for $-1 \leq \mu < 0$ and has a unique stable periodic solution for $0 < \mu < c$.

5.3 Bifurcation Analysis of Two Gene Networks



A SCHEMATIC DIAGRAM OF A TWO GENE NETWORK WITH TWO REPRESSORS.

A network of two mutually inhibitory genes that acts as a switch by some mechanism as a control switching from one basin to another.

Two gene networks in figure can be described by,

$$\frac{dx}{dt} = F(y) - ax$$

$$\frac{dy}{dt} = G(x) - by \tag{5.3.1}$$

Where $F(y)$ and $G(x)$ are Hill type functions and these equations are,

The jacobian matrix J at an equilibrium (x_0, y_0) is ,

$$J = \begin{pmatrix} -a & F'(y_0) \\ G'(x_0) & -b \end{pmatrix}$$

In this case $F' < 0, G' < 0$, since F & G are repressors. Let $Q = F'G'$ thus $Q > 0$,

The characteristic equation of the matrix J at (x_0, y_0) is given by,

$$(\lambda + a)(\lambda + b) = Q$$

Eigen values at equilibrium (x_0, y_0) are given by,

$$\begin{aligned} \lambda_1 &= -\frac{1}{2}(a + b) + \frac{1}{2}\sqrt{(a - b)^2 + 4Q} \\ \lambda_2 &= -\frac{1}{2}(a + b) - \frac{1}{2}\sqrt{(a - b)^2 + 4Q} \end{aligned} \tag{5.3.2}$$

$$\det(J) = ab - Q$$

So, if $\det(J) = 0$, then $Q = ab$ and $\lambda_1 = 0$ and $\lambda_2 < 0$

It consisted of two genes, which they described as,

$$\begin{aligned} \frac{dx}{dt} &= \frac{\alpha_1}{1 + y^m} - x \\ \frac{dy}{dt} &= \frac{\alpha_2}{1 + x^n} - y \end{aligned} \tag{5.3.3}$$

If $n = 0$, the equilibrium is $x = \frac{\alpha_1}{2}$, $y = \frac{\alpha_2}{2}$ and the eigen values of the Jacobian are negative. If $\alpha_1 < 2 \max(x)$ and $\alpha_2 < 2 \max(y)$, this equilibrium is feasible. The system has a unique global stable equilibrium. The bifurcation parameter *or* $\mu < \mu_0$, the system has a stable equilibrium. At μ_0 we assume a bifurcation.

Take m and n to be bifurcating parameters, $(m, n) = (m_\mu, n_\mu)$, $(m_0, n_0) = (0, 0)$ the initial value problem of the bifurcation parameter. If there is a first bifurcation with $\det(J_\mu) = 0$, it is a pitchfork.

5.3.1 Theorem

Suppose F_μ is represented by

$$\begin{aligned}\frac{dx}{dt} &= \frac{\alpha_1}{1+y^m} - x \\ \frac{dy}{dt} &= \frac{\alpha_2}{1+x^n} - y\end{aligned}\tag{5.3.4}$$

With μ described .let the first bifurcation given by $\det(J_\mu) = 0$. Then there is a pitchfork bifurcation at that .

Proof :

The existence of a pitchfork bifurcation in the two gene case ,

When $\alpha_1 = \alpha_2 = 2$ and $n > 0$, the system is 5.3.4 can be written as ,

$$\begin{aligned}\frac{dx}{dt} &= \frac{2}{1+y^m} - x \\ \frac{dy}{dt} &= \frac{2}{1+x^n} - y \quad , x, y \geq 0\end{aligned}\tag{5.3.5}$$

For $0 \leq m \leq 2$, then every equilibria must be (1,1) . This can be proved by numerics.

