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Steady State Configurations of Cells Connected by Cadherin Sites

Jared Adam McBride

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of
Master of Science

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ABSTRACT

Steady State Configurations of Cells Connected by Cadherin Sites

Jared Adam McBride

Department of Mathematics, BYU

Master of Science

Many cells employ cadherin complexes (*c*-sites) on the cell membrane to attach to neighboring cells, as well as integrin complexes (*i*-sites) to attach to a substrate in order to accomplish cell migration. This paper analyzes a model for the motion of a group of cells connected by *c*-sites. We begin with two cells connected by a single *c*-site and analyze the resultant motion of the system. We find that the system is irrotational. We present a result for reducing the number of *c*-sites in a system with *c*-sites between pairs of cells. This greatly simplifies the general system, and provides an exact solution for the motion of a system of two cells and several *c*-sites.

Then a method for analyzing the general cell system is presented. This method involves 0-row-sum, symmetric matrices. A few results are presented as well as conjectures made that we feel will greatly simplify such analyses. The thesis concludes with the proposal of a framework for analyzing a dynamic cell system in which stochastic processes govern the attachment and detachment of *c*-sites.

Keywords: Differential Equations, Nondimensionalization, Stochastics.

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I am extremely grateful for the hard work of those involved in my education and offer much thanks to them and especially to my committee. I would like to start by expressing my appreciation for Dr. John Dallon for getting me started and helping me to realize my hope of doing research in math biology. It was he who first posed the problem addressed here and excited my interest in this model. He is an excellent adviser. Dr. Christopher Grant has also been an invaluable resource for not only questions in the mathematics but also in the typesetting and formatting of the thesis. His door was always open and I greatly appreciate that. It was also a great opportunity to work with Dr. Emily Evans; her insights were ever on point and very helpful.

It was from Dr. Bakker that I took my first course in applied mathematics. This course was full of most of the techniques necessary to make any progress in this problem. Much of what is accomplished here is the result of his instruction and generous time outside of the classroom.

I also offer my thanks to my dad, Dr. Don McBride for his encouragement and support. My officemates Kevin Johnston and Devin McGhie also provided insights in a variety of aspects, not the least of which improved the readability of the piece. Lastly, I would like to express my gratitude for the support, encouragement, and patience of my wife, Erin.

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CHAPTER 1. INTRODUCTION AND SETTING

1.1 INTRODUCTION

Currently there is great interest in studying simple organisms that display specific aspects of much more complex organisms. Such simple organisms, called model organisms, are vastly more accessible to research and provide insights in understanding more complex organisms. The research here began with the study of just such an organism, *Dictyostelium discoideum*.

In the summer of 1933 Kenneth B. Raper, just before arriving as a graduate student at Harvard University, went on a brief vacation to North Carolina. Raper was among the rare sort who would, while hiking in the Appalachian Mountains, collect samples of forest leaf mold. From litter collected from western North Carolina's Craggy Mountains, he isolated a remarkable new species of cellular slime mold in the genus *Dictyostelium*. Raper named the new species *Dictyostelium discoideum* (Dd) , when he described it in a paper in the Journal of Agricultural Research in 1935 [1], [2]. A slime mold is a eukaryotic amoeba that transitions from a collection of single cellular organisms into a multinucleated slug. Dd on the other hand as a cellular slime mold spends most of its life as uninucleated cells, that form a slug but retain, for the most part their cell membranes. The transition from a isolated cell to a multicellular slug is based on several factors including scarcity of resources. It has since been designated a model organism by the National Institutes of Health for the many areas of research to which its study has contributed. These areas include cell differentiation, chemotaxis and thermotaxis, programmed cell death, and DNA repair [3].

Motility in Dd involves periodic extension and retraction of pseudopodia with coordinated adhesion to propel cellular movement in random directions [4]. The adhesion here referred to is explained in great detail by Siu et al [3]. There, they identify cell-to-cell adhesion molecules and note that a few of these molecules are dependent on the adhesion molecule DdCAD-1, a form of cadherin. These attachment complexes reside at the end of pseudopodia. These complexes will simply be referred to as c-sites (for cadherin), when they attach to other cells.

When a cell attaches to a substrate the adhesion molecule are typically integrin based, for this reason these adhesion sites are referred to as i-sites.

For the past 8 years, Dr. John Dallon (BYU) has been doing research on Dd, and has employed undergraduate students in developing computer simulations in order to better understand the movement of a population of cells like Dd.

The computer models referenced above involve a collection of cells reaching out to neighboring cells as well as to the substrate (simulating both c-site and i-site attachment behavior). The pseudopodia are modeled as a Hookean spring of zero rest length, meaning they exert forces on both the c-site or i-site and the cell center that is directly proportional to their distance apart. The tendency for a cell to attach to either a cell or the substrate both involve random processes.

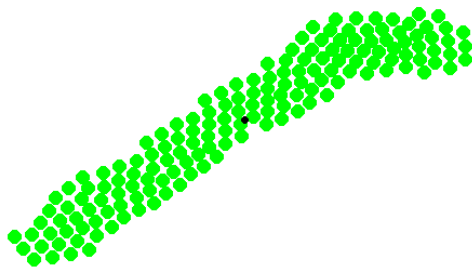


Figure 1.1: Here is a Dd slug *in silico* displaying the typical elongated structure. This structure seems to be a steady state of the model.

These simulations have produced interesting results such as the elongated steady state exhibited in Figure 1.1. This thesis was born out a desire to better understand this behavior of the slug *in silico*.

The purpose of this study is to analyze the movement of these cell centers under assumptions similar to the computer model, but from a strictly theoretically perspective. Here, the reaching of the pseudopodia is restricted to only other cells. These cells are thought of as being in suspension with no substrate to latch on to. The result of this restriction is that only c-sites and no i-sites are considered in the model. The exact assumptions used in the majority of this work are now listed. (1) The cell centers are all two dimensional, identically

shaped, objects in the plane. This means that, in the equations used to govern the motion of these objects, cell centers have the same drag coefficient. (2) The c-sites are likewise two dimensional and identically shaped objects in the plane, and, therefore, also all have the same drag coefficient (different from the cell center drag coefficient). It is also supposed that the c-sites are much smaller than the cells. (3) The spring constant for the springs that model the pseudopodia are all the same. Also, the pseudopodia may be arbitrarily long. (4) The cells possess an inhibition to occupy the same space. The cells should be thought of not as overlapping but rather as deforming as they bump up against each other. The force on the centers of two cells that are squashed together increases (continuously) as the distance between the centers decreases. It is not assumed that the force here described changes linearly with the distance between the cell centers but only that the force gets large as the distance becomes small. (5) There is no boundary to the plane on which the cell centers reside. Another rather significant assumption that greatly simplifies the problem is that (6) the c-sites are constantly attached to the cells. A more accurate and sophisticated model would employ random variables, as switching terms, to govern the attachment and detachment of the c-sites to various cells as well as random variables (times) to determine where the c-sites move in the plane between attachments. As such, an approach to a formulation of such a model involving stochastics has been considered and a framework for this approach has been included in Chapter Five.

1.2 FORMULATION OF THE MODEL, NOTATION AND DEFINITIONS

The objects in the model are defined mathematically as follows. The cell centers and the c-sites will be represented by points in \mathbb{R}^2 . Let $\mathbf{x}_i = \mathbf{x}_i(t)$, for real $t \geq 0$ and for $i = 1, 2, \dots, n$, be points in \mathbb{R}^2 that denote the locations of the centers of n cells at time t . The coordinates for the cell locations will be designated by $\mathbf{x}_i = (x_i, y_i)$. Similarly, let $\mathbf{c}_{i,j,k} = \mathbf{c}_{i,j,k}(t)$ be the point in \mathbb{R}^2 that represents the location of the center of the k th c-site that is attached to both the i th and the j th cell centers (so, $\mathbf{c}_{i,j,k} = \mathbf{c}_{j,i,k}$). The integer $n_{i,j}$ will denote the number

of c -sites connecting the i th and the j th cells; m will denote the total number of c -sites, so $m = \sum_{i < j} n_{i,j}$. The coordinates will be denoted $\mathbf{c}_{i,j,k} = (x_{i,j,k}, y_{i,j,k})$. As mentioned above, with regards to the assumptions in our model, cells are connected to c -sites by pseudopodia which here is represented as a spring.

Now, we think of the network of cells and c -sites as a graph together with any information relevant to its evolution in the plane. This is roughly what we mean when we refer to a cell system (this will be defined more precisely below). So, in total a cell system includes data about the drag of the cells in the group and the elasticity of areas of the cell, the size of the c -sites etc. as well as information of which cells are connected by which c -sites, all this is in a cell system. An illustration of a cell system is displayed in Figure 1.2.

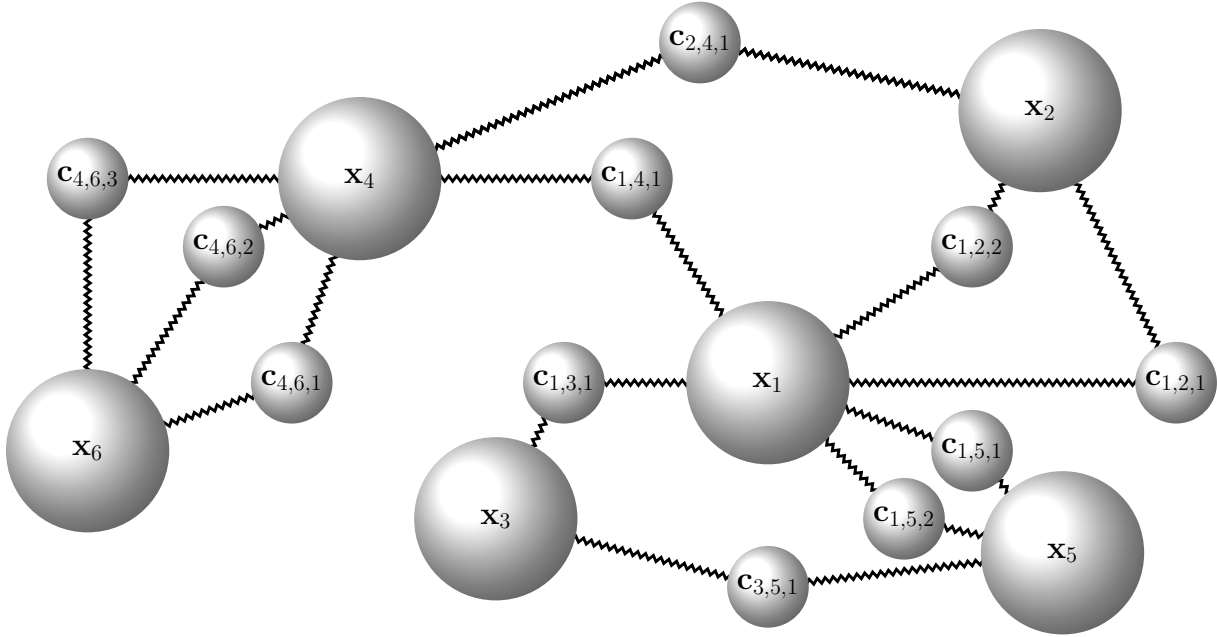


Figure 1.2: This is a representation of a cell system. There are six cells and eleven c -sites, they are interconnected, as seen above. The location of each body is given. The drag coefficients of the cells are γ_1 and that of the c -sites are γ_2 . All the pseudopodia spring constants are α and the body force is given by f . All this information is necessary in determining a cell system.

Now, given any cell system it is handy to consider what we call the *cell adjacency graph* of the cell system. This graph is associated with a cell system and has adjacency matrix $M = [n_{ij}]$ that is to say the matrix whose i, j -entry is the number $n_{i,j}$ (recall $n_{i,j}$ is defined to be 0 if there are no c -sites connecting to the i th and the j th cells.) The edges of the graph will correspond to the c -sites that connect the various cells. So, the cell adjacency graph

associated with the cell system in Figure 1.2 is shown in Figure 1.3. The cell adjacency graph of a system will be useful in Chapter Four where more general systems are discussed.

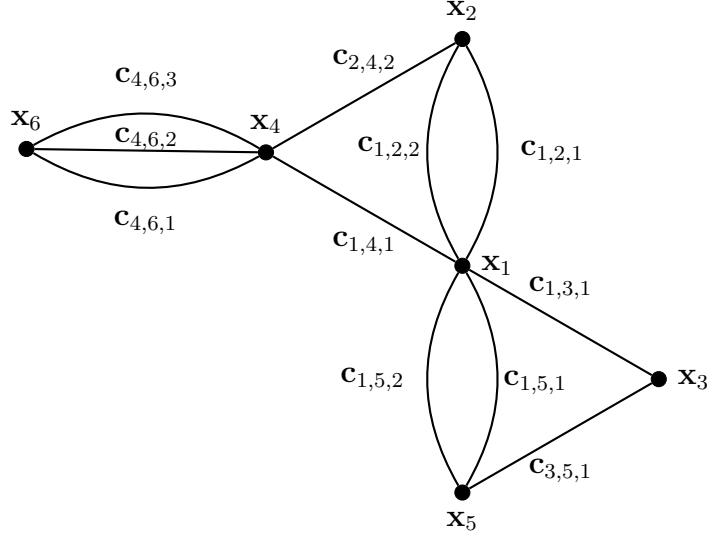


Figure 1.3: The cell incidence graph of the cell system with six cells and eleven c-sites depicted in Figure 1.2.

The number $m_{i,j}$ will be defined as follows

$$m_{i,j} = \begin{cases} 0 & \text{If } n_{i,j} = 0, \\ 1 & \text{If } n_{i,j} \neq 0. \end{cases} \quad (1.1)$$

These are the entries of the adjacency matrix for the graph associated with a cell system in which the multiple edges of the cell adjacency graph have been removed, it is called the *reduced cell adjacency graph*.

Since we consider all cell centers to be identical, as mentioned above, they have the same drag coefficient as do the c-sites of the model. The drag coefficient for the cells will be denoted $\gamma_1 \in (0, \infty)$, and for the c-sites, $\gamma_2 \in (0, \infty)$.

Once attached, a c-site and a cell center, connected by the pseudopodia of the cell with the c-site on the end, tug on each other. We will approximate this as being directly proportional to the distance between the cell center and the c-site, as if they were connected by a Hookean spring of zero rest length. The spring constant to the spring modeling the pseudopodia for all the individual c-sites will be assumed to be the same and will be denoted by $\alpha \in (0, \infty)$.

We have just discussed the objects of the model and now describe in greater detail how these objects relate to each other. The cells will have a body force that keeps them from passing through each other. Let $f : [0, \infty) \rightarrow [0, \infty]$ be a continuously differentiable function, with $f(0) = \infty$, and with support $[0, r]$ for some real number $r > 0$. This function will denote the magnitude of the body force or the force that repels any two cells as soon as their centers become too close to each other (i.e. the distance between the centers of the cells is less than r). Since the cells are assumed to be identical, only one body force function is necessary throughout a single system. The input of the function f will be thought of as the distance between two cells, in this case, the Euclidean 2-norm will be used, which will be denoted simply by $\|\cdot\|$. We will sometimes write $\Delta x_{i,j}$ to mean $\|\mathbf{x}_j - \mathbf{x}_i\|$. So, below it will be seen that the factor $f(\|\mathbf{x}_j - \mathbf{x}_i\|)$ will ever be multiplied by the unit vector along the line connecting the two cells \mathbf{x}_i and \mathbf{x}_j . Since the closer the cell centers get to each other the more they repel each other, f may be assumed to be decreasing and even convex. With these assumptions in hand it follows then that $f > 0$ and $f' < 0$ on $(0, r)$.

The proposed model (so far, free from any stochastic terms) is derived from Newton's Second Law of Motion. The equation for a single cell may be thought of in the context of the sum of the forces acting on the cell producing an acceleration. The principal forces acting on the cell are (1) the body force (which vanishes when the cell centers are sufficiently far away from each other), (2) the forces generated by the c-sites (linear forces), and (3) the force of drag which in this environment is proportional to the velocity of the cell, but in the direction opposite the velocity. So, in general, the equation (for a cell of mass μ) of motion associated with the cell system is

$$\mu \ddot{\mathbf{x}}_i = \sum_{\substack{j=1 \\ j \neq i}}^n f(\|\mathbf{x}_i - \mathbf{x}_j\|) \frac{\mathbf{x}_i - \mathbf{x}_j}{\|\mathbf{x}_i - \mathbf{x}_j\|} + \sum_{j=1}^n \sum_{k=1}^{n_{i,j}} \alpha(\mathbf{c}_{i,j,k} - \mathbf{x}_i) - \gamma_1 \dot{\mathbf{x}}_i.$$

The first sum ranges over the indices of all the cells in the cell system. And the second sum ranges over the c-sites attached to the i th cell. Now, because of the medium through which

the cell travels and the cell's small size the Reynolds number is very small. As a result, the acceleration term is negligible. The equation for the c-site is similar but without the body force term. Writing an equations for each body, yields the following system:

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_1 = \sum_{\substack{j=1 \\ j \neq i}}^n f(\|\mathbf{x}_1 - \mathbf{x}_j\|) \frac{\mathbf{x}_1 - \mathbf{x}_j}{\|\mathbf{x}_1 - \mathbf{x}_j\|} + \sum_{j=1}^n \sum_{k=1}^{n_{1,j}} \alpha m_{1,j} (\mathbf{c}_{1,j,k} - \mathbf{x}_1) \\ \vdots \\ \gamma_1 \dot{\mathbf{x}}_n = \sum_{\substack{j=1 \\ j \neq i}}^n f(\|\mathbf{x}_n - \mathbf{x}_j\|) \frac{\mathbf{x}_n - \mathbf{x}_j}{\|\mathbf{x}_n - \mathbf{x}_j\|} + \sum_{j=1}^n \sum_{k=1}^{n_{n,j}} \alpha m_{n,j} (\mathbf{c}_{n,j,k} - \mathbf{x}_n) \\ \vdots \\ \gamma_2 \dot{\mathbf{c}}_{i,j,k} = \alpha (\mathbf{x}_i - \mathbf{c}_{i,j,k}) + \alpha (\mathbf{x}_j - \mathbf{c}_{i,j,k}) \\ \vdots \end{array} \right. \quad (1.2)$$

where $\mathbf{c}_{i,j,k}$ ranges over all the c-sites.

We conclude this section by summarizing the above in a few definitions.

1.2.1 Definitions.

Definition 1. *A cell system is a connected bipartite graph, together with some additional information associated with elements of the graph. One of the partite groups represents the c-sites, the other, the cells. The c-site partite group is bivalent¹ and incident with no multi-edges². The additional information coupled with the graph is as follows:*

1. *The location, on the plane, of each vertex ($\mathbf{x}_i \in \mathbb{R}^2$ for vertices in the cell partite and $\mathbf{c}_{i,j,k} \in \mathbb{R}^2$ for vertices in the c-site partite).*
2. *A positive value $\gamma_i > 0$ associated with each vertex in the cell partite and $\gamma_{i,j,k} > 0$*

¹This means each vertex in the partite group has degree two.

²A multi-edge is an edge whose endpoints are the same as the endpoints of some other edge in the graph. Also, a vertex is incident to an edge if it is one of the endpoints of the edge. This condition is equivalent to saying the bipartite graph has girth at least 4, or in other words that there are no cycles of length smaller than four.

associated with each vertex in the c -site partaite (the drag coefficient). The index on γ corresponds with the vertex with which it is associated.

3. A function $\mathbf{a}_{i,j,k,l} : \mathbb{R}^4 \rightarrow \mathbb{R}^2$ associated with each edge modeling the attractive force of the cell and the c -site incident to that edge. The function $\mathbf{a}_{i,j,k,l}$ is thought of as having for arguments locations of the cell and the c -site that form its endpoints. The c -site is always the k th c -site attached to both the i th and j th cells. However, which cell is the argument depends on the value of l , if $l = 1$ then the location of the i th cell center in graph is the argument, if $l = 2$ then the location of the j th cell center is used. The output of $\mathbf{a}_{i,j,k,l}$ is a scalar multiple of the difference of the arguments being used. See figure 1.4.

4. A function $\mathbf{f}_{i,j} : \mathbb{R}^4 \rightarrow \mathbb{R}^2$ associated with a pair of vertices in the cell partite group which models the repulsive body force of the cells in the pair. Hence the arguments of $\mathbf{f}_{i,j}$ are simply the locations of the i th and j th cell centers and its output is a scalar multiple of their difference.

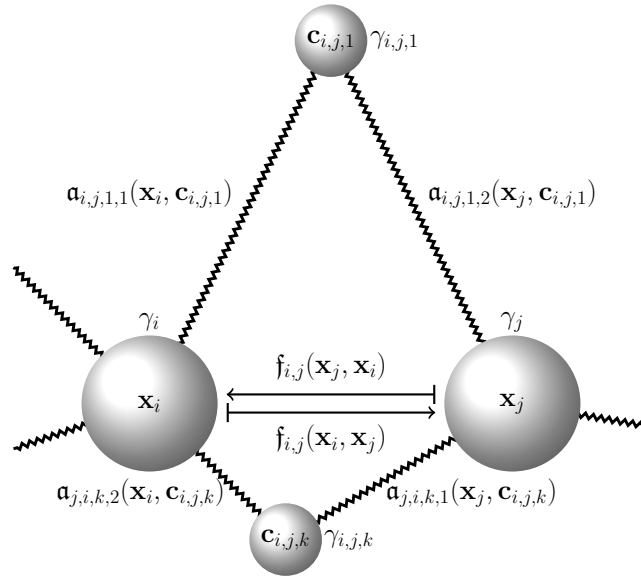


Figure 1.4: A portion of a cell system. Note, the indices on \mathbf{a}

Notice, in the above definition there are some identities:

$$\begin{aligned}\mathbf{c}_{i,j,k} &= \mathbf{c}_{j,i,k} \\ \gamma_{i,j,k} &= \gamma_{j,i,k} \\ \mathbf{a}_{i,j,k,1} &= \mathbf{a}_{j,i,k,2} \\ \mathbf{f}_{i,j} &= \mathbf{f}_{j,i}.\end{aligned}$$

We impose the laws of Newtonian mechanics in low Reynolds number, to dictate the evolution of the cell system. We now define a means of evaluating or studying the evolution of a cell system. With all the information given above pertaining to a cell system we define a force based system of differential equations as follows:

Definition 2. A cell system model is an initial value problem (IVP) associated with a cell system formulated this way

$$\left\{ \begin{array}{l} \gamma_i \dot{\mathbf{x}}_i = \sum_{j=1}^n \mathbf{f}_{i,j}(\mathbf{x}_i, \mathbf{x}_j) - \sum_{j=1}^n \sum_{k=1}^{n_{i,j}} \mathbf{a}_{i,j,k,1}(\mathbf{x}_i, \mathbf{c}_{i,j,k}) \\ \gamma_{i,j,k} \dot{\mathbf{c}}_{i,j,k} = \mathbf{a}_{i,j,k,1}(\mathbf{x}_i, \mathbf{c}_{i,j,k}) + \mathbf{a}_{i,j,k,2}(\mathbf{x}_j, \mathbf{c}_{i,j,k}) \end{array} \right. \quad (1.3)$$

Let $\mathbf{x} = (\mathbf{x}_1, \dots, \mathbf{x}_n, \dots, \mathbf{c}_{i,j,k}, \dots) \in \mathbb{R}^{2n+2m}$ be the state variable of the system. Then let $\mathbf{f} : \mathbb{R}^{2n+2m} \rightarrow \mathbb{R}^{2n+2m}$ be such that system (1.3) may be written as $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$. This is accomplished by assigning the right hand side of the l th equation of (1.3) as the l th component of \mathbf{f} . Here \mathbf{f} is said to be a cell system model force function and $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ is referred to as the ordinary differential equation (ODE) of the cell system model. The initial condition will be the state \mathbf{x}^0 (value of the state variable) of the cell system at some initial time t_0 .

So, the cell system model is simply the IVP

$$\left\{ \begin{array}{l} \dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}) \\ \mathbf{x}(t_0) = \mathbf{x}^0. \end{array} \right. \quad (1.4)$$

In regards to (1.3), for conciseness we display only the general forms of each group of equations that form the system, there are two groups of equations in these cell system models: cell equations and c-site equations. It is then left to the reader to flesh out the full system. For instance, system (1.3) has $n + m$ equations (each equation equates elements of \mathbb{R}^2); n for the cell equations denoted by the first line of (1.3) as j ranges from 1 to n , and $m = \sum_{i < j} n_{i,j}$ for each c-site equation.

Throughout the text we employ a useful convention, functions with their range lying in the state space of a cell system model are denoted in bold italics such as \mathbf{x} , \mathbf{y} , \mathbf{c} , and \mathbf{f} . Functions of elements in \mathbb{R}^2 are denoted by boldface characters such as \mathbf{x} , \mathbf{y} , \mathbf{c} , and \mathbf{f} . Elements of \mathbb{R} are simply written in normal type such as x , y , c , t , and f .

Definition 3. A Hookean cell system is a cell system in which

$$\begin{aligned} \mathbf{a}_{i,j,k,1}(\mathbf{x}_i, \mathbf{c}_{i,j,k}) &= \alpha_{i,j,k}(\mathbf{x}_i - \mathbf{c}_{i,j,k}) \\ \mathbf{a}_{i,j,k,2}(\mathbf{x}_j, \mathbf{c}_{i,j,k}) &= \alpha_{i,j,k}(\mathbf{x}_j - \mathbf{c}_{i,j,k}). \end{aligned} \tag{1.5}$$

This we refer to as the Hookean condition.

Definition 4. A Hookean cell system will be said to be of type 1 if

1. $\gamma_i = \gamma_1$ for each cell, i.e. for $i = 1, 2, \dots, n$ (in which case, relabel all to γ_1) and each $\gamma_{i,j,k} = \gamma_2$ for each c-site (in which case, relabel all to γ_2),
- 2.

$$\mathbf{f}_{i,j}(\mathbf{x}_i, \mathbf{x}_j) = f(\|\mathbf{x}_i - \mathbf{x}_j\|) \frac{\mathbf{x}_i - \mathbf{x}_j}{\|\mathbf{x}_i - \mathbf{x}_j\|}$$

for each $i, j = 1, 2, \dots, n$ for some $f : [0, \infty) \rightarrow [0, \infty]$ with the following properties:

- (a) $f(0) = \infty$,
- (b) for some $r > 0$, f has support $[0, r]$,
- (c) f is convex,
- (d) f is decreasing,

(e) f is C^1 on $(0, 1)$.

In this case f will be referred to as the generating function.

3. each $\alpha_{i,j,k} = \alpha m_{i,j}$ (in which case, relabel).

Definition 5. A Hookean cell system will be said to be of type 2 if

1. each $\gamma_i = \gamma_1$ for $i = 1, 2, \dots, n$ and

2. each $\mathfrak{f}_{i,j}$ is as in the definition of a Hookean cell system of type 1.

There are a few things worth pointing out at this point. First, note that all Hookean cell system of type 1 are also type 2. Second, the conditions in the definition of type 1 and type 2 pertaining to $\mathfrak{f}_{i,j}$ make it antisymmetric, meaning $\mathfrak{f}_{i,j} = -\mathfrak{f}_{j,i}$. This is important as it provides cancellation should some equations be added together.

More simply stated, in a Hookean cell system, the force representing the attraction between a cell and a c-site is linear with respect to their difference (the vector connecting the two bodies), notice also by the Hookean condition (1.5) the force $\mathbf{a}_{i,j,k,1} = \mathbf{a}_{i,j,k,2}$ thus the pseudopod spring constants are the same for each pseudopod connected to the same c-site.

The careful reader will observe that there may be some ambiguity in the definition of γ_1 and γ_2 . In the definition of a Hookean cell system of type 1 γ_1 is used to denote the common drag coefficient of the cells and γ_2 is used for the common drag coefficient of the c-sites. However in cell systems not of type 1 or 2 γ_1 and γ_2 are used for the drag coefficients of two particular cells. We feel that the context makes this naming system sufficiently transparent as to avoid any confusion.

Definition 6. A Hookean cell system model is a cell system model associated with a Hookean cell system. Hookean cell system models of type 1 and 2 are similarly defined according to the Hookean cell systems with which the model is associated.

For convenience a Hookean cell system and its corresponding model will be denoted by the fraktur character \mathfrak{H} , and when it is important to vary the initial conditions without

changing the underlying differential equation, we will specify the initial conditions by writing $\mathfrak{H}(t_0, \mathbf{x}^0)$.

And lastly, as will be important in chapters three and four.

Definition 7. *A cell system (cell system model) is said to be simple if each pair of cell centers have at most one c-site connecting them, that is $n_{i,j} \leq 1$ for all pairs $i, j = 1, 2, \dots, n$.*

1.3 EXISTENCE AND UNIQUENESS RESULTS

In this section we present a version of the famous existence and uniqueness theorem of ordinary differential equations tailored to Hookean cell system models of type 2. This theorem is used extensively in chapters two and three. We begin with an interesting observation.

1.3.1 Conservation of the Center of Drag. There is a useful property inherent in Hookean cell systems of type 2. There is a conservation of what we call the “center of drag.”

Definition 8. *In a cell system with $\mathbf{x} = (\mathbf{x}_1, \dots, \mathbf{x}_n, \dots, \mathbf{c}_{i,j,k}, \dots) \in \mathbb{R}^{2n+2m}$ the center of drag of the cell system is defined to be the point*

$$\mathbf{x}_{cod} = \frac{\sum_{i=1}^n \gamma_i \mathbf{x}_i + \sum_{i < j} \sum_{k=1}^{n_{i,j}} \gamma_{i,j,k} \mathbf{c}_{i,j,k}}{\sum_{i=1}^n \gamma_i + \sum_{i < j} \sum_{k=1}^{n_{i,j}} \gamma_{i,j,k}}.$$

This point is something of an analog to the center of mass.

Proposition 1.3.1. *Given a Hookean cell system of type 2, the center of drag is conserved throughout the entire evolution of that system.*

Proof. Consider the derivative of the center of drag with respect to time

$$\begin{aligned}
\dot{\mathbf{x}}_{\text{cod}} &= \left(\frac{\sum_{i=1}^n \gamma_i \mathbf{x}_i + \sum_{i < j} \sum_{k=1}^{n_{i,j}} \gamma_{i,j,k} \mathbf{c}_{i,j,k}}{\sum_{i=1}^n \gamma_i + \sum_{i < j} \sum_{k=1}^{n_{i,j}} \gamma_{i,j,k}} \right) \\
&= \left(\sum_{i=1}^n \gamma_i + \sum_{i < j} \sum_{k=1}^{n_{i,j}} \gamma_{i,j,k} \right)^{-1} \left(\sum_{i=1}^n \gamma_i \dot{\mathbf{x}}_i + \sum_{i < j} \sum_{k=1}^{n_{i,j}} \gamma_{i,j,k} \dot{\mathbf{c}}_{i,j,k} \right) \\
&= \mathbf{0}.
\end{aligned}$$

That $\sum_{i=1}^n \gamma_i \dot{\mathbf{x}}_i + \sum_{i < j} \sum_{k=1}^{n_{i,j}} \gamma_{i,j,k} \dot{\mathbf{c}}_{i,j,k} = \mathbf{0}$ can be seen from the definition of a Hookean cell system of type 2, since the body forces are anti-symmetric and all the c-site forces in the cell equations appear in the c-site equations with opposite sign. Indeed adding up all the equations in (1.3) reveals that the right hand sides sum to zero. So, $\mathbf{x}_{\text{cod}} = \mathbf{C}$ where $\mathbf{C} \in \mathbb{R}^2$ is a constant. \square

In fact, this law applies to more robust systems than those that are Hookean cell system models of type 2, we will see that the first condition for type 2 may be discarded and the second relaxed $\mathbf{f}_{i,j}(\mathbf{x}_i, \mathbf{x}_j) = -\mathbf{f}_{j,i}(\mathbf{x}_j, \mathbf{x}_i)$ (an anti-symmetry of the body forces). However, since this paper is mainly concerned with Hookean cell system of type 2 we state the law for that class of cell system.

This principle is a direct result of the conservation of force. A useful consequence of this fact is the following.

Proposition 1.3.2. *If $\mathbf{x}(t)$ is a solution to a Hookean cell system model \mathfrak{H} , then there exist an $L > 0$ which depends on \mathbf{x}^0 such that*

$$\|\mathbf{x}(t)\| < L$$

for all t .

Proof. Let \mathbf{x}^0 be the initial state of \mathfrak{H} and let L_0 be such that $\|\mathbf{x}^0\| < L_0$. Now, it is important to point out that the c-sites have no tendency to become further from the midpoint of the two cell centers to which they are attached. Likewise the cell centers are only ever forced no more than r units from another cell, by its body force. These facts together make it apparent that any solution to \mathfrak{H} will not at any point have norm greater than $L_0 + nr$. Hence, $L := L_0 + nr$ is the distance that is the farthestmost any cell and c-site could possibly be apart, given the initial state of a system with condition $\|\mathbf{x}^0\| < L_0$. So, as will be employed later, if \mathbf{x} is a solution to the \mathfrak{H} and $\|\mathbf{x}^0\| < L_0$ then $\|\mathbf{x}(t)\| < L$ and $\|\mathbf{x} - \mathbf{x}^0\| < L_0 + L$. \square

1.3.2 Some important sets. These models necessitate a family of sets that will be important to the analysis to follow. They arise naturally, from the avoidance of the case in which two cell centers are in the same location. Here is one such set:

$$\Theta_n = \{ \mathbf{x} = (\mathbf{x}_1, \mathbf{x}_2, \dots, \mathbf{x}_n) \in \mathbb{R}^{2n} : \|\mathbf{x}_i - \mathbf{x}_j\| \neq 0 \text{ for all } 1 \leq i \neq j \leq n \}$$

An element of the set $\Theta_n \times \mathbb{R}^{2m} \subset \mathbb{R}^{2n+2m}$ (which set should be thought of as being contained in the state space) corresponds to a cell system in which no two cell centers are at the same location (no such consideration is made for the c-sites). This is an invariant set for any Hookean cell system model of type 2, as we here explain. From the physical interpretation, the body force repelling any two cell centers will eventually overcome any c-site force (or even any collection of c-site forces). This is because the body force is unbounded as the distance between the two cell centers becomes small and the pseudopodia forces are generally decreasing. Hence no pseudopodia forces will eventually overpower the body force; the cell centers will, then, eventually, be forced apart or at least stop attracting.

Proposition 1.3.3. *The set Θ_n is open and connected.*

Proof. Let $\mathbf{x} = (\mathbf{x}_1, \dots, \mathbf{x}_n) \in \Theta_n$ and pick $\epsilon = \frac{1}{2} \min_{i \neq j} \|\mathbf{x}_i - \mathbf{x}_j\|$. Now suppose $\mathbf{y} \in B(\mathbf{x}, \epsilon) :=$

$\{\mathbf{y} \in \mathbb{R}^{2n} : \|\mathbf{y} - \mathbf{x}\| < \epsilon\}$. Observe that

$$\left(\frac{1}{2} \min_{i \neq j} \|\mathbf{x}_i - \mathbf{x}_j\|\right)^2 = \epsilon^2 > \|\mathbf{y} - \mathbf{x}\|^2 = \sum_{i=1}^n \|\mathbf{y}_i - \mathbf{x}_i\|^2 \geq \|\mathbf{y}_i - \mathbf{x}_i\|^2.$$

and, so, for any i , $\|\mathbf{y}_i - \mathbf{x}_i\| < \frac{1}{2} \min_{i \neq j} \|\mathbf{x}_i - \mathbf{x}_j\|$. Now suppose there exist an i and j with $i \neq j$ so that $\mathbf{y}_i = \mathbf{y}_j$ then

$$\|\mathbf{x}_i - \mathbf{x}_j\| = \|\mathbf{x}_i - \mathbf{y}_i + \mathbf{y}_j - \mathbf{x}_j\| \leq \|\mathbf{x}_i - \mathbf{y}_i\| + \|\mathbf{y}_j - \mathbf{x}_j\| < \min_{i \neq j} \|\mathbf{x}_i - \mathbf{x}_j\|$$

a contradiction. So, $\mathbf{y} \in \Theta_n$ and $B(\mathbf{x}, \epsilon) \subset \Theta_n$, hence Θ_n is open.

To see that Θ_n is connected, it is sufficient to show it is path connected. To do this consider any two points $\mathbf{y}^0, \mathbf{x}^0 \in \Theta_n$ and a series of paths $\phi_i(\mathbf{x}, \mathbf{y}) : [0, 1] \rightarrow \Theta_n$ for $i = 1, 2, \dots, n$ so that $\phi_i(\mathbf{x}, \mathbf{y})(0) = \mathbf{x}$ and $\phi_i(\mathbf{x}, \mathbf{y})(1) = (\mathbf{x}_1, \dots, \mathbf{x}_{i-1}, \mathbf{y}_i, \mathbf{x}_{i+1}, \dots, \mathbf{x}_n)$ each continuously deforming the i th component of \mathbf{x} to the i th component of \mathbf{y} leaving the other components constant and avoiding equality with any other component of \mathbf{x} . See Figure 1.5.