The Jacobian matrix J at (1,1)

$$\begin{aligned}J &= \begin{pmatrix} -1 & -m \frac{\alpha y^{m-1}}{(y^m + 1)^2} \\ -m \frac{\alpha x^m}{(x^m + 1)^2} & -1 \end{pmatrix} \\ &= \begin{pmatrix} -1 & -\frac{1}{2}m \\ -\frac{1}{2}m & -1 \end{pmatrix}\end{aligned}$$

And the $\det(J) = 1 - \frac{1}{4}m^2$

$\therefore 0 \leq m < 2$, $\det(J) > 0$ and $m = 2$, $\det(J) = 0$

This is a condition for a pitchfork bifurcation

5.4 Bifurcation Analysis of Three Gene Networks :

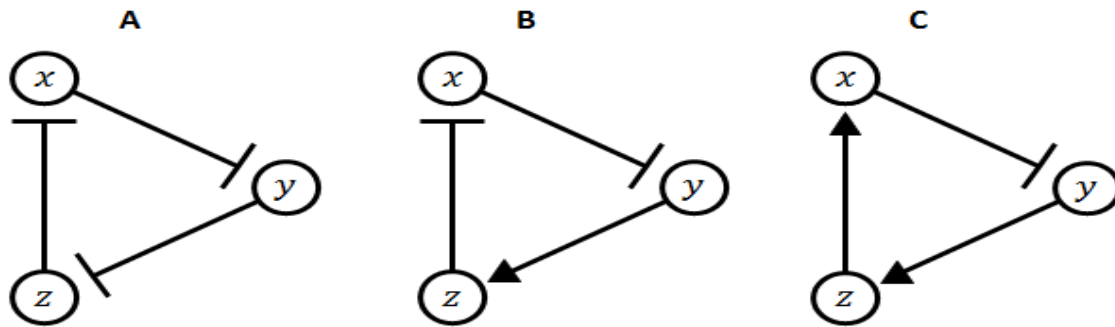


Figure: Gene circuits: A) A network with three inhibitory genes (The Depreciator). B) A network with two inhibitory genes and one excitatory gene. C) A network with two excitatory genes and one inhibitory gene. The dynamics are the same as for network A.

This is a network of two mutually excitatory genes and one inhibitory gene, which produces similar to a depreciator.

Our three gene model is described by ODE of the form:

$$\begin{aligned} \frac{dx}{dt} &= F(z) - ax \\ \frac{dy}{dt} &= G(x) - by \\ \frac{dz}{dt} &= H(x) - cz \end{aligned} \tag{5.4.1}$$

$x, y, z \in \mathbb{R}^+$ and $a, b, c > 0$ are constants. Here F, G and H are Hill functions for the transcription factors.

The Jacobian matrix J_μ at an equilibrium (x_0, y_0, z_0) is

$$J_\mu = \begin{pmatrix} -a & 0 & F'(z_0) \\ G'(x_0) & -b & 0 \\ 0 & H'(y_0) & -c \end{pmatrix}$$

Let $Q = F'G'H'$

$$\text{Det}(J_\mu) = Q - abc$$

The characteristic equation is given by $\det(J_\mu - \lambda I) = 0$.

We expand the equation and obtain,

$$(\lambda + a)(\lambda + b)(\lambda + c) = Q \tag{5.4.2}$$

Similarly take $a = b = c = \alpha$ where $\alpha = \frac{(a+b+c)}{3}$ is the mean.

The characteristic equation is given by,

$$(\alpha + \lambda)^3 = Q \quad (5.4.3)$$

The system has a parameter μ for $\mu < \mu_0$ the equilibrium is stable and it loses stability immediately after $\mu = \mu_0$, thus $Q = Q(\mu)$.

5.4.1 Remark

The dichotomy of pitchfork and Hopf corresponds to $Q > 0, Q < 0$ where Q is the value at μ_0 .

Proof:

let $m =$ largest real cube root of $|Q|$

CASE: 1 For example the depreciator $F' < 0, G' < 0, H' < 0$

Another for case 1:

When $F' > 0, G' > 0, H' < 0$

Eigen values at the equilibrium $(x_0, y_0, z_0)\mu$ are given by

$$\begin{aligned}\lambda_1 &= -\alpha - m \\ \lambda_2 &= -\alpha + \frac{1}{2}m + \frac{1}{2}i\sqrt{3}m \\ \lambda_3 &= -\alpha + \frac{1}{2}m - \frac{1}{2}i\sqrt{3}m\end{aligned}$$

The points $\lambda_1 + \alpha, \lambda_2 + \alpha$ and $\lambda_3 + \alpha$ corresponding to points in a circle of radius one.