Let

$$\begin{aligned} \mathbf{x}^1 &= \phi_1(\mathbf{x}^0, \mathbf{y}^0)(1) \\ \mathbf{x}^2 &= \phi_2(\mathbf{x}^1, \mathbf{y}^0)(1) \\ &\vdots \\ \mathbf{x}^i &= \phi_i(\mathbf{x}^{i-1}, \mathbf{y}^0)(1) \\ &\vdots \\ \mathbf{x}^n &= \phi_n(\mathbf{x}^{n-1}, \mathbf{y}^0)(1) \end{aligned}$$

then the path

$$\mathbf{x}^0 \xrightarrow{\phi_1(\mathbf{x}^0, \mathbf{y}^0)} \mathbf{x}^1 \xrightarrow{\phi_2(\mathbf{x}^1, \mathbf{y}^0)} \dots \xrightarrow{\phi_{n-1}(\mathbf{x}^{n-2}, \mathbf{y}^0)} \mathbf{x}^{n-1} \xrightarrow{\phi_n(\mathbf{x}^{n-1}, \mathbf{y}^0)} \mathbf{x}^n = \mathbf{y}^0$$

is a continuous deformation from \mathbf{x}^0 to \mathbf{y}^0 which remains in Θ_n □

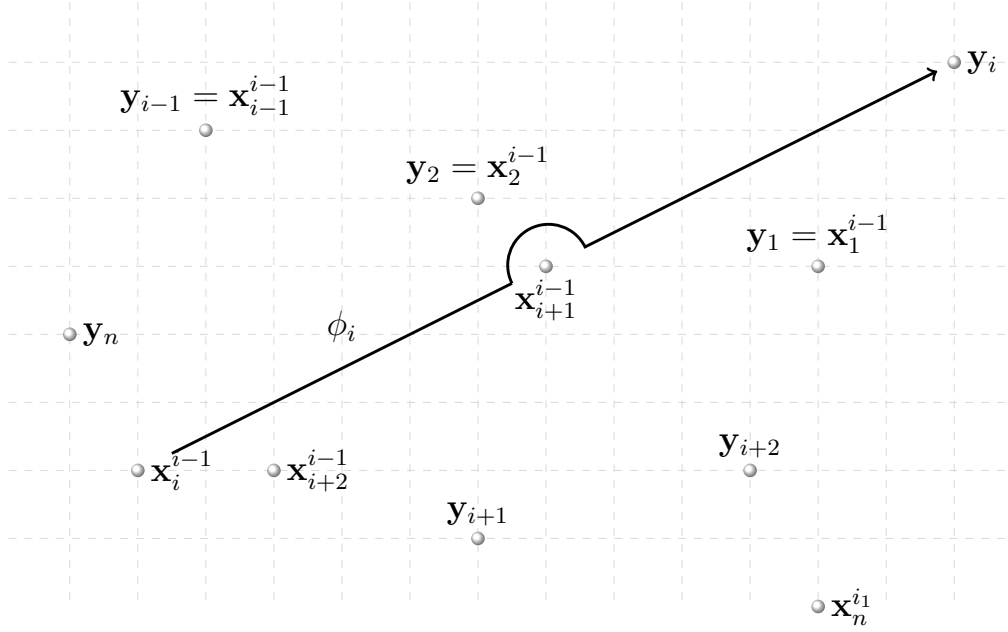


Figure 1.5: A demonstration of the continuous path $\phi_i(\mathbf{x}^{i-1}, \mathbf{y}^0)$ that is used as the i th component of ϕ_i (the other components being the identity on \mathbb{R}^2) so that $\phi_i(\mathbf{x}^{i-1}, \mathbf{y}^0)(0) = \mathbf{x}^{i-1} = (\mathbf{y}_1, \dots, \mathbf{y}_{i-1}, \mathbf{x}_i, \mathbf{x}_{i+1}, \dots, \mathbf{x}_n)$ and $\phi_i(\mathbf{x}^{i-1}, \mathbf{y}^0)(1) = \mathbf{x}^i = (\mathbf{y}_1, \dots, \mathbf{y}_{i-1}, \mathbf{y}_i, \mathbf{x}_{i+1}, \dots, \mathbf{x}_n)$. Notice that because the components of \mathbf{x}^{i-1} are in the plane and finite there is always a continuous path from \mathbf{x}_i^{i-1} to \mathbf{y}_i which does not intersect any other component of \mathbf{x}^{i-1} .

In the interest of building an existence and uniqueness result for a Hookean cell system of type 2 \mathfrak{H} , it will be helpful for the force function \mathbf{f} of \mathfrak{H} to be uniformly Lipschitz. Because of the singularities that occur when two cell centers approach the same location it is necessary to find a more restrictive set on which \mathbf{f} is better behaved and which still possess an invariance property. To that end, let $\epsilon > 0$ and let

$$\Theta_{n,\epsilon} = \{ \mathbf{x} = (\mathbf{x}_1, \mathbf{x}_2, \dots, \mathbf{x}_n) \in \mathbb{R}^{2n} : \|\mathbf{x}_i - \mathbf{x}_j\| > \epsilon \text{ for all } 1 \leq i < j \leq n \}$$

These sets are not necessarily invariants sets for the ODE of some Hookean cell system model \mathfrak{H} since cell centers generally do become closer together as the system evolves, but it may be shown that for any given Hookean cell system model \mathfrak{H} it is impossible for the cell centers to be forced within a particular distance. This is because there is, basically, a maximum to the force that the c-sites can exert on a system. This is a result of Proposition 1.3.2; the c-sites can only be so far from the cells. This is made precise in the following lemma:

Lemma 1.3.4. *Given the Hookean cell system model, \mathfrak{H} , there exists an $\epsilon > 0$ for which if there is a solution to \mathfrak{H} it will remain in $\Theta_{n,\epsilon} \times \mathbb{R}^{2m}$.*

Proof. Proposition 1.3.2 gives an L such that for any solution \mathbf{x} of \mathfrak{H} we have $\|\mathbf{x}\| < L$. This implies that for any cell center and c-site of the cell system \mathbf{x}_i and $\mathbf{c}_{ij,k}$, $\|\mathbf{x}_i - \mathbf{c}_{ij,k}\| < 2L$. Now, for each cell \mathbf{x}_i pick $r_i > 0$ so that

$$f(r_i) = \sum_{j=1}^n \sum_{k=1}^{n_{i,j}} 2\alpha_{i,j,k}(2L), \quad (1.6)$$

(since f is continuous on $(0, r)$, $f(0) = \infty$, and $f(r) = 0$ such an $r_i > 0$ exists for each \mathbf{x}_i) choose $\epsilon_1 = \min_i r_i$, $\epsilon_2 = \min_{i \neq j} \|\mathbf{x}_i^0 - \mathbf{x}_j^0\|$ (for $\mathbf{x}^0 = (\mathbf{x}_1^0, \dots, \mathbf{x}_n^0, \dots, \mathbf{x}_{i,j,k}^0, \dots)$ the initial condition of \mathfrak{H} ; we are concerned with only the cells in this initial condition for our formulation of ϵ_2), and $\epsilon = \min\{\epsilon_1, \epsilon_2\}$. Observe that the RHS of (1.6) provides a very crude upper bound for the sum of all possible pseudopodia forces acting on the i th cell. By way of explanation, if all the c-sites in the whole cell system were attached to that one cell and they were stretched as far as possible from the cell, the resulting total force would be the RHS of (1.6). The ϵ is chosen to be the minimum since because the function f is decreasing $f(\epsilon)$ will be larger than the RHS of (1.6) for any i . Thus, the first time the distance of any two cell centers approach ϵ (this would approach from above as all the cell started out farther then ϵ apart) the body force of the cells would overpower all other possible forces of attraction, the velocity of the cell centers would immediately be in a direction to increase their distance apart. And so, the solution \mathbf{x} remains safely in the set $\Theta_{n,\epsilon}$. \square

Proposition 1.3.5. *The set $\Theta_{n,\epsilon}$ is open and connected.*

Proof. Let $\mathbf{x} \in \Theta_{n,\epsilon}$, so then $\|\mathbf{x}_i - \mathbf{x}_j\| > \epsilon$ for all $1 \leq i < j \leq n$. Let $\delta = \frac{1}{2}(\min_{i \neq j} \|\mathbf{x}_i - \mathbf{x}_j\| - \epsilon)$. Now suppose $\mathbf{y} \in B(\mathbf{x}, \delta)$ then

$$\frac{1}{2}(\min_{i \neq j} \|\mathbf{x}_i - \mathbf{x}_j\| - \epsilon) = \delta > \|\mathbf{y} - \mathbf{x}\| = \left(\sum_{i=1}^n \|\mathbf{y}_i - \mathbf{x}_i\|^2 \right)^{\frac{1}{2}} \geq \|\mathbf{y}_i - \mathbf{x}_i\|.$$

and

$$\begin{aligned}
\min_{i \neq j} \|\mathbf{x}_i - \mathbf{x}_j\| &\leq \|\mathbf{x}_i - \mathbf{x}_j\| = \|\mathbf{x}_i - \mathbf{y}_i + \mathbf{y}_i - \mathbf{y}_j + \mathbf{y}_j - \mathbf{x}_j\| \\
&\leq \|\mathbf{x}_i - \mathbf{y}_i\| + \|\mathbf{y}_i - \mathbf{y}_j\| + \|\mathbf{y}_j - \mathbf{x}_j\| \\
&< 2\delta + \|\mathbf{y}_i - \mathbf{y}_j\| \\
&< \min_{i \neq j} \|\mathbf{x}_i - \mathbf{x}_j\| - \epsilon + \|\mathbf{y}_i - \mathbf{y}_j\|.
\end{aligned}$$

So, $\|\mathbf{y}_i - \mathbf{y}_j\| > \epsilon$ for any $i \neq j$. Hence, $\mathbf{y} \in \Theta_{n,\epsilon}$ so $B(\mathbf{x}, \delta) \subset \Theta_{n,\epsilon}$ and $\Theta_{n,\epsilon}$ is open.

The proof that $\Theta_{n,\epsilon}$ is connected is almost identical to that of Θ_n being connected, the only difference is that some care may need to be taken in choosing the paths. Notice that for any element $\mathbf{x} \in \Theta_{n,\epsilon}$ there is a path in $\Theta_{n,\epsilon}$ from \mathbf{x} to an element with the components in a line with the components sufficiently far apart. This provides an intermediate step from which any element of $\Theta_{n,\epsilon}$ may be reached. \square

Before proceeding there is a small fact that should be pointed out

Lemma 1.3.6. *For any $a_i \in \mathbb{R}$ for $i = 1, 2, \dots, n$, $(\sum_{i=1}^n a_i)^2 \leq n \sum_{i=1}^n a_i^2$.*

Proof. Young's inequality provides that $a_i a_j \leq \frac{a_i^2}{2} + \frac{a_j^2}{2}$ so

$$\left(\sum_{i=1}^n a_i \right)^2 \leq \sum_{i=1}^n a_i^2 + \sum_{i < j} (a_i^2 + a_j^2) \leq \sum_{i=1}^n a_i^2 + \sum_{i=1}^n (n-1)a_i^2 = n \sum_{i=1}^n a_i^2.$$

\square

We are now in a position to show that for any $\epsilon > 0$, \mathbf{f} is uniformly Lipschitz on any open ball contained in $\Theta_{n,\epsilon}$ (with n appropriately chosen according to the domain of \mathbf{f}).

Proposition 1.3.7. *For any $\epsilon > 0$ and Hookean cell system model of type 1 \mathfrak{H} , the force function \mathbf{f} of \mathfrak{H} is uniformly Lipschitz on any open ball contained in $\Theta_{n,\epsilon}$.*

Proof. Let $\hat{\mathbf{x}} \in \Theta_{n,\epsilon}$ be arbitrary and pick any $r > 0$ such that $B(\hat{\mathbf{x}}, r) \subset \Theta_{n,\epsilon}$. Now, note that there is a nonlinear function \mathbf{N} and a linear function \mathbf{L} both in $C([0, \infty); \mathbb{R}^{2n+2m})$ such that $\mathbf{f} = \mathbf{N} + \mathbf{L}$. Namely,

$$\mathbf{N}(\mathbf{x}) = \begin{pmatrix} \frac{1}{\gamma_1} \sum_{i=1}^n f(\|\mathbf{x}_j - \mathbf{x}_i\|) \frac{\mathbf{x}_j - \mathbf{x}_i}{\|\mathbf{x}_j - \mathbf{x}_i\|} \\ \mathbf{0} \end{pmatrix}, \quad \mathbf{L}(\mathbf{x}) = \begin{pmatrix} \frac{1}{\gamma_1} \sum_{i=1}^n \left(\sum_{k=1}^{n_{i,j}} \alpha_{i,j,k} (\mathbf{c}_{i,j,k} - \mathbf{x}_j) \right) \\ \frac{1}{\gamma_2} \alpha_{i,j,k} (\mathbf{x}_i + \mathbf{x}_j - 2\mathbf{c}_{i,j,k}) \end{pmatrix}.$$

Now, \mathbf{L} is Lipschitz everywhere because it is a bounded linear operator. It will here be shown that \mathbf{N} is Lipschitz in $B(\hat{\mathbf{x}}, r)$. Because f is decreasing, convex, and continuously differentiable $|f'|$ is decreasing, so let $M > f(\epsilon)$ and $M' > |f'(\epsilon)|$. Observe that so long as $\mathbf{x} \in \Theta_{n,\epsilon}$, $\|\mathbf{x}_i - \mathbf{x}_j\| > \epsilon$. Now, consider the following:

$$\begin{aligned} & \|\mathbf{N}(\mathbf{x}^2) - \mathbf{N}(\mathbf{x}^1)\|^2 \\ &= \sum_{j=1}^n \left\| \frac{1}{\gamma_1} \sum_{\substack{i=1 \\ i \neq j}}^n \left(f(\|\mathbf{x}_i^2 - \mathbf{x}_j^2\|) \frac{\mathbf{x}_i^2 - \mathbf{x}_j^2}{\|\mathbf{x}_i^2 - \mathbf{x}_j^2\|} - f(\|\mathbf{x}_i^1 - \mathbf{x}_j^1\|) \frac{\mathbf{x}_i^1 - \mathbf{x}_j^1}{\|\mathbf{x}_i^1 - \mathbf{x}_j^1\|} \right) \right\|^2 \\ &\leq \sum_{j=1}^n \left(\frac{1}{\gamma_1} \sum_{\substack{i=1 \\ i \neq j}}^n \left\| \left(f(\|\mathbf{x}_i^2 - \mathbf{x}_j^2\|) \frac{\mathbf{x}_i^2 - \mathbf{x}_j^2}{\|\mathbf{x}_i^2 - \mathbf{x}_j^2\|} - f(\|\mathbf{x}_i^1 - \mathbf{x}_j^1\|) \frac{\mathbf{x}_i^1 - \mathbf{x}_j^1}{\|\mathbf{x}_i^1 - \mathbf{x}_j^1\|} \right) \right\| \right)^2 \\ &\leq \frac{n-1}{\gamma_1^2} \sum_{j=1}^n \sum_{\substack{i=1 \\ i \neq j}}^n \left\| f(\|\mathbf{x}_i^2 - \mathbf{x}_j^2\|) \frac{\mathbf{x}_i^2 - \mathbf{x}_j^2}{\|\mathbf{x}_i^2 - \mathbf{x}_j^2\|} - f(\|\mathbf{x}_i^1 - \mathbf{x}_j^1\|) \frac{\mathbf{x}_i^1 - \mathbf{x}_j^1}{\|\mathbf{x}_i^1 - \mathbf{x}_j^1\|} \right\|^2. \end{aligned} \quad (1.7)$$

Let us here consider

$$\left\| f(\|\mathbf{x}_i^2 - \mathbf{x}_j^2\|) \frac{\mathbf{x}_i^2 - \mathbf{x}_j^2}{\|\mathbf{x}_i^2 - \mathbf{x}_j^2\|} - f(\|\mathbf{x}_i^1 - \mathbf{x}_j^1\|) \frac{\mathbf{x}_i^1 - \mathbf{x}_j^1}{\|\mathbf{x}_i^1 - \mathbf{x}_j^1\|} \right\|. \quad (1.8)$$

Letting $\boldsymbol{\xi}^k = \mathbf{x}_i^k - \mathbf{x}_j^k$ for $k = 1, 2$ and letting $\mathbf{g}(\boldsymbol{\xi}) = \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \boldsymbol{\xi}$, (1.8) becomes simply

$$\|\mathbf{g}(\boldsymbol{\xi}^2) - \mathbf{g}(\boldsymbol{\xi}^1)\|. \quad (1.9)$$

Now, by the Mean Value Theorem [5]

$$\|\mathbf{g}(\boldsymbol{\xi}^2) - \mathbf{g}(\boldsymbol{\xi}^1)\| \leq \sup_{t \in [0,1]} \|\mathbf{Dg}(\boldsymbol{\xi}^1 + t(\boldsymbol{\xi}^2 - \boldsymbol{\xi}^1))\| \|\boldsymbol{\xi}^2 - \boldsymbol{\xi}^1\| \quad (1.10)$$

provided $\mathbf{Dg}(\boldsymbol{\xi}^1 + t(\boldsymbol{\xi}^2 - \boldsymbol{\xi}^1))$ exists for all $t \in [0, 1]$. To determine $\|\mathbf{Dg}(\boldsymbol{\xi}^1 + t(\boldsymbol{\xi}^2 - \boldsymbol{\xi}^1))\|$, let $\boldsymbol{\xi} = \boldsymbol{\xi}^1 + t(\boldsymbol{\xi}^2 - \boldsymbol{\xi}^1)$ and then observe that

$$\begin{aligned} \|\boldsymbol{\xi}\| &= \|\boldsymbol{\xi}^1 + t(\boldsymbol{\xi}^2 - \boldsymbol{\xi}^1)\| \\ &= \|\mathbf{x}_i^1 - \mathbf{x}_j^1 + t(\mathbf{x}_i^2 - \mathbf{x}_j^2 - (\mathbf{x}_i^1 - \mathbf{x}_j^1))\| \\ &= \|\mathbf{x}_i^1 + t(\mathbf{x}_i^2 - \mathbf{x}_i^1) - (\mathbf{x}_j^1 + t(\mathbf{x}_j^2 - \mathbf{x}_j^1))\| \\ &= \|(\mathbf{x}^1 + t(\mathbf{x}^2 - \mathbf{x}^1))_i - (\mathbf{x}^1 + t(\mathbf{x}^2 - \mathbf{x}^1))_j\| \\ &> \epsilon \end{aligned} \quad (1.11)$$

for all $t \in [0, 1]$. Line (1.11) is by the convexity of $B(\hat{\mathbf{x}}, r)$ which is in $\Theta_{n,\epsilon}$. Since $\mathbf{x}^2, \mathbf{x}^1 \in B(\hat{\mathbf{x}}, r)$, $\mathbf{x}^1 + t(\mathbf{x}^2 - \mathbf{x}^1) \in B(\hat{\mathbf{x}}, r) \subset \Theta_{n,\epsilon}$. Thus, for all $t \in [0, 1]$, $\boldsymbol{\xi}$ is never zero and the following calculations are valid for any $\boldsymbol{\xi}$ in the understood context. To calculate the Jacobian matrix of \mathbf{g} let $\mathbf{g} = (g_1, g_2)^T$, and $\boldsymbol{\xi} = (\xi_1, \xi_2)^T$ then,

$$\begin{aligned} \frac{\partial}{\partial \xi_1} \left(\frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \right) &= \frac{f'(\|\boldsymbol{\xi}\|)\xi_1}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)\xi_1}{\|\boldsymbol{\xi}\|^3} \\ &= \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_1 \end{aligned}$$

and (recall we are using the Euclidean norm in \mathbb{R}^2)

$$\frac{\partial}{\partial \xi_2} \left(\frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \right) = - \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_2.$$

Utilizing these we find

$$\begin{aligned}
\frac{\partial g_1}{\partial \xi_1} &= \frac{\partial}{\partial \xi_1} \left(\frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \xi_1 \right) \\
&= \frac{\partial}{\partial \xi_1} \left(\frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \right) \xi_1 + \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \\
&= \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_1^2 + \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \\
\frac{\partial g_1}{\partial \xi_2} &= \frac{\partial}{\partial \xi_2} \left(\frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \xi_1 \right) \\
&= - \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_1 \xi_2 \\
\frac{\partial g_2}{\partial \xi_1} &= \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_1 \xi_2 \\
\frac{\partial g_2}{\partial \xi_2} &= \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_2^2 + \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|}.
\end{aligned}$$

So that,

$$\mathbf{Dg}(\boldsymbol{\xi}) = \begin{pmatrix} \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_1^2 + \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} & - \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_1 \xi_2 \\ \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_1 \xi_2 & \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_2^2 + \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \end{pmatrix}.$$

The Mean Value Theorem referenced above employs the operator norm on $\mathbf{Dg}(\boldsymbol{\xi}) \in \mathcal{L}(\mathbb{R}^2)$ (where $\mathcal{L}(\mathbb{R}^2)$ is the set of all bounded linear operators on \mathbb{R}^2). Since this space is finite dimensional, norms on this space are topologically equivalent. Here, we choose to work with the Forbenius norm (written $\|\cdot\|_{\text{Forb}}$). If a bound can be found on $\mathbf{Dg}(\boldsymbol{\xi})$ under the Forbenius norm then there will exist a bound on $\mathbf{Dg}(\boldsymbol{\xi})$ under any other norm (that bound depends

on the particular norm). So,

$$\begin{aligned}
\|\mathbf{Dg}(\boldsymbol{\xi})\|_{\text{Forb}}^2 &= \left\| \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_1^2 + \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \right\|^2 + 2 \left\| \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_1 \xi_2 \right\|^2 \\
&\quad + \left\| \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_2^2 + \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \right\|^2 \\
&\leq \left(\left\| \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_1^2 \right\| + \left\| \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \right\| \right)^2 + 2 \left\| \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_1 \xi_2 \right\|^2 \\
&\quad + \left(\left\| \left(\frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right) \xi_2^2 \right\| + \left\| \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \right\| \right)^2 \\
&\leq 2 \left\| \frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right\|^2 |\xi_1|^4 + 2 \left\| \frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right\|^2 |\xi_1|^2 |\xi_2|^2 \\
&\quad + 2 \left\| \frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right\|^2 |\xi_2|^4 + 4 \left\| \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|} \right\|^2 \\
&\leq 6 \left\| \frac{f'(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^2} - \frac{f(\|\boldsymbol{\xi}\|)}{\|\boldsymbol{\xi}\|^3} \right\|^2 L^4 + 4 \left(\frac{M}{\epsilon} \right)^2 \\
&\leq 6 \left(\frac{M'}{\epsilon^2} + \frac{M}{\epsilon^3} \right)^2 L^4 + 4 \left(\frac{M}{\epsilon} \right)^2.
\end{aligned}$$

Pick $\kappa \in \mathbb{R}$ according to the definition of equivalent norms so that for all $\mathbf{f} \in \mathcal{L}(\mathbb{R}^2)$, $\|\mathbf{f}\| \leq \kappa \|\mathbf{f}\|_{\text{Forb}}$. So, from the above together with (1.9), (1.10), and (1.11) we find that (1.8) is bounded above by

$$\kappa \left(6 \left(\frac{M'}{\epsilon^2} + \frac{M}{\epsilon^3} \right)^2 L^4 + 4 \left(\frac{M}{\epsilon} \right)^2 \right) \|\mathbf{x}_i^1 - \mathbf{x}_j^1 - (\mathbf{x}_i^2 - \mathbf{x}_j^2)\|.$$

So, continuing from (1.7),

$$\begin{aligned}
& \|\mathbf{N}(\mathbf{x}^2) - \mathbf{N}(\mathbf{x}^1)\|^2 \\
& \leq \kappa^2 \frac{n-1}{\gamma_1^2} \sum_{j=1}^n \sum_{i=1}^n \left(6 \left(\frac{M'}{\epsilon^2} + \frac{M}{\epsilon^3} \right)^2 L^4 + 4 \left(\frac{M}{\epsilon} \right)^2 \right)^2 \|\mathbf{x}_i^1 - \mathbf{x}_j^1 - (\mathbf{x}_i^2 - \mathbf{x}_j^2)\|^2 \\
& \leq \kappa^2 \frac{n-1}{\gamma_1^2} \sum_{j=1}^n \sum_{i=1}^n \left(6 \left(\frac{M'}{\epsilon^2} + \frac{M}{\epsilon^3} \right)^2 L^4 + 4 \left(\frac{M}{\epsilon} \right)^2 \right)^2 \|\mathbf{x}_i^1 - \mathbf{x}_i^2 - (\mathbf{x}_j^1 - \mathbf{x}_j^2)\|^2 \\
& \leq \kappa^2 \frac{n-1}{\gamma_1^2} \sum_{j=1}^n \sum_{i=1}^n \left(6 \left(\frac{M'}{\epsilon^2} + \frac{M}{\epsilon^3} \right)^2 L^4 + 4 \left(\frac{M}{\epsilon} \right)^2 \right)^2 (\|\mathbf{x}_i^1 - \mathbf{x}_i^2\| + \|\mathbf{x}_j^1 - \mathbf{x}_j^2\|)^2 \\
& \leq \kappa^2 \frac{n-1}{\gamma_1^2} \sum_{j=1}^n \sum_{i=1}^n 2 \left(6 \left(\frac{M'}{\epsilon^2} + \frac{M}{\epsilon^3} \right)^2 L^4 + 4 \left(\frac{M}{\epsilon} \right)^2 \right)^2 (\|\mathbf{x}_i^1 - \mathbf{x}_i^2\|^2 + \|\mathbf{x}_j^1 - \mathbf{x}_j^2\|^2) \\
& = \kappa^2 \frac{n-1}{\gamma_1^2} 2 \left(6 \left(\frac{M'}{\epsilon^2} + \frac{M}{\epsilon^3} \right)^2 L^4 + 4 \left(\frac{M}{\epsilon} \right)^2 \right)^2 (2n \|\mathbf{x}^1 - \mathbf{x}^2\|^2) \\
& = \kappa^2 \frac{16n(n-1)}{\gamma_1^2} \left(3L^4 \left(\frac{M'}{\epsilon^2} + \frac{M}{\epsilon^3} \right) + 2 \left(\frac{M}{\epsilon} \right)^2 \right)^2 \|\mathbf{x}^1 - \mathbf{x}^2\|^2.
\end{aligned}$$

So, \mathbf{N} is Lipschitz in $B(\hat{\mathbf{x}}, r)$. And since the sum of two Lipschitz continuous functions is itself Lipschitz, \mathbf{f} is Lipschitz in $B(\hat{\mathbf{x}}, r)$. \square

Notice, the fact that \mathbf{f} is Lipschitz does not depend on the initial condition \mathbf{x}^0 . However, there exists a bound on $\|\mathbf{f}(\mathbf{x})\|$, and this bound does depend on the initial condition of \mathfrak{H} . This dependence is in the sense that a bound L on $\|\mathbf{x}\|$ according to Proposition 1.3.2 depends on \mathbf{x}^0 and it is in the sense that we require an $\epsilon > 0$ according to Lemma 1.3.4 for which \mathbf{x} remains in $\Theta_{n,\epsilon}$. That being said, let \mathfrak{H} be given and pick $\epsilon > 0$ by Lemma 1.3.4 according to \mathbf{x}^0 and L (produced by Proposition 1.3.2). Pick $M > f(\epsilon)$, and let

$\alpha = \max_{i,j,k} \alpha_{i,j,k}$ then, if $\mathbf{x} \in \Theta_{n,\epsilon} \times \mathbb{R}^{2m}$, we get that

$$\begin{aligned}
\|\mathbf{f}(\mathbf{x})\|^2 &= \sum_j \left\| \frac{1}{\gamma_1} \left(\sum_{\substack{i=1 \\ i \neq j}}^n f(\|\mathbf{x}_j - \mathbf{x}_i\|) \frac{\mathbf{x}_j - \mathbf{x}_i}{\|\mathbf{x}_j - \mathbf{x}_i\|} + \sum_{i=1}^n \left(\sum_{k=1}^{n_{i,j}} \alpha_{i,j,k} (\mathbf{c}_{i,j,k} - \mathbf{x}_j) \right) \right) \right\|^2 \\
&\quad + \sum_{i,j,k} \left\| \frac{1}{\gamma_2} (\alpha_{i,j,k} (\mathbf{x}_i - \mathbf{c}_{i,j,k}) + \alpha_{i,j,k} (\mathbf{x}_j - \mathbf{c}_{i,j,k})) \right\|^2 \\
&\leq \frac{2}{\gamma_1^2} \sum_j \left(\left\| \sum_{\substack{i=1 \\ i \neq j}}^n f(\|\mathbf{x}_j - \mathbf{x}_i\|) \frac{\mathbf{x}_j - \mathbf{x}_i}{\|\mathbf{x}_j - \mathbf{x}_i\|} \right\|^2 + \left\| \sum_{i=1}^n \left(\sum_{k=1}^{n_{i,j}} \alpha_{i,j,k} (\mathbf{c}_{i,j,k} - \mathbf{x}_j) \right) \right\|^2 \right) \\
&\quad + \frac{1}{\gamma_2^2} \sum_{i,j,k} \|\alpha_{i,j,k} (\mathbf{x}_i + \mathbf{x}_j - 2\mathbf{c}_{i,j,k})\|^2 \\
&< \frac{2}{\gamma_1^2} \sum_j ((n-1)^2 M^2 + (2m\alpha L)^2) + \frac{1}{\gamma_2^2} \sum_{i,j,k} 18(\alpha L)^2 \\
&= \frac{2n}{\gamma_1^2} ((nM)^2 + (2m\alpha L)^2) + \frac{m}{\gamma_2^2} 18(\alpha L)^2 := N^2.
\end{aligned}$$

So, N is an upper bound of $\|\mathbf{f}(\mathbf{x})\|$ for $\mathbf{x} \in \Theta_{n,\epsilon}$ and $\|\mathbf{x}\| < L$. Now, we state and prove a local existence and uniqueness theorem we will use to get the global version.

Theorem 1.3.8. *For any Hookean cell system model of type 2 \mathfrak{H} , there exists a $\delta > 0$ such that \mathfrak{H} has a unique solution $\mathbf{x}(t)$ on $[t_0, t_0 + \delta]$.*

The theorem and associated proof is very similar to the existence theorem for a Lipschitz function on a parallelepiped found in [6].

Proof. Pick $\epsilon > 0$ according to Lemma 1.3.4 so that $\mathbf{x}^0 \in \Theta_{n,\epsilon}$ and any solutions to \mathfrak{H} remain in $\Theta_{n,\epsilon}$. Pick $r > 0$, by $\Theta_{n,\epsilon}$ being open (Proposition 1.3.5), so that $B(\mathbf{x}_0, r) \subset \Theta_{n,\epsilon}$. It has been show that \mathbf{f} is uniformly Lipschitz on $B(\mathbf{x}_0, r)$ (Proposition 1.3.7).

Now, set $\delta = \frac{r}{N}$ (recall $\|\mathbf{f}(x)\| < N$ for $\mathbf{x} \in \Theta_{n,\epsilon}$). Let $\mathbf{x}^0(t) = \mathbf{x}^0$, and put

$$\mathbf{x}^{k+1}(t) = \mathbf{x}^0 + \int_{t_0}^t \mathbf{f}(\mathbf{x}^k(s)) ds \quad \text{for } k = 0, 1, 2, \dots \quad (1.12)$$

Notice that each $\mathbf{x}^{k+1}(t)$ is defined and continuous on $[t_0, t_0 + \delta]$, since each $\mathbf{f}(\mathbf{x}^k(t))$ is. Furthermore,

$$\|\mathbf{x}^{k+1}(t) - \mathbf{x}^0\| = \left\| \int_{t_0}^t \mathbf{f}(\mathbf{x}^k(s)) ds \right\| \leq \int_{t_0}^t \|\mathbf{f}(\mathbf{x}^k(s))\| ds < N\delta = r$$

So, each $\mathbf{x}^k \in B(\mathbf{x}^0, r) \subset \Theta_{n,\epsilon}$. This defines a sequence of continuous functions on $[t_0, t_0 + \delta]$. Now, it will be show by induction that

$$\|\mathbf{x}^{k+1}(t) - \mathbf{x}^k(t)\| < \frac{NK^k(t - t_0)^{k+1}}{(k + 1)!} \quad (1.13)$$

where K is the Lipschitz constant for \mathbf{f} on $B(\mathbf{x}^0, r)$. The inequality is clearly true when $k = 0$, so suppose it is true for some nonnegative integer k , then

$$\begin{aligned} \|\mathbf{x}^{k+2}(t) - \mathbf{x}^{k+1}(t)\| &= \left\| \int_{t_0}^t \mathbf{f}(\mathbf{x}^{k+1}(s)) - \mathbf{f}(\mathbf{x}^k(s)) ds \right\| \\ &\leq \int_{t_0}^t \|\mathbf{f}(\mathbf{x}^{k+1}(s)) - \mathbf{f}(\mathbf{x}^k(s))\| ds \\ &\leq K \int_{t_0}^t \|\mathbf{x}^{k+1}(s) - \mathbf{x}^k(s)\| ds \\ &< K \int_{t_0}^t \frac{NK^k(s - t_0)^{k+1}}{(k + 1)!} ds \\ &= \frac{NK^{k+1}(t - t_0)^{k+2}}{(k + 2)!}. \end{aligned}$$

Hence, (1.13) is true for all $k = 0, 1, 2, \dots$. The above shows then, that,

$$\mathbf{x}^0 + \sum_{i=0}^{\infty} (\mathbf{x}^{i+1}(t) - \mathbf{x}^i(t))$$

converges uniformly. And so,

$$\mathbf{x}(t) = \mathbf{x}^0 + \sum_{i=0}^{\infty} (\mathbf{x}^{i+1}(t) - \mathbf{x}^i(t)) = \lim_{k \rightarrow \infty} \mathbf{x}^k(t)$$

exists uniformly for all $t \in [t_0, t_0 + \delta]$. Then by uniform convergence

$$\mathbf{x}(t) = \mathbf{x}^0 + \int_{t_0}^t \mathbf{f}(\mathbf{x}(s)) ds. \quad (1.14)$$

And so, $\mathbf{x}(t)$ satisfies \mathfrak{H} .

To prove uniqueness, let $\mathbf{z}(t)$ also be a solution to \mathfrak{H} and therefore (1.14) also on $[t_0, t_0 + \delta]$. Then it can be shown by induction that

$$\|\mathbf{x}_n(t) - \mathbf{z}(t)\| < \frac{NK^k(t - t_0)^{k+1}}{(k + 1)!}$$

and taking the limit of both sides as $n \rightarrow \infty$ reveals $\|\mathbf{x}(t) - \mathbf{z}(t)\| \leq 0$, so, $\mathbf{x}(t) = \mathbf{z}(t)$ on $[t_0, t_0 + \delta]$. \square

We now discuss a global existence and uniqueness result, that is, we entertain the question: given a Hookean cell system model of type 2 \mathfrak{H} with $t_0 = 0$ does there exist a unique solution on the interval $[0, \infty)$? To answer this, consider the existence of a maximal half open interval of existence $[0, T)$ (possibly infinite) of a solution to $\mathfrak{H}(0, \mathbf{x}^0)$. Here by maximal we mean that there exists no strictly larger (half open) interval on which there is a solutions to $\mathfrak{H}(0, \mathbf{x}^0)$. Defining the interval is fairly straightforward. Let $\mathcal{T} = \cup\{[0, \delta)\}$ be the union of the collection of all intervals $[0, \delta)$ for which there exists a solution to $\mathfrak{H}(0, \mathbf{x}^0)$. From Theorem 1.3.8 there exists at least one such interval so \mathcal{T} is not empty. Furthermore, \mathcal{T} is itself an interval with left endpoint 0; Let $\mathcal{T} = [0, T)$. And certainly every interval of existence is in fact a subinterval of \mathcal{T} so no larger interval may exist. However, is there a unique solution on \mathcal{T} ?

To address this, we begin by considering any two intervals from the union which constructs \mathcal{T} , name them $[0, \delta_1)$ and $[0, \delta_2)$, and with no loss of generality suppose $\delta_1 \leq \delta_2$. Each of these intervals has at least one solution which we will call $\mathbf{x}_1(t)$ for $[0, \delta_1)$ and $\mathbf{x}_2(t)$ for $[0, \delta_2)$. Now, let $\hat{t} = \inf\{t : \mathbf{x}_1(t) \neq \mathbf{x}_2(t)\}$. If $\hat{t} < \delta_1$, then the continuity of both solutions gives $\mathbf{x}_1(\hat{t}) = \mathbf{x}_2(\hat{t})$ and Theorem 1.3.8 applied to $\mathfrak{H}(\hat{t}, \mathbf{x}_1(\hat{t}))$ provides a $\delta > 0$ for which there is a

unique solution $\mathbf{x}(t)$ on $[\hat{t}, \hat{t} + \delta]$. So, $\mathbf{x}(t) = \mathbf{x}_1(t) = \mathbf{x}_2(t)$ on $[\hat{t}, \hat{t} + \delta]$. But, the definition of \hat{t} implies $\mathbf{x}_1(t) = \mathbf{x}_2(t)$ on $[0, \hat{t}]$, so

$$\hat{t} = \inf\{t : \mathbf{x}_1(t) \neq \mathbf{x}_2(t)\} \geq \hat{t} + \delta,$$

a contradiction. We conclude $\hat{t} \geq \delta_1$. This means that any two solutions to $\mathfrak{H}(0, \mathbf{x}^0)$ on a common interval containing 0 agree on that interval (notice, this demonstrates that no interval can have more than one solution). Ultimately, this implies that there is a unique solution \mathbf{x} to $\mathfrak{H}(0, \mathbf{x}^0)$ on $[0, T)$. Suppose otherwise, let

$$\hat{\delta} = \sup\{\delta : \mathbf{x}(t) \text{ is a solution to } \mathfrak{H}(0, \mathbf{x}^0) \text{ on } [0, \delta)\}$$

now suppose $\hat{\delta} < T$. Then there exists a $\hat{\delta} < \delta < T$ and from the argument above there is a unique solution $\mathbf{x}(t)$ to $\mathfrak{H}(0, \mathbf{x}^0)$ on $[0, \delta)$, a contradiction. So, $\hat{\delta} \geq T$. However, if $\hat{\delta} > T$ this would contradict the definition of $\mathcal{T} = [0, T)$; we conclude therefore $\hat{\delta} = T$. And so there is a maximal interval of existence and a unique solution to $\mathfrak{H}(0, \mathbf{x}^0)$ on that interval.