When $\frac{m}{2} < \alpha$, then $\lambda_1 < 0$ and the real part of $\lambda_2, \lambda_3 < 0$.

When $\frac{m}{2} < \alpha$, $\lambda_1 < 0$ and λ_2, λ_3 are purely imaginary.

When $\frac{m}{2} > \alpha$, $\lambda_1 < 0$ and the real part of $\lambda_2, \lambda_3 > 0$.

These are sufficient for a generic Hopf bifurcation.

5.4.2 Example

The existence of a Hopf bifurcation in the three gene case. Depreciator can be written as

$$\begin{aligned}\frac{dx}{dt} &= \frac{\alpha}{1 + z^m} - x \\ \frac{dy}{dt} &= \frac{\alpha}{1 + x^m} - y\end{aligned}$$

$$\frac{dz}{dt} = \frac{\alpha}{1+y^m} - z, x, y, z \geq 0 \quad (5.4.4)$$

The diagonal $x = y = z = s$ is parameterized by s . The coordinated of an equilibrium state are (s, s, s) and equilibrium path is described by,

$$s + s^{m+1} - \alpha = 0 \quad (5.4.5)$$

The Jacobian matrix J at (s, s, s) is,

$$J = \begin{pmatrix} -1 & 0 & \frac{-ms^m}{(s^m + 1)} \\ \frac{-ms^m}{(s^m + 1)} & -1 & 0 \\ 0 & \frac{-ms^m}{(s^m + 1)} & -1 \end{pmatrix}$$

The real part of complex eigen values is,

$$Re(\lambda) = -\frac{1}{2} \left(\frac{-ms^m}{(s^m + 1)} \right) - 1$$

The condition for a Hopf bifurcation is thus,

$$-\frac{1}{2} \left(\frac{-ms^m}{(s^m + 1)} \right) - 1 = 0$$

$s^m(2 - m) = -2$ and for any $m > 2$ the bifurcation value for s .

$$s = \sqrt[m]{\frac{2}{m-2}}$$

This satisfies the conditions for a generic Hopf bifurcation.

CASE: 2 For example, $F' < 0, G' < 0, H' > 0$, Eigenvalues at the equilibrium (x_0, y_0, z_0) corresponding to the bifurcation value μ are given by,

$$\lambda_1 = -\alpha + m$$

$$\lambda_2 = -\alpha - \frac{1}{2}m + \frac{1}{2}i\sqrt{3}m$$

$$\lambda_3 = -\alpha - \frac{1}{2}m - \frac{1}{2}i\sqrt{3}m$$

When $m < \alpha$, then $\lambda_1 < 0$ and real part $\lambda_2, \lambda_3 < 0$.

When $m = \alpha$, then $\lambda_1 = 0$ and real part $\lambda_2, \lambda_3 < 0$. (since $-\alpha - \frac{1}{2}m < 0$)

When $m > \alpha$, then $\lambda_1 > 0$ and real part $\lambda_2, \lambda_3 < 0$

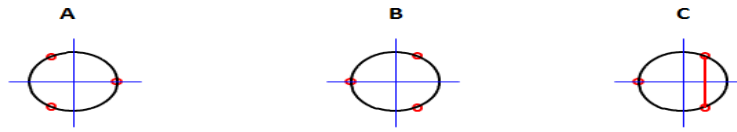


Figure: Two main bifurcations from a stable equilibrium for the three gene network. A: $Q > 0$ (pitchfork bifurcation), B: $Q < 0$ (Hopfbifurcation). C: illustration of the Hopf bifurcation point. The radius of the circle is one and the marked points are the cube roots of 1 column A and -1 in B and C.

5.4.3 Example

The existence of a Pitchfork bifurcation in the three gene case.

$$\begin{aligned} \frac{dx}{dt} &= \frac{2}{1+z^m} - x \\ \frac{dy}{dt} &= \frac{2x^m}{1+x^m} - y \\ \frac{dz}{dt} &= \frac{2}{1+y^m} - z \end{aligned} \tag{5.4.6}$$

The equilibrium of the system are

$$\begin{aligned} x &= \frac{2}{1+z^m} \\ y &= \frac{2x^m}{1+x^m} \\ z &= \frac{2}{1+y^m} \end{aligned} \tag{5.4.7}$$

$0 \leq m \leq 2$, then all equilibria (x, y, z) must be $(1,1,1)$. This can be proved by numerica.