Now, suppose $T < \infty$. Recall that if $\mathbf{x} \in \Theta_{n,\epsilon}$ for any $\epsilon > 0$ there exist an N such that $\|\mathbf{f}(\mathbf{x})\| < N$. Then, if $\mathbf{x}(t)$ is a solution to $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ (\mathbf{f} , the force functions of \mathfrak{H}) the mean value theorem gives $\|\mathbf{x}(t) - \mathbf{x}(s)\| < N|t - s|$ for any $s, t \in [0, T)$ which implies $\mathbf{x}(t)$ is uniformly continuous on $[0, T)$ and therefore continuously extendable to the closure $[0, T]$. furthermore, since $\mathbf{x}(t)$ is continuous on $[0, T]$ it is uniformly continuous there. Now, it is not apparent that $\mathbf{x}(T)$ lies in $\Theta_{n,\epsilon}$ however it is in $\overline{\Theta}_{n,\epsilon}$ (the closure of $\Theta_{n,\epsilon}$). But for $0 < \hat{\epsilon} < \epsilon$ it is clear that $\overline{\Theta}_{n,\epsilon} \subset \Theta_{n,\hat{\epsilon}}$. So, pick $r > 0$ so that $B(\mathbf{x}(T), r) \subset \Theta_{n,\hat{\epsilon}}$ in this ball, Proposition 1.3.7 applies so that \mathbf{f} is Lipschitz continuous. Now consider

$$\lim_{t \uparrow T} \dot{\mathbf{x}}(t) = \lim_{t \uparrow T} \mathbf{f}(\mathbf{x}(t)) = \mathbf{f}(\mathbf{x}(T)).$$

Thus the $\lim_{t \uparrow T} \dot{\mathbf{x}}(t)$ exists and

$$\dot{\mathbf{x}}(T) = \lim_{t \uparrow T} \frac{\mathbf{x}(T) - \mathbf{x}(t)}{T - t} = \lim_{c \uparrow T} \dot{\mathbf{x}}(c) = \lim_{c \uparrow T} \mathbf{f}(\mathbf{x}(c)) = \mathbf{f}(\mathbf{x}(T)).$$

So, it may be deduced that the $\mathbf{x}(t)$ as solution to $\mathfrak{H}(0, \mathbf{x}^0)$ may be extended to $[0, T]$. Now, apply Theorem 1.3.8, noting that $\mathbf{x}(T) \in \Theta_{n, \epsilon}$ (as solutions remain in $\Theta_{n, \epsilon}$, $\hat{\epsilon}$ is no longer necessary), to $\mathfrak{H}(T, \mathbf{x}(T))$. We get that there exists a $\delta > 0$ such that there is a solution to $\mathfrak{H}(T, \mathbf{x}(T))$ on $[T, T + \delta)$; meaning there exist a solution to $\mathfrak{H}(0, \mathbf{x}^0)$ on $[0, T + \delta)$ this contradicts the definition of \mathcal{T} . We conclude that $T = \infty$. The above provides a proof for the global existence and uniqueness theorem for any Hookean cell system model, $\mathfrak{H}(0, \mathbf{x}^0)$.

Theorem 1.3.9 (Global Existence and Uniqueness for Hookean Cell System Models of Type 2). *Given Hookean cell system model of type 2 \mathfrak{H} there exist a unique solution on $[0, \infty)$.*

1.4 OVERVIEW

Chapter Two considers a highly simplified instance of this problem in which there are only two cells and one c-site. The behavior of this simplified system is then explored in a variety of ways. First, because the system presented does not have many equations, the exact solutions may be computed in the case that the cell centers are sufficiently far from each other ($\Delta x = \|\mathbf{x}_i - \mathbf{x}_j\| > r$). This way the system is linear as no nonlinear body force exists until the cell centers become close. Analysis in this case provides some interesting findings and helps develop intuition for the evolution of such a system when the nonlinear term is included. It then is shown that y -values of the system are not affected by the body force. This will be used to conclude that there is no rotation through the system. The case in which the nonlinear body force has not vanished (i.e. when the cell centers are close enough together to stimulate a body force, $\|\mathbf{x}_1 - \mathbf{x}_j\| < r$) is then addressed and the equilibria of the system are calculated. It is possible to explicitly determine the set of all possible equilibria. It turns out that this set is a smooth submanifold of the state space. The stability of these

equilibria is then considered. This is done by computing the derivative of the system at a given equilibria (fixed point) and analyzing it, it is shown that the center manifold of the system is exactly the set of fixed points. Since there is no unstable manifold the dynamics of the system are not difficult to obtain. Chapter Two concludes with a summary. This chapter represents much of the intuition-building which is able to motivate what is to follow.

Chapter Three focuses on the systems with a pair of cells but multiple c -sites between them. The main result of this chapter addresses the possibility of reducing such a system to an equivalent one of only a single “average” c -site. We present the statement of the c -site reduction theorem with proof and provide an example, as verification. Following this it is show that the theorem may be extended to a system involving more than two cells. The general c -site reduction theorem is then presented with proof. The chapter concludes with a discussion of which of the results of Chapter Two may be applied and further implications of the theorem are discussed.

By Chapter Four we begin our analysis of system of n cells with an arbitrary number of c -sites connecting various cells. Thanks to the general c -site reduction theorem, we consider the system as having at most one c -site connecting any two cells (though the parameters for each c -site may not all be the same). Motivated by seeking the equilibria of such systems we develop the problem into solving the matrix equation $0 = B\mathbf{x}$, where B is a symmetric matrix of 0-row-sums that depends on \mathbf{x} . This proves to be a highly complex question and the theory for solving such an equation is only partially developed in this piece. Finding are reported and conjectures are posited that will aid in the future study of these problems.

In Chapter Five a framework for the motion of these systems involving stochastic processes is provided along with a discussion on how the work here can be of use to the investigation of the more robust model.

CHAPTER 2. TWO CELLS ATTACHED BY ONE C-SITE

A study of the cell system of only two cells and one c-site is useful in the development of intuition for the behavior of larger cell systems. We begin our study by recognizing that in this analysis only the configuration of the cell centers and c-sites (really only the cell centers) is of concern and no reference need be made to any external objects. It is for this reason that, with no loss of generality, it may be assumed that the starting location of one of the two cells of the cell system has its center at the origin and the other, on the positive x -axis. The starting location of the c-site (since there is only one, it will be denoted as $\mathbf{c}_{1,2,1}(t) = \mathbf{c}(t)$) will be restricted only to the closed upper half plane $\mathbb{R} \times \mathbb{R}^+$. This means $\mathbf{x}_1(0) = (0, 0)$, $\mathbf{x}_2(0) = (l, 0)$ for some real $l > 0$, and $\mathbf{c}(0) = (x_c(0), (y_c(0))$ with $y_c(0) \geq 0$ (or $\mathbf{x}^0 = (0, 0, l, 0, x_c(0), (y_c(0)))$). So, in studying the evolution of a general Hookean cell system of type 1 it is sufficient to study the cell system model $\hat{\mathfrak{H}}$ given explicitly by

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_1 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_1 - \mathbf{x}_2}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha(\mathbf{c} - \mathbf{x}_1) \\ \gamma_1 \dot{\mathbf{x}}_2 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_2 - \mathbf{x}_1}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha(\mathbf{c} - \mathbf{x}_2) \\ \gamma_2 \dot{\mathbf{c}} = \alpha(\mathbf{x}_1 - \mathbf{c}) + \alpha(\mathbf{x}_2 - \mathbf{c}) \\ \mathbf{x}_1(0) = (0, 0), \quad \mathbf{x}_2(0) = (l, 0), \quad \text{and} \quad \mathbf{c}(0) = (x_c(0), y_c(0)), \end{array} \right. \quad (2.1)$$

where f is as in the definition of a Hookean cell system of type 1. By Theorem 1.3.9 there is a solution \mathbf{x} to $\hat{\mathfrak{H}}$. The goal now becomes to determine as much as possible about \mathbf{x} . A picture of the cell system, represented by $\hat{\mathfrak{H}}$, at time $t = 0$ is shown in Figure 2.1 .

Since (2.1) is not too large it is possible to analyze it quite thoroughly. To do this it will be convenient to divide the problem into two regimes. The first regime will consider the case in which the cell centers of $\hat{\mathfrak{H}}$ are sufficiently far apart as to make the body force trivial, that is when $\|\mathbf{x}_2 - \mathbf{x}_1\| \geq r$ (recall r is the smallest value for which $f(r) = 0$; see page 11). This is favorable as it reduces (2.1) to a linear system in which elementary methods may be used to obtain an explicit solution, which will have to agree with \mathbf{x} as far as the cell centers are sufficiently far apart. This case will be described as $\hat{\mathfrak{H}}$ being “beyond the support of f .”

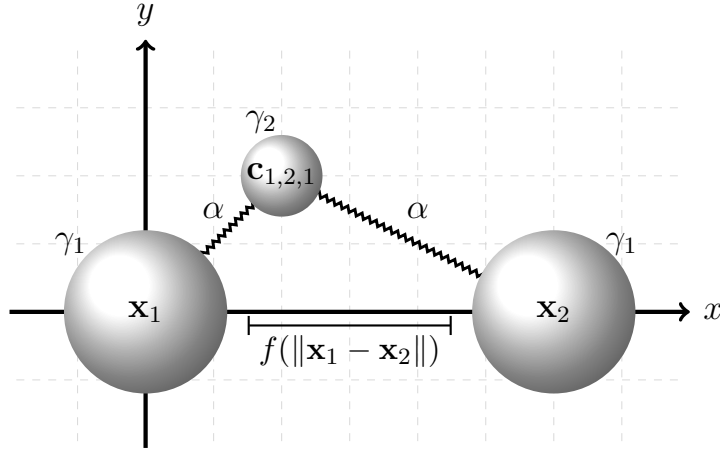


Figure 2.1: Example of a cell system with two cell centers and one c-site placed on the coordinate grid.

The second regime considers the case in which the cell centers are close enough to produce a positive body force, so, when $\|\mathbf{x}_2 - \mathbf{x}_1\| < r$. In this regime $\hat{\mathfrak{H}}$ is referred to as being “within the support of f .” Here, $\hat{\mathfrak{H}}$ is possibly non-linear, so the analysis of it will be much different from the analysis of $\hat{\mathfrak{H}}$ while in the first regime. It is not as convenient in this case to find an explicit solution to $\hat{\mathfrak{H}}$; however, it will be shown that because of some remarkable symmetries inherent in $\hat{\mathfrak{H}}$ it is possible to obtain explicit solutions for the motion of the cell system within the support of f .

It is natural to divide the problem into these regimes because of how $\hat{\mathfrak{H}}$ evolves. The system usually begins with the cell centers far enough apart as to experience no body force. The attached c-site then pulls the cell centers close enough together to incite the body force (at which point $\hat{\mathfrak{H}}$ becomes in the support of f). Once the proximity of the cell centers incites the body force they will not be forced clear of the effective range of the force. This is because the body force (or rather the generating function f of the force function of $\hat{\mathfrak{H}}$) is continuous with the magnitude of the force approaching zero as the distance between the two cell centers approaches r , the force generated by the attached c-site however remains close to $r\alpha (> 0)$ when the distance between the two cell centers is near r (see Figure 2.2).

With this in mind also recall that the cells are in a low Reynold’s number environment. Thus, the inertial terms are very small, which means that there is no drifting. So, at any given time the motion of a cell center is exactly determined by the forces acting on it at

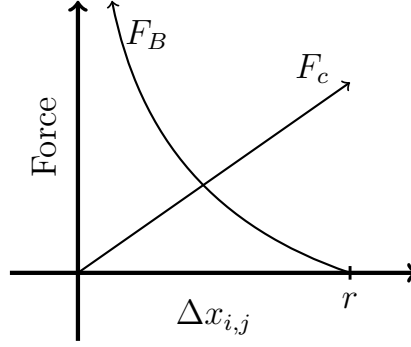


Figure 2.2: A illustrative graph for the relationship between the distance the cell centers are apart ($\Delta x_{i,j}$) and the magnitude of the body force (F_B) and the magnitude of the force enacted by the c-site (F_c).

exactly that moment. For a $\Delta x_{i,j}$ close enough to zero the body force will be larger in magnitude than that of the c-site force (even when the c-site is directly between the two cell centers), and the cell centers will move apart. However, for $0 \ll \Delta x_{i,j} < r$ the body force will be small and the c-site force much larger; so, the cell centers move toward each other. In fact, the cell will not be able to leave the effective range of the body force. This means that it would not be possible, in $\hat{\mathfrak{H}}$, for the cell centers to be forced apart to a distance beyond the support of the body force. As a result, the system will remain structurally the same till the end of time. Thus there is a time in which the system goes from regime one to regime two where it remains.

2.1 BEYOND THE SUPPORT OF f , A LINEAR SYSTEM

Here the system is analyzed under the assumption that $\|\mathbf{x}_2 - \mathbf{x}_1\| \geq r$. In this scenario the term containing the possibly non-linear body force vanishes and system (2.1) becomes

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_1 = \alpha(\mathbf{c} - \mathbf{x}_1) \\ \gamma_1 \dot{\mathbf{x}}_2 = \alpha(\mathbf{c} - \mathbf{x}_2) \\ \gamma_2 \dot{\mathbf{c}} = \alpha(\mathbf{x}_1 - \mathbf{c}) + \alpha(\mathbf{x}_2 - \mathbf{c}) \\ \mathbf{x}_1(0) = (0, 0), \quad \mathbf{x}_2(0) = (l, 0), \quad \text{and} \quad \mathbf{c}(0) = (x_c(0), y_c(0)). \end{array} \right. \quad (2.2)$$

The initial conditions have been included to facilitate the nondimensionalization of the system, which is done now to greatly simplify further calculations. Notice, there are five parameters above: γ_1 , γ_2 , α , l , $x_c(0)$, and $y_c(0)$. These have dimensions¹ as follows:

$$[\gamma_1] = \frac{M}{T}, \quad [\gamma_2] = \frac{M}{T}, \quad [\alpha] = \frac{M}{T^2}, \quad [l] = L, \quad [x_c(0)] = L, \quad \text{and} \quad [y_c(0)] = L.$$

In order to arrive at a quantity using these parameters that has the dimension of time, take the characteristic time to be $t_c = \gamma_1/\alpha$. In the characteristic time, γ_1 is chosen over γ_2 in order to get more cancellation in the first two equations. For the characteristic length take l .

Now, to begin the nondimensionalization of the system (2.2), set $\tau = t/t_c$,

$$\boldsymbol{\xi}_i(\tau) = \frac{1}{l}\mathbf{x}_i(t_c\tau) = \frac{1}{l}\mathbf{x}_i(t)$$

and take the derivative with respect to τ . This achieves the following: (The derivative with respect to τ will be denoted by the usual apostrophe)

$$\boldsymbol{\xi}'_i(\tau) = \frac{d}{d\tau} \left(\frac{1}{l}\mathbf{x}_i(t_c\tau) \right) = \frac{1}{l}\dot{\mathbf{x}}_i(t_c\tau)t_c = \frac{t_c}{l}\dot{\mathbf{x}}_i(t).$$

Likewise, for the c-sites, put

$$\boldsymbol{\sigma}(\tau) = \frac{1}{l}\mathbf{c}(t_c\tau) = \frac{1}{l}\mathbf{c}(t).$$

Taking the derivative of this yields

$$\boldsymbol{\sigma}'(\tau) = \frac{d}{d\tau} \left(\frac{1}{l}\mathbf{c}(t_c\tau) \right) = \frac{1}{l}\dot{\mathbf{c}}(t_c\tau)t_c = \frac{t_c}{l}\dot{\mathbf{c}}(t).$$

¹Here the we employ the notation of J. David Logan found in [7]. In which, brackets around a quantity are used to denote the dimension of the quantity. These dimensions can be written in terms of the following fundamental dimensions: M for mass, T for time, and L for length.

Making the appropriate substitutions into system (2.2) produces the following,

$$\begin{cases} \gamma_1 l \frac{\alpha}{\gamma_1} \boldsymbol{\xi}'_1(\tau) = \alpha(l\boldsymbol{\sigma}(\tau) - l\boldsymbol{\xi}_1(\tau)) \\ \gamma_1 l \frac{\alpha}{\gamma_1} \boldsymbol{\xi}'_2(\tau) = \alpha(l\boldsymbol{\sigma}(\tau) - l\boldsymbol{\xi}_2(\tau)) \\ \gamma_2 l \frac{\alpha}{\gamma_1} \boldsymbol{\sigma}'(\tau) = \alpha(l\boldsymbol{\xi}_1(\tau) - l\boldsymbol{\sigma}(\tau)) + \alpha(l\boldsymbol{\xi}_2(\tau) - l\boldsymbol{\sigma}(\tau)) \\ \boldsymbol{\xi}_1(0) = (0, 0), \quad \boldsymbol{\xi}_2(0) = (1, 0), \quad \text{and} \quad \boldsymbol{\sigma}(0) = \left(\frac{x_c(0)}{l}, \frac{y_c(0)}{l}\right). \end{cases}$$

Simplifying, letting $\gamma = \frac{\gamma_1}{\gamma_2}$, and suppressing τ dependence produces a dimensionless system equivalent to (2.2),

$$\begin{cases} \boldsymbol{\xi}'_1 = \boldsymbol{\sigma} - \boldsymbol{\xi}_1 \\ \boldsymbol{\xi}'_2 = \boldsymbol{\sigma} - \boldsymbol{\xi}_2 \\ \boldsymbol{\sigma}' = \gamma(\boldsymbol{\xi}_1 - \boldsymbol{\sigma}) + \gamma(\boldsymbol{\xi}_2 - \boldsymbol{\sigma}) \\ \boldsymbol{\xi}_1(0) = (0, 0), \quad \boldsymbol{\xi}_2(0) = (1, 0), \quad \text{and} \quad \boldsymbol{\sigma}(0) = \left(\frac{x_c(0)}{l}, \frac{y_c(0)}{l}\right). \end{cases} \quad (2.3)$$

Because the system is linear it may be expressed in matrix form. With the notation $\boldsymbol{\xi}_1 = (\xi_1, \eta_1)$, $\boldsymbol{\xi}_2 = (\xi_2, \eta_2)$, and $\boldsymbol{\sigma} = (\xi_\sigma, \eta_\sigma)$ along with

$$\boldsymbol{\Xi} = \begin{pmatrix} \xi_1 \\ \eta_1 \\ \xi_2 \\ \eta_2 \\ \xi_\sigma \\ \eta_\sigma \end{pmatrix} \quad \text{and} \quad \mathbf{A} = \begin{pmatrix} -1 & 0 & 0 & 0 & 1 & 0 \\ 0 & -1 & 0 & 0 & 0 & 1 \\ 0 & 0 & -1 & 0 & 1 & 0 \\ 0 & 0 & 0 & -1 & 0 & 1 \\ \gamma & 0 & \gamma & 0 & -2\gamma & 0 \\ 0 & \gamma & 0 & \gamma & 0 & -2\gamma \end{pmatrix}$$

system (2.3) becomes, simply,

$$\boldsymbol{\Xi}' = \mathbf{A}\boldsymbol{\Xi}, \quad (2.4)$$

with the initial condition

$$\Xi(0) = \begin{pmatrix} 0 \\ 0 \\ 1 \\ 0 \\ \frac{x_c(0)}{l} \\ \frac{y_c(0)}{l} \end{pmatrix}. \quad (2.5)$$

The eigenvalues² of \mathbf{A} are 0, -1, and $-1-2\gamma$ each with multiplicity two and the associated eigenvectors are: for $\lambda = 0$,

$$\hat{\xi}_1 = \begin{pmatrix} 0 \\ 1 \\ 0 \\ 1 \\ 0 \\ 1 \end{pmatrix} \quad \text{and} \quad \hat{\xi}_2 = \begin{pmatrix} 1 \\ 0 \\ 1 \\ 0 \\ 1 \\ 0 \end{pmatrix};$$

for $\lambda = -1$,

$$\hat{\xi}_3 = \begin{pmatrix} 0 \\ -1 \\ 0 \\ 1 \\ 0 \\ 0 \end{pmatrix} \quad \text{and} \quad \hat{\xi}_4 = \begin{pmatrix} -1 \\ 0 \\ 1 \\ 0 \\ 0 \\ 0 \end{pmatrix};$$

²The computation of the eigenvalues of \mathbf{A} as well as their associated eigenvectors was performed by *Mathematica*.

and for $\lambda = -1 - 2\gamma$,

$$\hat{\xi}_5 = \begin{pmatrix} 0 \\ -\frac{1}{2\gamma} \\ 0 \\ -\frac{1}{2\gamma} \\ 0 \\ 1 \end{pmatrix} \quad \text{and} \quad \hat{\xi}_6 = \begin{pmatrix} -\frac{1}{2\gamma} \\ 0 \\ -\frac{1}{2\gamma} \\ 0 \\ 1 \\ 0 \end{pmatrix}.$$

The fundamental matrix³ for the solution may then be written as

$$\Psi(\tau) = \begin{pmatrix} 0 & 1 & 0 & -e^{-t} & 0 & -\frac{1}{2\gamma}e^{-(1+2\gamma)\tau} \\ 1 & 0 & -e^{-t} & 0 & -\frac{1}{2\gamma}e^{-(1+2\gamma)\tau} & 0 \\ 0 & 1 & 0 & e^{-t} & 0 & -\frac{1}{2\gamma}e^{-(1+2\gamma)\tau} \\ 1 & 0 & e^{-t} & 0 & -\frac{1}{2\gamma}e^{-(1+2\gamma)\tau} & 0 \\ 0 & 1 & 0 & 0 & 0 & e^{-(1+2\gamma)\tau} \\ 1 & 0 & 0 & 0 & e^{-(1+2\gamma)\tau} & 0 \end{pmatrix}.$$

Notice that $\Xi(\tau) = \Psi(\tau)\mathbf{k}$ is a solution for any $\mathbf{k} \in \mathbb{R}^6$. However, a specific solution Ξ to equation (2.4) that satisfies the initial condition (2.5) is sought. Happily, the matrix $\Psi(0)$ (shown below) is invertible⁴. Thus, the vector $\mathbf{k} = \Psi(0)^{-1}\Xi(0)$ may be chosen. Now,

$$\Psi(0) = \begin{pmatrix} 0 & 1 & 0 & -1 & 0 & -\frac{1}{2\gamma} \\ 1 & 0 & -1 & 0 & -\frac{1}{2\gamma} & 0 \\ 0 & 1 & 0 & 1 & 0 & -\frac{1}{2\gamma} \\ 1 & 0 & 1 & 0 & -\frac{1}{2\gamma} & 0 \\ 0 & 1 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 1 & 0 \end{pmatrix}$$

³Throughout the process of finding the solution for system (2.3) we use the terminology and techniques found in Boyce and DiPrima's text on Elementary Differential Equations [8]

⁴The computation of the inverse of $\Psi(0)$ was performed by *Mathematica*.

and

$$\mathbf{\Psi}(0)^{-1} = \begin{pmatrix} 0 & \frac{\gamma}{1+2\gamma} & 0 & \frac{\gamma}{1+2\gamma} & 0 & \frac{1}{1+2\gamma} \\ \frac{\gamma}{1+2\gamma} & 0 & \frac{\gamma}{1+2\gamma} & 0 & \frac{1}{1+2\gamma} & 0 \\ 0 & -\frac{1}{2} & 0 & \frac{1}{2} & 0 & 0 \\ -\frac{1}{2} & 0 & \frac{1}{2} & 0 & 0 & 0 \\ 0 & -\frac{\gamma}{1+2\gamma} & 0 & -\frac{\gamma}{1+2\gamma} & 0 & \frac{2\gamma}{1+2\gamma} \\ -\frac{\gamma}{1+2\gamma} & 0 & -\frac{\gamma}{1+2\gamma} & 0 & \frac{2\gamma}{1+2\gamma} & 0 \end{pmatrix}.$$

So,

$$\mathbf{k} = \mathbf{\Psi}(0)^{-1}\mathbf{\Xi}(0) = \begin{pmatrix} \frac{y_c(0)}{l(1+2\gamma)} \\ \frac{x_c(0)+l\gamma}{l(1+2\gamma)} \\ 0 \\ \frac{1}{2} \\ \frac{2y_c(0)\gamma}{l(1+2\gamma)} \\ \frac{2x_c(0)\gamma-l\gamma}{l(1+2\gamma)} \end{pmatrix}.$$

The solution, then, to the IVP (2.3) is $\mathbf{\Xi}(\tau) = \mathbf{\Psi}(\tau)\mathbf{\Psi}(0)^{-1}\mathbf{\Xi}(0)$ and its components are

$$\xi_1(\tau) = \frac{x_c(0) + l\gamma}{l(1+2\gamma)} - \frac{1}{2}e^{-\tau} - \frac{x_c(0) - l/2}{l(1+2\gamma)}e^{-(1+2\gamma)\tau},$$

$$\eta_1(\tau) = \frac{y_c(0)}{l(1+2\gamma)} - \frac{y_c(0)}{l(1+2\gamma)}e^{-(1+2\gamma)\tau},$$

$$\xi_2(\tau) = \frac{x_c(0) + l\gamma}{l(1+2\gamma)} + \frac{1}{2}e^{-\tau} - \frac{x_c(0) - l/2}{l(1+2\gamma)}e^{-(1+2\gamma)\tau},$$

$$\eta_2(\tau) = \frac{y_c(0)}{l(1+2\gamma)} - \frac{y_c(0)}{l(1+2\gamma)}e^{-(1+2\gamma)\tau},$$

$$\xi_\sigma(\tau) = \frac{x_c(0) + l\gamma}{l(1+2\gamma)} + \frac{2x_c(0)\gamma - l\gamma}{l(1+2\gamma)}e^{-(1+2\gamma)\tau},$$

$$\eta_\sigma(\tau) = \frac{y_c(0)}{l(1+2\gamma)} + \frac{2y_c(0)\gamma}{l(1+2\gamma)}e^{-(1+2\gamma)\tau}.$$

Then, substituting the original dimensioned variables back into this solution produces a solution to system (2.2) shown below: (γ_1 and γ_2 are used rather than γ)

$$x_1(t) = \frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} - \frac{l}{2}e^{-\alpha t/\gamma_1} - \frac{2x_c(0)\gamma_2 - l\gamma_2}{2(2\gamma_1 + \gamma_2)}e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t}, \quad (2.6)$$

$$y_1(t) = \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} - \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2}e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t}, \quad (2.7)$$

$$x_2(t) = \frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} + \frac{l}{2}e^{-\alpha t/\gamma_1} - \frac{2x_c(0)\gamma_2 - l\gamma_2}{2(2\gamma_1 + \gamma_2)}e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t}, \quad (2.8)$$

$$y_2(t) = \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} - \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2}e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t}, \quad (2.9)$$

$$x_c(t) = \frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} + \frac{2x_c(0)\gamma_1 - l\gamma_1}{2\gamma_1 + \gamma_2}e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t}, \quad (2.10)$$

$$y_c(t) = \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} + \frac{2y_c(0)\gamma_1}{2\gamma_1 + \gamma_2}e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t}. \quad (2.11)$$

This then provides the exact values of \mathbf{x} , at least until \mathbf{x} leaves the set $\Theta_{2,r} \times \mathbb{R}^2$.

2.1.1 Qualitative Findings of the Behavior of the Solution to the Linear System.

Here an interesting fact becomes apparent: the path that \mathbf{c} travels is a line. Indeed, both equations (2.10) and (2.11) may be set equal to $\gamma_1 e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t}$. Equating these yields

$$\frac{x_c(t)(2\gamma_1 + \gamma_2) - x_c(0)\gamma_2 - l\gamma_1}{2x_c(0) - l} = \frac{y_c(t)(2\gamma_1 + \gamma_2) - y_c(0)\gamma_2}{2y_c(0)}.$$

With a bit of manipulation the following is achieved (suppressing dependence on t)

$$y_c = x_c \left(\frac{2y_c(0)(2\gamma_1 + \gamma_2)}{2x_c(0) - l} \right) + \left(y_c(0)\gamma_2 - \frac{2x_c(0)y_c(0)\gamma_2 - y_c(0)l\gamma_1}{2x_c(0) - l} \right).$$

The careful reader will recognize that any point $(x_c(t), y_c(t)) \in \mathbb{R}^2$ will satisfy the above equation and therefore be found somewhere on this line. Since the solution is continuous the

point \mathbf{c} starts at $(x_c(0), y_c(0))$ and travels in line to the point

$$\left(\frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2}, \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} \right),$$

which is determined by simply taking the limit as $t \rightarrow \infty$. In fact, all the bodies in the system tend to this point (this is seen also by taking the limit as $t \rightarrow \infty$ for each equation (2.6-2.11)), for that reason we will call the above point \mathbf{x}_e , or the equilibrium point. We must keep in mind that this is only the equilibrium of the linear system in which the body force is completely ignored (because the cell centers are supposed to be sufficiently far apart). It is not even the equilibrium of the linearization of the original system, so it is important to realize that this point has rather limited usefulness in the solving of this original system. However, in system (2.1) the equations (2.6-2.11) above are valid until the cell centers become close enough to engage the body force. It will be shown that, in fact, the solutions $y_1(t)$, $y_2(t)$, $x_c(t)$, and $y_c(t)$ to the linear system above are the same as their analog solutions to the nonlinear case of regime two.

This point \mathbf{x}_e is a weighted average of the locations of the bodies weighted according to their drag coefficients. It is the center of drag, as discussed in Section 1.3. Notice that the center of drag of the system at $t = 0$ is the equilibrium \mathbf{x}_e . Indeed, using the explicit solution found above this may be verified (at least as long as these solutions are valid). Checking this for the y -components yields

$$\begin{aligned} \frac{\gamma_1 y_1(t) + \gamma_1 y_2(t) + \gamma_2 y_c(t)}{\gamma_1 + \gamma_1 + \gamma_2} &= \frac{1}{2\gamma_1 + \gamma_2} \left(2\gamma_1 \left(\frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} - \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} e^{-\alpha(\frac{1}{\gamma_1} + 2\frac{2}{\gamma_1})t} \right) \right. \\ &\quad \left. + \gamma_2 \left(\frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} + \frac{2y_c(0)\gamma_1}{2\gamma_1 + \gamma_2} e^{-\alpha(\frac{1}{\gamma_1} + 2\frac{2}{\gamma_1})t} \right) \right) \\ &= \frac{1}{2\gamma_1 + \gamma_2} \left((2\gamma_1 + \gamma_2) \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} \right) \\ &= \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2}. \end{aligned}$$

And likewise for the x -components

$$\begin{aligned}
\frac{\gamma_2 x_c(t) + \gamma_1(x_1(t) + x_2(t))}{\gamma_2 + 2\gamma_1} &= \frac{1}{2\gamma_1 + \gamma_2} \left(\gamma_2 \left(\frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} + \frac{2x_c(0)\gamma_1 - l\gamma_1}{2\gamma_1 + \gamma_2} e^{-\alpha(\frac{1}{\gamma_1} + \frac{2}{\gamma_1})t} \right) \right. \\
&+ \gamma_1 \left(\frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} + \frac{l}{2} e^{-\frac{\alpha t}{\gamma_1}} - \frac{2x_c(0)\gamma_2 - l\gamma_2}{2(2\gamma_1 + \gamma_2)} e^{-\alpha(\frac{1}{\gamma_1} + \frac{2}{\gamma_1})t} \right) \\
&+ \left. \gamma_1 \left(\frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} - \frac{l}{2} e^{-\frac{\alpha t}{\gamma_1}} - \frac{2x_c(0)\gamma_2 - l\gamma_2}{2(2\gamma_1 + \gamma_2)} e^{-\alpha(\frac{1}{\gamma_1} + \frac{2}{\gamma_1})t} \right) \right) \\
&= \frac{1}{2\gamma_1 + \gamma_2} \left((\gamma_2 + 2\gamma_1) \left(\frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} \right) \right. \\
&+ \gamma_2 \left(\frac{2x_c(0)\gamma_1 - l\gamma_1}{2\gamma_1 + \gamma_2} e^{-\alpha(\frac{1}{\gamma_1} + \frac{2}{\gamma_1})t} \right) \\
&- \left. \gamma_1 \left(\frac{2x_c(0)\gamma_2 - l\gamma_2}{2\gamma_1 + \gamma_2} e^{-\alpha(\frac{1}{\gamma_1} + \frac{2}{\gamma_1})t} \right) \right) \\
&= \frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2}.
\end{aligned}$$

The above demonstrates that, the solutions to the system with no body force still conserves the center of drag.

With the solutions to the system (2.2), we now seek to find the time at which the distance between the two cell centers enters the support of the body function f . We get the following formula for the distance between the two cell centers as they evolve through regime one:

$$\|\mathbf{x}_1(t) - \mathbf{x}_2(t)\| = l e^{-\alpha t/\gamma_1}.$$

This allows us to determine precisely where the cell centers will be as soon as the body force becomes nonzero. This is also useful as it provides precisely the time regime one ends and regime two begins. Let t_r be the time in which, $\|\mathbf{x}_1(t) - \mathbf{x}_2(t)\| = r$. This may be solved and yields

$$t_r = \frac{\gamma_1}{\alpha} \ln \frac{l}{r}.$$

Some interesting formulas are now available; such as, the location of the cell centers and c-site precisely at the time the body force turns on. These provide the bridge between regime

one and regime two.

$$\begin{aligned}\mathbf{x}_1(t_r) &= \begin{pmatrix} \frac{x_c(0)\gamma_2+l\gamma_1}{2\gamma_1+\gamma_2} - \frac{r}{2} - \frac{2x_c(0)\gamma_2-l\gamma_2}{2(2\gamma_1+\gamma_2)} \left(\frac{r}{l}\right)^{\frac{2\gamma_1}{\gamma_2}+1} \\ \frac{y_c(0)\gamma_2}{2\gamma_1+\gamma_2} - \frac{y_c(0)\gamma_2}{2\gamma_1+\gamma_2} \left(\frac{r}{l}\right)^{\frac{2\gamma_1}{\gamma_2}+1} \end{pmatrix}, \\ \mathbf{x}_2(t_r) &= \begin{pmatrix} \frac{x_c(0)\gamma_2+l\gamma_1}{2\gamma_1+\gamma_2} + \frac{r}{2} - \frac{2x_c(0)\gamma_2-l\gamma_2}{2(2\gamma_1+\gamma_2)} \left(\frac{r}{l}\right)^{\frac{2\gamma_1}{\gamma_2}+1} \\ \frac{y_c(0)\gamma_2}{2\gamma_1+\gamma_2} - \frac{y_c(0)\gamma_2}{2\gamma_1+\gamma_2} \left(\frac{r}{l}\right)^{\frac{2\gamma_1}{\gamma_2}+1} \end{pmatrix}, \\ \mathbf{c}(t_r) &= \begin{pmatrix} \frac{x_c(0)\gamma_2+l\gamma_1}{2\gamma_1+\gamma_2} + \frac{2x_c(0)\gamma_1-l\gamma_1}{2\gamma_1+\gamma_2} \left(\frac{r}{l}\right)^{\frac{2\gamma_1}{\gamma_2}+1} \\ \frac{y_c(0)\gamma_2}{2\gamma_1+\gamma_2} + \frac{2y_c(0)\gamma_1}{2\gamma_1+\gamma_2} \left(\frac{r}{l}\right)^{\frac{2\gamma_1}{\gamma_2}+1} \end{pmatrix}.\end{aligned}$$

Notice that when the cell centers reach the threshold of the body force the y -values are the same, and the difference between the y -value of the cell centers and that of the c-site is

$$y_c(t_r) - y_1(t_r) = y_c(0) \left(\frac{r}{l}\right)^{\frac{2\gamma_1}{\gamma_2}+1}.$$

This value may be made arbitrarily large by increasing the $y_c(0)$. The distances the bodies are from the equilibrium point,

$$\mathbf{x}_e = \left(\frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2}, \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} \right)$$

when the body force turns on are also provided below:

$$\|\mathbf{x}_e - \mathbf{c}(t_r)\| = \left(\frac{r}{l}\right)^{\frac{\gamma_1}{\gamma_2}+1} \left(\frac{2\gamma_1}{2\gamma_1 + \gamma_2}\right) \sqrt{\left(x_c(0) - \frac{l}{2}\right)^2 + (y_c(0))^2},$$

$$\|\mathbf{x}_e - \mathbf{x}_1(t_r)\| = \left(\frac{r}{l}\right)^{\frac{\gamma_1}{\gamma_2}+1} \left(\frac{2\gamma_1}{2\gamma_1 + \gamma_2}\right) \sqrt{\left(\left(x_c(0) - \frac{l}{2}\right) + \left(\frac{l}{r}\right)^{\frac{\gamma_1}{\gamma_2}+1} \frac{l(2\gamma_1 + \gamma_2)}{2\gamma_2}\right)^2 + (y_c(0))^2},$$

$$\|\mathbf{x}_e - \mathbf{x}_2(t_r)\| = \left(\frac{r}{l}\right)^{\frac{\gamma_1}{\gamma_2}+1} \left(\frac{2\gamma_1}{2\gamma_1 + \gamma_2}\right) \sqrt{\left(\left(x_c(0) - \frac{l}{2}\right) - \left(\frac{l}{r}\right)^{\frac{\gamma_1}{\gamma_2}+1} \frac{l(2\gamma_1 + \gamma_2)}{2\gamma_2}\right)^2 + (y_c(0))^2}.$$

With this in hand, we are ready to discuss the case in which the distance between the two cell centers enters the support of f , or, in the notation established, when $\Delta x_{1,2} = \|\mathbf{x}_2(t) - \mathbf{x}_1(t)\| \leq r$.

2.2 WITHIN THE SUPPORT OF f , A NONLINEAR SYSTEM

We analyze this nonlinear system in two steps. First, the set of equilibria for the system is identified and studied and the stability of the equilibria is explored. In this discussion of the equilibria initial conditions have no bearing, so rather than talking about it in terms of $\hat{\mathfrak{H}}$, it is discussed in terms of \mathbf{f} , the force function of $\hat{\mathfrak{H}}$. The second step includes a method for finding explicit solutions. This is done by proposing guesses based on our analysis of the system in regime one. The existence and uniqueness theorem (Theorem 1.3.9) then establishes the guesses as the unique solution to $\hat{\mathfrak{H}}$.