The Jacobian matrix is,

$$J = \begin{pmatrix} -1 & 0 & -2m \frac{z^{m-1}}{(z^m+1)^2} \\ 2m \frac{x^{m-1}}{(x^m+1)^2} & -1 & 0 \\ 0 & -2m \frac{y^{m-1}}{(y^m+1)^2} & -1 \end{pmatrix}$$

$$= \begin{pmatrix} -1 & 0 & -\frac{1}{2}m \\ \frac{1}{2}m & -1 & 0 \\ 0 & -\frac{1}{2}m & -1 \end{pmatrix}$$

$\det(J) = \frac{1}{8}m^3 - 1$, which is zero exactly when $m = 2$.

This satisfies the conditions for the existence of a pitchfork bifurcation.

5.5 N-Dimensional Theory

A network of order n , consider the model described by ODE of the form ,

$$\begin{aligned} \frac{dx_1}{dt} &= F_1(x_n) - \alpha_1 x_1 \\ \frac{dx_2}{dt} &= F_2(x_1) - \alpha_2 x_2 \\ &\vdots \\ \frac{dx_n}{dt} &= F_n(x_{n-1}) - \alpha_n x_n \end{aligned} \tag{5.5.1}$$

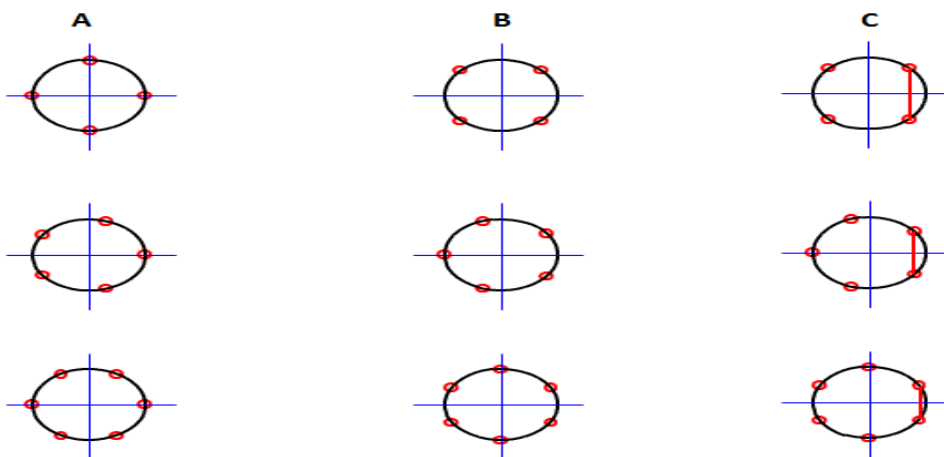


Figure: Two main bifurcations from a stable equilibrium.

Column A: $Q > 0$ (pitchfork bifurcation), column B: $Q < 0$ (Hopf bifurcation). Column C: illustration of the Hopf bifurcation point. Rows show dimensions 4,5 and 6 from the top to bottom. The radius of the circle is one and the marked points are the cube roots of 1 column A and -1 in B and C.

let x_0 be an equilibrium and J at x_0 .

Then let $Q = \prod F_i'$ and the determinant of

$$J = -1^n \times Q - \prod \alpha_i$$

The characteristic equation for a n –dimensional system can be written as ,

Where each α_i represents the absolute value of a diagonal term in J and is a degradation constant. If we replace α_i 's with the mean,

ie), $\alpha = \frac{1}{n} \sum_i \alpha_i$, then equation (5.5.2) is simplified to the form,

$$(\lambda + \alpha)^n = -1^n \times Q .$$

Finally, we constructed a network for the genome and defined the concept of a core and laying in the network.

5 Conclusion

We constructed a dynamical system on gens expression levels from the network. For these dynamics two main bifurcations from a stable equilibrium. Last we presented preliminary work toward understanding the bifurcations in n –dimensions. This work will contribute to a deep understanding of the genome and its controllability.

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