Once the distance between the two cell centers enters the support of f the nonlinear repulsive body force becomes nonzero and the system returns to $\hat{\mathfrak{H}}$

$$\begin{cases} \gamma_1 \dot{\mathbf{x}}_1 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_1 - \mathbf{x}_2}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha(\mathbf{c} - \mathbf{x}_1) \\ \gamma_1 \dot{\mathbf{x}}_2 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_2 - \mathbf{x}_1}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha(\mathbf{c} - \mathbf{x}_2) \\ \gamma_2 \dot{\mathbf{c}} = \alpha(\mathbf{x}_1 - \mathbf{c}) + \alpha(\mathbf{x}_2 - \mathbf{c}). \end{cases}$$

or rather, in the notation of the force function⁵

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}). \quad (2.12)$$

To solve for the equilibria (if any) of the nonlinear system set the derivative terms equal to $\mathbf{0}$. So, that

$$\mathbf{0} = \mathbf{f}(\mathbf{x})$$

⁵Recall the definition on page 11

or

$$\begin{cases} \mathbf{0} = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_1 - \mathbf{x}_2}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha(\mathbf{c} - \mathbf{x}_1) \\ \mathbf{0} = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_2 - \mathbf{x}_1}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha(\mathbf{c} - \mathbf{x}_2) \\ \mathbf{0} = \alpha(\mathbf{x}_1 - \mathbf{c}) + \alpha(\mathbf{x}_2 - \mathbf{c}). \end{cases}$$

The last equation will only be satisfied if

$$\mathbf{c} = \frac{\mathbf{x}_1 + \mathbf{x}_2}{2}.$$

Substituting this for \mathbf{c} into the first and second equations reduces the system to

$$\begin{cases} \mathbf{0} = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_1 - \mathbf{x}_2}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha \left(\frac{\mathbf{x}_2 - \mathbf{x}_1}{2} \right) \\ \mathbf{0} = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_2 - \mathbf{x}_1}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha \left(\frac{\mathbf{x}_1 - \mathbf{x}_2}{2} \right) \end{cases}$$

or more simply

$$\begin{cases} \mathbf{0} = \left(\frac{f(\|\mathbf{x}_1 - \mathbf{x}_2\|)}{\|\mathbf{x}_1 - \mathbf{x}_2\|} - \frac{\alpha}{2} \right) (\mathbf{x}_1 - \mathbf{x}_2) \\ \mathbf{0} = \left(\frac{f(\|\mathbf{x}_1 - \mathbf{x}_2\|)}{\|\mathbf{x}_1 - \mathbf{x}_2\|} - \frac{\alpha}{2} \right) (\mathbf{x}_2 - \mathbf{x}_1). \end{cases}$$

By Lemma 1.3.4 there exists an $\epsilon > 0$ for which $\mathbf{x}(t) \in \Theta_{2,\epsilon} \times \mathbb{R}^2$. Hence, $\|\mathbf{x}_1 - \mathbf{x}_2\|$ is bounded away from 0. So, it can only be the case that

$$\frac{f(\|\mathbf{x}_1 - \mathbf{x}_2\|)}{\|\mathbf{x}_1 - \mathbf{x}_2\|} - \frac{\alpha}{2} = 0.$$

Using $\Delta x_{1,2} = \|\mathbf{x}_1 - \mathbf{x}_2\|$, we require then

$$2f(\Delta x_{1,2}) = \alpha \Delta x_{1,2}.$$

Now, it can be shown that $\frac{2}{\alpha}f$ has a unique fixed point; let r_0 be that point.

Here then are both necessary and sufficient conditions for the equilibrium points of system

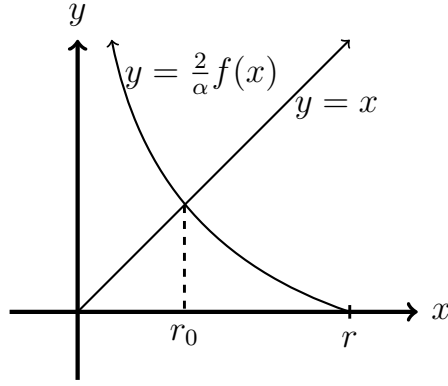


Figure 2.3: A illustrative graph for existence of a fixed point of $\frac{2}{\alpha}f$. A rigorous proof is very straightforward use of the intermediate value theorem of elementary calculus.

(2.12). The equilibrium points of this system are all the points $\mathbf{x} \in \mathbb{R}^6$ such that

$$(1) \quad \mathbf{c} = \frac{\mathbf{x}_1 + \mathbf{x}_2}{2} \quad \text{and} \quad (2.13)$$

$$(2) \quad \|\mathbf{x}_2 - \mathbf{x}_1\| = r_0. \quad (2.14)$$

From the work above one can see that if system (2.12) has equilibrium points they must satisfy conditions (2.13) and (2.14). Conversely, any point $\mathbf{x} \in \mathbb{R}^6$ that satisfies these conditions is, in fact, an equilibrium for that system. Such a characterization of the equilibria is then precise but not very useful. We seek to formulate the set of equilibria in a more meaningful way. Let $e(\mathbf{f})^6$ be the set of all the equilibria of \mathbf{f} . Suppose $\mathbf{x} \in e(\mathbf{f})$, $\mathbf{a} \in \mathbb{R}^2$ and $\mathbf{a} = (\mathbf{a}, \mathbf{a}, \mathbf{a})^T$ then

$$\mathbf{x} + \mathbf{a} = \begin{pmatrix} \mathbf{x}_1 + \mathbf{a} \\ \mathbf{x}_2 + \mathbf{a} \\ \mathbf{c} + \mathbf{a} \end{pmatrix}$$

and observe that from

$$(1) \quad \mathbf{c} + \mathbf{a} = \frac{\mathbf{x}_1 + \mathbf{a} + \mathbf{x}_2 + \mathbf{a}}{2} \quad \text{and} \quad (2.15)$$

$$(2) \quad \|\mathbf{x}_1 + \mathbf{a} - (\mathbf{x}_2 + \mathbf{a})\| = \|\mathbf{x}_1 - \mathbf{x}_2\| = r_0, \quad (2.16)$$

⁶This notation is used since the set depends only on the force function \mathbf{f} of $\hat{\mathcal{H}}$.

$\mathbf{x} + \mathbf{a} \in e(\mathbf{f})$. So, the three points in \mathbb{R}^2 that represent an equilibrium of \mathbf{f} may be translated by the same vector and remain an equilibrium. Now, suppose the points in \mathbb{R}^2 that correspond to an equilibrium of \mathbf{f} are rotated θ radians counterclockwise about the point \mathbf{c} . To check that the result would also satisfy conditions (2.13) and (2.14), consider the following.

Let

$$T = \begin{pmatrix} 1 & 0 & 0 & 0 & -1 & 0 \\ 0 & 1 & 0 & 0 & 0 & -1 \\ 0 & 0 & 1 & 0 & -1 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix},$$

$$S_\theta = \begin{pmatrix} \cos \theta & -\sin \theta & 0 & 0 & 0 & 0 \\ \sin \theta & \cos \theta & 0 & 0 & 0 & 0 \\ 0 & 0 & \cos \theta & -\sin \theta & 0 & 0 \\ 0 & 0 & \sin \theta & \cos \theta & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

and

$$L_\theta = T^{-1}S_\theta T.$$

What is going on here is that T translates points in \mathbb{R}^2 of an equilibrium to where they would be if the c-site were at the origin, the location of the c-site itself, however, remains unchanged. Then, S_θ rotates the cell centers of the translated system θ radians counterclockwise. The inverse of T then undoes the translation and the result of these three operators together is

simply a rotation about the c-site. Now, if $\mathbf{x} \in e(\mathbf{f})$ and $\theta \in [0, 2\pi)$ then let $\tilde{\mathbf{x}} = L_\theta \mathbf{x}$.

$$\tilde{\mathbf{x}}_i = \begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix} (\mathbf{x}_i - \mathbf{c}) + \mathbf{c} \quad \text{for } i = 1, 2$$

and, of course $\tilde{\mathbf{c}} = \mathbf{c}$. Notice then that

$$\begin{aligned} \frac{\tilde{\mathbf{x}}_1 + \tilde{\mathbf{x}}_2}{2} &= \frac{1}{2} \left(\begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix} (\mathbf{x}_1 - \mathbf{c}) + \mathbf{c} + \begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix} (\mathbf{x}_2 - \mathbf{c}) + \mathbf{c} \right) \\ &= \frac{1}{2} \begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix} (\mathbf{x}_1 + \mathbf{x}_2 - 2\mathbf{c}) + \mathbf{c} \\ &= \frac{1}{2} \begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix} (2\mathbf{c} - 2\mathbf{c}) + \mathbf{c} \quad \text{since } \mathbf{x} \in e(\mathbf{f}) \\ &= \mathbf{c} = \tilde{\mathbf{c}} \end{aligned}$$

and

$$\begin{aligned} \|\tilde{\mathbf{x}}_2 - \tilde{\mathbf{x}}_1\| &= \left\| \begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix} (\mathbf{x}_2 - \mathbf{c}) + \mathbf{c} - \left(\begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix} (\mathbf{x}_1 - \mathbf{c}) + \mathbf{c} \right) \right\| \\ &= \left\| \begin{pmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{pmatrix} (\mathbf{x}_2 - \mathbf{x}_1) \right\| \\ &= \|\mathbf{x}_2 - \mathbf{x}_1\| = r_0. \end{aligned}$$

The third equal sign is because the matrix is orthogonal. This shows that the set $e(\mathbf{f})$ is invariant under the operator L_θ , that is $L_\theta(e(\mathbf{f})) \subset e(\mathbf{f})$ for all real θ .

Now to write out this set formally. Let

$$W = \text{span} \left\{ \begin{pmatrix} 1 \\ 0 \\ 1 \\ 0 \\ 1 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ 1 \\ 0 \\ 1 \\ 0 \\ 1 \end{pmatrix} \right\}, \quad \text{and} \quad \mathbf{x}^0 = \begin{pmatrix} 0 \\ 0 \\ r_0 \\ 0 \\ \frac{r_0}{2} \\ 0 \end{pmatrix}.$$

We then seek to show

$$\bigcup_{\theta \in \mathbb{R}} L_\theta(\mathbf{x}_0 + W) = e(\mathbf{f}). \quad (2.17)$$

From the above, since clearly $\mathbf{x}^0 \in e(\mathbf{f})$,

$$\bigcup_{\theta \in \mathbb{R}} L_\theta(\mathbf{x}_0 + W) \subset e(\mathbf{f}).$$

To get the inclusion in the other direction suppose $\mathbf{x} = (x_1, y_1, x_2, y_2, x_c, y_c)^T \in e(\mathbf{f})$, and note that it must satisfy conditions (2.13) and (2.14). Then let $\mathbf{a} = (x_c, y_c)^T - (\frac{r_0}{2}, 0)^T$, $\mathbf{a} = (\mathbf{a}, \mathbf{a}, \mathbf{a})^T$ and $\theta = \tan^{-1} \left(\frac{y_2 - y_1}{x_2 - x_1} \right)$, if $\mathbf{x}_1 = \mathbf{x}_2$ let $\theta = \pm \frac{\pi}{2}$. From this we can then recover \mathbf{x}

$$L_\theta(\mathbf{x}_0 + \mathbf{a}) = L_\theta \begin{pmatrix} x_c - \frac{r_0}{2} \\ y_c \\ x_c + \frac{r_0}{2} \\ y_c \\ x_c \\ y_c \end{pmatrix} = \begin{pmatrix} x_c - \frac{r_0}{2} \cos \theta \\ y_c - \frac{r_0}{2} \sin \theta \\ x_c + \frac{r_0}{2} \cos \theta \\ y_c + \frac{r_0}{2} \sin \theta \\ x_c \\ y_c \end{pmatrix} = \begin{pmatrix} \frac{(x_2 + x_1)}{2} - \frac{(x_2 - x_1)}{2} \\ \frac{(y_2 + y_1)}{2} - \frac{(y_2 - y_1)}{2} \\ \frac{(x_2 + x_1)}{2} + \frac{(x_2 - x_1)}{2} \\ \frac{(y_2 + y_1)}{2} + \frac{(y_2 - y_1)}{2} \\ x_c \\ y_c \end{pmatrix} = \begin{pmatrix} x_1 \\ y_1 \\ x_2 \\ y_2 \\ x_c \\ y_c \end{pmatrix} = \mathbf{x}.$$

The third equality results from the definition of θ and the fact that \mathbf{x} is an equilibrium of \mathbf{f} . See Figure 2.4.

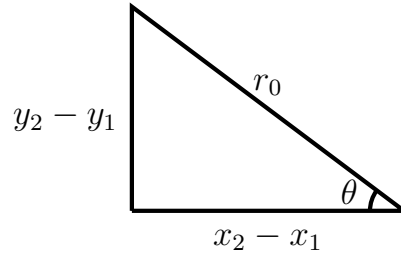


Figure 2.4: A triangle demonstrating the relation between r_0 , $y_2 - y_1$, $x_2 - x_1$, and θ . Notice then that $r_0 \cos \theta = x_2 - x_1$.

Now that the set of equilibria is written explicitly by equation (2.17), we seek to understand the structure of this set. It will be particularly useful if this set is a manifold. To verify that this is indeed the case, consider the following as a proposed atlas for the proposed manifold $e(\mathbf{f})$:

$$U_1 = \bigcup_{-\frac{\pi}{2} < \theta < \frac{\pi}{2}} \mathbf{L}_\theta(\mathbf{X}_0 + W)$$

$$U_2 = \bigcup_{0 < \theta < \pi} \mathbf{L}_\theta(\mathbf{X}_0 + W)$$

$$U_3 = \bigcup_{\frac{\pi}{2} < \theta < \frac{3\pi}{2}} \mathbf{L}_\theta(\mathbf{X}_0 + W)$$

$$U_4 = \bigcup_{\pi < \theta < 2\pi} \mathbf{L}_\theta(\mathbf{X}_0 + W)$$

With (if $\mathbf{p} = (x_1, y_1, x_2, y_2, x_c, y_c)^T \in e(\mathbf{f})$)

$$\begin{aligned} \varphi_1 : p \mapsto & \begin{pmatrix} x_c - \frac{r_0}{2} \\ y_c \\ \sin^{-1}\left(\frac{y_1 - y_c}{r_0/2}\right) \end{pmatrix} & \varphi_2 : p \mapsto & \begin{pmatrix} x_c - \frac{r_0}{2} \\ y_c \\ \cos^{-1}\left(\frac{x_1 - x_c}{r_0/2}\right) \end{pmatrix} \\ \varphi_3 : p \mapsto & \begin{pmatrix} x_c - \frac{r_0}{2} \\ y_c \\ \sin^{-1}\left(\frac{y_1 - y_c}{r_0/2}\right) + \pi \end{pmatrix} & \varphi_4 : p \mapsto & \begin{pmatrix} x_c - \frac{r_0}{2} \\ y_c \\ \cos^{-1}\left(\frac{x_1 - x_c}{r_0/2}\right) + \pi \end{pmatrix} \end{aligned}$$

Note also,

$$\begin{aligned} \varphi_1(U_1) &= \mathbb{R}^2 \times \left(-\frac{\pi}{2}, \frac{\pi}{2}\right) \\ \varphi_2(U_2) &= \mathbb{R}^2 \times (0, \pi) \\ \varphi_3(U_3) &= \mathbb{R}^2 \times \left(\frac{\pi}{2}, \frac{3\pi}{2}\right) \\ \varphi_4(U_4) &= \mathbb{R}^2 \times (\pi, 2\pi). \end{aligned}$$

Now, define $G : \mathbb{R}^3 \rightarrow e(\mathbf{f}) \subset \mathbb{R}^6$ by

$$G(x_a, y_a, \theta) = \begin{pmatrix} \frac{r_0}{2} \cos \theta + \frac{r_0}{2} + x_a \\ \frac{r_0}{2} \sin \theta + y_a \\ \frac{r_0}{2} \cos(\theta + \pi) + \frac{r_0}{2} + x_a \\ \frac{r_0}{2} \sin(\theta + \pi) + y_a \\ x_a + \frac{r_0}{2} \\ y_a \end{pmatrix}, \quad (2.18)$$

and notice

$$\varphi_i \circ G = G \circ \varphi_i = \text{Id} \quad \text{for } i = 1, 2, 3, 4.$$

So, each transition map

$$\varphi_j \circ \varphi_i^{-1} : \varphi_i(U_i \cap U_j) \rightarrow \varphi_j(U_i \cap U_j)$$

is the identity map and therefore smooth. This gives that $e(\mathbf{f})$ has a smooth atlas and therefore a smooth structure (see [9]). Hence it is a smooth manifold.

Let us consider the tangent space of this 3-submanifold of \mathbb{R}^6 .

$$G_{x_a} = \begin{pmatrix} 1 \\ 0 \\ 1 \\ 0 \\ 1 \\ 0 \end{pmatrix}, \quad G_{y_a} = \begin{pmatrix} 0 \\ 1 \\ 0 \\ 1 \\ 0 \\ 1 \end{pmatrix}, \quad \text{and} \quad G_\theta = \begin{pmatrix} -\frac{r_0}{2} \sin \theta \\ \frac{r_0}{2} \cos \theta \\ -\frac{r_0}{2} \sin(\theta + \pi) \\ \frac{r_0}{2} \cos(\theta + \pi) \\ 0 \\ 0 \end{pmatrix}.$$

Simplifying G_θ the basis of the tangent space of $e(\mathbf{f})$ at some point (x_a, y_a, θ) is

$$\left\{ \begin{pmatrix} 1 \\ 0 \\ 1 \\ 0 \\ 1 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ 1 \\ 0 \\ 1 \\ 0 \\ 1 \end{pmatrix}, \begin{pmatrix} \tan \theta \\ -1 \\ -\tan \theta \\ 1 \\ 0 \\ 0 \end{pmatrix} \right\}. \quad (2.19)$$

It has been shown that the set of equilibria have a smooth 3-manifold structure.

2.2.1 Stability of the equilibria. In order to study the stability of these equilibria or fixed points⁷ it will be useful to simplify \mathbf{f} by defining a function $g : \mathbb{R}^4 \rightarrow \mathbb{R}$ as

$$g(x_1, y_1, x_2, y_2) = g(\mathbf{x}_1, \mathbf{x}_2) = \frac{f(\|\mathbf{x}_1 - \mathbf{x}_2\|)}{\gamma_1 \|\mathbf{x}_1 - \mathbf{x}_2\|}.$$

This way,

$$\mathbf{f}(\mathbf{x}) = \begin{pmatrix} \left(g(\mathbf{x}_1, \mathbf{x}_2) - \frac{\alpha}{\gamma_1}\right) \mathbf{x}_1 & -g(\mathbf{x}_1, \mathbf{x}_2) \mathbf{x}_2 & + \frac{\alpha}{\gamma_1} \mathbf{c} \\ -g(\mathbf{x}_1, \mathbf{x}_2) \mathbf{x}_1 & + \left(g(\mathbf{x}_1, \mathbf{x}_2) - \frac{\alpha}{\gamma_1}\right) \mathbf{x}_2 & + \frac{\alpha}{\gamma_1} \mathbf{c} \\ \frac{\alpha}{\gamma_2} \mathbf{x}_1 & + \frac{\alpha}{\gamma_2} \mathbf{x}_2 & - \frac{2\alpha}{\gamma_2} \mathbf{c} \end{pmatrix}. \quad (2.20)$$

To analyze the stability of a fixed point $\tilde{\mathbf{x}}$ consider the change of variable to the variable $\mathbf{y} \in \mathbb{R}^6$ defined as $\mathbf{y} = \mathbf{x} - \tilde{\mathbf{x}}$. So, $\mathbf{x} = \mathbf{y} + \tilde{\mathbf{x}}$ and $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ becomes

$$\dot{\mathbf{y}} = \mathbf{f}(\mathbf{y} + \tilde{\mathbf{x}}),$$

we have shifted the equilibrium we wish to study to the origin. Using a Taylor expansion provides

$$\begin{aligned} \dot{\mathbf{y}} &= \mathbf{f}(\tilde{\mathbf{x}}) + \mathbf{Df}(\tilde{\mathbf{x}})\mathbf{y} + \mathcal{O}(\|\mathbf{y}\|^2) \\ &= \mathbf{Df}(\tilde{\mathbf{x}})\mathbf{y} + \mathcal{O}(\|\mathbf{y}\|^2). \end{aligned}$$

So, it is sufficient to determine the dynamics of \mathbf{y} close to $\mathbf{0}$. For this we look at the linear part, $\mathbf{Df}(\tilde{\mathbf{x}})\mathbf{y}$. Before taking the derivative of \mathbf{f} at $\tilde{\mathbf{x}}$ it may be helpful to express $\mathbf{f}(\mathbf{x})$ like

⁷The term “fixed points” is more common in the literature surrounding the techniques to follow. See [10].

this:

$$\mathbf{f}(\mathbf{x}) = \begin{pmatrix} \left(g - \frac{\alpha}{\gamma_1}\right) x_1 - gx_2 + \frac{\alpha}{\gamma_1} x_c \\ \left(g - \frac{\alpha}{\gamma_1}\right) y_1 - gy_2 + \frac{\alpha}{\gamma_1} y_c \\ -gx_1 + \left(g - \frac{\alpha}{\gamma_1}\right) x_2 + \frac{\alpha}{\gamma_1} x_c \\ -gy_1 + \left(g - \frac{\alpha}{\gamma_1}\right) y_2 + \frac{\alpha}{\gamma_1} y_c \\ \frac{\alpha}{\gamma_2} x_1 + \frac{\alpha}{\gamma_2} x_2 - \frac{2\alpha}{\gamma_2} x_c \\ \frac{\alpha}{\gamma_2} y_1 + \frac{\alpha}{\gamma_2} y_2 - \frac{2\alpha}{\gamma_2} y_c \end{pmatrix}.$$

With this in hand we proceed to formulate the derivative matrix

$$\mathbf{Df}(\mathbf{x}) = \begin{pmatrix} \frac{\partial g}{\partial x_1} x_1 + g - \frac{\alpha}{\gamma_1} - \frac{\partial g}{\partial x_1} x_2 & \frac{\partial g}{\partial y_1} x_1 - \frac{\partial g}{\partial y_1} x_2 & \frac{\partial g}{\partial x_2} x_1 - \frac{\partial g}{\partial x_2} x_2 - g & \frac{\partial g}{\partial y_2} x_1 - \frac{\partial g}{\partial y_2} x_2 & 0 \\ \frac{\partial g}{\partial x_1} y_1 - \frac{\partial g}{\partial x_1} y_2 & \frac{\partial g}{\partial y_1} y_1 + g - \frac{\alpha}{\gamma_1} - \frac{\partial g}{\partial y_1} y_2 & \frac{\partial g}{\partial x_2} y_1 - \frac{\partial g}{\partial x_2} y_2 & \frac{\partial g}{\partial y_2} y_1 - \frac{\partial g}{\partial y_2} y_2 - g & \frac{\alpha}{\gamma_1} \\ -\frac{\partial g}{\partial x_1} x_1 - g + \frac{\partial g}{\partial x_1} x_2 & -\frac{\partial g}{\partial y_1} x_1 + \frac{\partial g}{\partial y_1} x_2 & -\frac{\partial g}{\partial x_2} x_1 + \frac{\partial g}{\partial x_2} x_2 + g - \frac{\alpha}{\gamma_1} & -\frac{\partial g}{\partial y_2} x_1 + \frac{\partial g}{\partial y_2} x_2 & 0 \\ -\frac{\partial g}{\partial x_1} y_1 + \frac{\partial g}{\partial x_1} y_2 & -\frac{\partial g}{\partial y_1} y_1 - g + \frac{\partial g}{\partial y_1} y_2 & -\frac{\partial g}{\partial x_2} y_1 + \frac{\partial g}{\partial x_2} y_2 & -\frac{\partial g}{\partial y_2} y_1 + \frac{\partial g}{\partial y_2} y_2 + g - \frac{\alpha}{\gamma_1} & 0 \\ \frac{\alpha}{\gamma_2} & 0 & \frac{\alpha}{\gamma_2} & 0 & -\frac{2\alpha}{\gamma_2} \\ 0 & \frac{\alpha}{\gamma_2} & 0 & \frac{\alpha}{\gamma_2} & 0 \end{pmatrix}.$$

Which simplifies to:

$$\mathbf{Df}(\mathbf{x}) = \begin{pmatrix} \frac{\partial g}{\partial x_1} (x_1 - x_2) + g - \frac{\alpha}{\gamma_1} & \frac{\partial g}{\partial y_1} (x_1 - x_2) & \frac{\partial g}{\partial x_2} (x_1 - x_2) - g & \frac{\partial g}{\partial y_2} (x_1 - x_2) & 0 \\ \frac{\partial g}{\partial x_1} (y_1 - y_2) & \frac{\partial g}{\partial y_1} (y_1 - y_2) + g - \frac{\alpha}{\gamma_1} & \frac{\partial g}{\partial x_2} (y_1 - y_2) & \frac{\partial g}{\partial y_2} (y_1 - y_2) - g & \frac{\alpha}{\gamma_1} \\ -\frac{\partial g}{\partial x_1} (x_1 - x_2) - g & -\frac{\partial g}{\partial y_1} (x_1 - x_2) & -\frac{\partial g}{\partial x_2} (x_1 - x_2) + g - \frac{\alpha}{\gamma_1} & -\frac{\partial g}{\partial y_2} (x_1 - x_2) & 0 \\ -\frac{\partial g}{\partial x_1} (y_1 - y_2) & -\frac{\partial g}{\partial y_1} (y_1 - y_2) - g & -\frac{\partial g}{\partial x_2} (y_1 - y_2) & -\frac{\partial g}{\partial y_2} (y_1 - y_2) + g - \frac{\alpha}{\gamma_1} & 0 \\ \frac{\alpha}{\gamma_2} & 0 & \frac{\alpha}{\gamma_2} & 0 & -\frac{2\alpha}{\gamma_2} \\ 0 & \frac{\alpha}{\gamma_2} & 0 & \frac{\alpha}{\gamma_2} & 0 \end{pmatrix}.$$

Recall that the above will only be useful if evaluated at an equilibrium $\tilde{\mathbf{x}} = (\tilde{x}_1, \tilde{y}_1, \tilde{x}_2, \tilde{y}_2, \tilde{x}_c, \tilde{y}_c) \in e(\mathbf{f})$. In which case notice that

$$\begin{aligned}
g &= g(\tilde{x}_1, \tilde{y}_1, \tilde{x}_2, \tilde{y}_2) \\
&= \frac{f(\|\tilde{\mathbf{x}}_1 - \tilde{\mathbf{x}}_2\|)}{\gamma_1 \|\tilde{\mathbf{x}}_1 - \tilde{\mathbf{x}}_2\|} \\
&= \frac{f(r_0)}{\gamma_1 r_0} && \text{from (2.14)} \\
&= \frac{\alpha r_0 / 2}{\gamma_1 r_0} && \text{by definition of } r_0 \\
&= \frac{\alpha}{2\gamma_1}.
\end{aligned}$$

Furthermore, the partials of g will be useful. From the definition of g the following is obtained:

$$\frac{d}{du} \left(\frac{f(u)}{\gamma_1 u} \right) = \frac{f'(u)u - f(u)}{\gamma_1 u^2}.$$

So then, if $u = \|\mathbf{x}_1 - \mathbf{x}_2\|$ (recall that is simply the Euclidean norm) then

$$\begin{aligned}
\frac{\partial g}{\partial x_1} &= \frac{d}{du} \left(\frac{f(u)}{\gamma_1 u} \right) \frac{\partial u}{\partial x_1} \\
&= \frac{f'(u)u - f(u)}{\gamma_1 u^2} \frac{\partial u}{\partial x_1} \\
&= \left(\frac{f'(u)u - f(u)}{\gamma_1 u^2} \right) \left(\frac{x_1 - x_2}{u} \right) \\
&= \frac{1}{\gamma_1 r_0^2} \left(f'(r_0) - \frac{\alpha}{2} \right) (x_1 - x_2).
\end{aligned}$$

and

$$\begin{aligned}
\frac{\partial g}{\partial x_2} &= \frac{d}{du} \left(\frac{f(u)}{\gamma_1 u} \right) \frac{\partial u}{\partial x_2} \\
&= \frac{f'(u)u - f(u)}{\gamma_1 u^2} \frac{\partial u}{\partial x_2} \\
&= \left(\frac{f'(u)u - f(u)}{\gamma_1 u^2} \right) \left(\frac{x_2 - x_1}{u} \right) \\
&= -\frac{1}{\gamma_1 r_0^2} \left(f'(r_0) - \frac{\alpha}{2} \right) (x_1 - x_2).
\end{aligned}$$

Similarly for

$$\frac{\partial g}{\partial y_1} = \frac{1}{\gamma_1 r_0^2} \left(f'(r_0) - \frac{\alpha}{2} \right) (y_1 - y_2)$$

and

$$\frac{\partial g}{\partial y_2} = -\frac{1}{\gamma_1 r_0^2} \left(f'(r_0) - \frac{\alpha}{2} \right) (y_1 - y_2).$$

The eigenvalues⁸ of $\mathbf{Df}(\tilde{\mathbf{x}})$ are $0, 0, 0, -\alpha \left(\frac{1}{\gamma_1} + \frac{2}{\gamma_2} \right), -\alpha \left(\frac{1}{\gamma_1} + \frac{2}{\gamma_2} \right), \frac{1}{\gamma_1} \left(f'(r_0) - \frac{\alpha}{2} \right)$.

The eigenvectors of the zero eigenvalues are:

$$\begin{pmatrix} 0 \\ 1 \\ 0 \\ 1 \\ 0 \\ 1 \end{pmatrix}, \quad \begin{pmatrix} 1 \\ 0 \\ 1 \\ 0 \\ 1 \\ 0 \end{pmatrix}, \quad \text{and} \quad \begin{pmatrix} \frac{y_1 - y_2}{x_1 - x_2} \\ -1 \\ -\frac{y_1 - y_2}{x_1 - x_2} \\ 1 \\ 0 \\ 0 \end{pmatrix}.$$

It should be noted that because θ from the parameterization of $e(\mathbf{f})$ by G (see (2.18) on page 49) was defined to be the angle from the positive x -axis the solution was rotated counterclockwise,

$$\frac{y_1 - y_2}{x_1 - x_2} = \tan \theta.$$

In the above, three eigenvalues are zero and their associated directions according to the eigenvectors are all tangent to the manifold $e(\mathbf{f})$ at that point. This may be seen by comparing these eigenvectors to the basis of the tangent space of $e(\mathbf{f})$ at a particular point found in (2.19) on page 50. The other three eigenvalues above are negative, so the dynamics in the directions associated with their eigenvectors are asymptotically stable. We conclude that this system possesses a stable manifold and a center manifold which is in fact the set of all equilibrium. So, any equilibrium point is stable but not asymptotically stable.

2.2.2 Qualitative Findings of the Behavior of the Solution to the Nonlinear

System. In this and the next section we present findings motivated by work in the first regime of the problem (the linear case). By a few shrewd guesses we identify the unique

⁸The eigenvalues of the above matrix were found by *Mathematica* in which the following variables were employed

$$a = (\tilde{x}_1 - \tilde{x}_2)^2, \quad b = (\tilde{x}_1 - \tilde{x}_2)(\tilde{y}_1 - \tilde{y}_2), \quad c = (\tilde{y}_1 - \tilde{y}_2)^2, \quad d = \frac{f'(r_0) - \frac{\alpha}{2}}{\gamma_1 r_0^2}, \quad \text{and} \quad e = \frac{\alpha}{2\gamma_1}.$$

solution to $\hat{\mathfrak{H}}$.

The system $\hat{\mathfrak{H}}$ is given below, where $l > 0$ and $y_c(0) \geq 0$

$$\begin{cases} \gamma_1 \dot{\mathbf{x}}_1 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_1 - \mathbf{x}_2}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha(\mathbf{c} - \mathbf{x}_1) \\ \gamma_1 \dot{\mathbf{x}}_2 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_2 - \mathbf{x}_1}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha(\mathbf{c} - \mathbf{x}_2) \\ \gamma_2 \dot{\mathbf{c}} = \alpha(\mathbf{x}_1 - \mathbf{c}) + \alpha(\mathbf{x}_2 - \mathbf{c}) \\ \mathbf{x}_1(0) = (0, 0), \quad \mathbf{x}_2(0) = (l, 0), \quad \text{and} \quad \mathbf{c}(0) = (x_c(0), y_c(0)). \end{cases} \quad (2.21)$$

By Theorem 1.3.9 there exists a unique solution to $\hat{\mathfrak{H}}$ on $[0, \infty)$. Let $\tilde{\mathbf{x}}(t) = (\tilde{x}_1(t), \tilde{y}_1(t), \tilde{x}_2(t), \tilde{y}_2(t), \tilde{x}_c(t), \tilde{y}_c(t))$ be that solution. For the sake of simplicity, let $g(x_1, x_2, y_1, y_2) = f(\|\mathbf{x}_1 - \mathbf{x}_2\|)/\|\mathbf{x}_1 - \mathbf{x}_2\|$. Expand (2.21) by writing the equation for each component of the vectors \mathbf{x}_1 , \mathbf{x}_2 , and \mathbf{c} . This produces an equivalent system of six equations together with initial conditions.

$$\begin{cases} \gamma_1 \dot{x}_1 = g(x_1, x_2, y_1, y_2)(x_1 - x_2) + \alpha(x_c - x_1) \\ \gamma_1 \dot{y}_1 = g(x_1, x_2, y_1, y_2)(y_1 - y_2) + \alpha(y_c - y_1) \\ \gamma_1 \dot{x}_2 = g(x_1, x_2, y_1, y_2)(x_2 - x_1) + \alpha(x_c - x_2) \\ \gamma_1 \dot{y}_2 = g(x_1, x_2, y_1, y_2)(y_2 - y_1) + \alpha(y_c - y_2) \\ \gamma_2 \dot{x}_c = \alpha(x_1 - x_c) + \alpha(x_2 - x_c) \\ \gamma_2 \dot{y}_c = \alpha(y_1 - y_c) + \alpha(y_2 - y_c). \\ x_1(0) = 0, \quad y_1(0) = 0, \quad x_2(0) = l, \quad y_2(0) = 0, \quad x_c(0) = c_x, \quad \text{and} \quad y_c(0) = c_y. \end{cases} \quad (2.22)$$

Now, separate the equations associated with the derivatives in the y directions from the equations with the derivatives in the x direction. This achieves two different coupled IVPs

$$\begin{cases} \gamma_1 \dot{y}_1 = g(x_1, x_2, y_1, y_2)(y_1 - y_2) + \alpha(y_c - y_1) \\ \gamma_1 \dot{y}_2 = g(x_1, x_2, y_1, y_2)(y_2 - y_1) + \alpha(y_c - y_2) \\ \gamma_2 \dot{y}_c = \alpha(y_1 - y_c) + \alpha(y_2 - y_c) \\ y_1(0) = y_2(0) = 0, \quad \text{and} \quad y_c(0) = c_y. \end{cases} \quad (2.23)$$

and

$$\begin{cases} \gamma_1 \dot{x}_1 = g(x_1, x_2, y_1, y_2)(x_1 - x_2) + \alpha(x_c - x_1) \\ \gamma_1 \dot{x}_2 = g(x_1, x_2, y_1, y_2)(x_2 - x_1) + \alpha(x_c - x_2) \\ \gamma_2 \dot{x}_c = \alpha(x_1 - x_c) + \alpha(x_2 - x_c) \\ x_1(0) = 0, \quad x_2(0) = l, \text{ and } x_c(0) = c_x. \end{cases} \quad (2.24)$$

Now, we will focus on each IVP individually.

We proceed to find an explicit solution to (2.23). First, consider as a guess, to be verified in course, $y_1(t) = y_2(t) = y(t)$ for all $t \geq 0$. To form the rest of the guess, solve for y and y_c . With the appropriate substitutions the first and second equations of (2.23) are seen to be identical so one may be omitted and the system here simplified becomes

$$\begin{cases} \gamma_1 \dot{y} = \alpha(y_c - y) \\ \gamma_2 \dot{y}_c = 2\alpha(y - y_c). \\ y(0) = 0, \text{ and } y_c(0) = c_y. \end{cases} \quad (2.25)$$

This equation may easily be solved as it is now linear. Let $\mathbf{y} = (y, y_c)^T$ and

$$A = \begin{pmatrix} -\frac{\alpha}{\gamma_1} & \frac{\alpha}{\gamma_1} \\ \frac{2\alpha}{\gamma_2} & -\frac{2\alpha}{\gamma_2} \end{pmatrix}.$$

So, we have $\dot{\mathbf{y}} = A\mathbf{y}$. The eigenvalues of A along with their respective eigenvectors are listed below⁹

$$\lambda_1 = 0, \quad \boldsymbol{\xi}_1 = \begin{pmatrix} 1 \\ 1 \end{pmatrix} \quad \text{and} \quad \lambda_2 = -\frac{\alpha}{\gamma_1} - \frac{2\alpha}{\gamma_2}, \quad \boldsymbol{\xi}_2 = \begin{pmatrix} -\frac{\gamma_2}{2\gamma_1} \\ 1 \end{pmatrix}$$

⁹the computation here was done in *Mathematica*.

So, the fundamental matrix for this system is

$$\mathbf{\Psi}(t) = \begin{pmatrix} 1 & -\frac{\gamma_2}{2\gamma_1} e^{-t(\frac{\alpha}{\gamma_1} + \frac{2\alpha}{\gamma_2})} \\ 1 & e^{-t(\frac{\alpha}{\gamma_1} + \frac{2\alpha}{\gamma_2})} \end{pmatrix}.$$

Note that for any $\mathbf{k} \in \mathbb{R}^2$ the solution $\mathbf{y}(t) = \mathbf{\Psi}(t)\mathbf{k}$ will also satisfy (2.25). In order, for the solution to satisfy the initial conditions \mathbf{k} will be chosen so that $\mathbf{\Psi}(0)\mathbf{k} = \mathbf{y}(0)$; hence its desirable for $\mathbf{k} = \mathbf{\Psi}(0)^{-1}\mathbf{y}(0)$. To that end note that

$$\mathbf{\Psi}(0) = \begin{pmatrix} 1 & -\frac{\gamma_2}{2\gamma_1} \\ 1 & 1 \end{pmatrix} \quad \text{and} \quad \mathbf{\Psi}(0)^{-1} = \begin{pmatrix} \frac{2\gamma_1}{2\gamma_1 + \gamma_2} & \frac{\gamma_2}{2\gamma_1 + \gamma_2} \\ -\frac{2\gamma_1}{2\gamma_1 + \gamma_2} & \frac{2\gamma_1}{2\gamma_1 + \gamma_2} \end{pmatrix}.$$

We may therefore let

$$\mathbf{k} = \begin{pmatrix} \frac{2\gamma_1}{2\gamma_1 + \gamma_2} & \frac{\gamma_2}{2\gamma_1 + \gamma_2} \\ -\frac{2\gamma_1}{2\gamma_1 + \gamma_2} & \frac{2\gamma_1}{2\gamma_1 + \gamma_2} \end{pmatrix} \begin{pmatrix} 0 \\ c_y \end{pmatrix} = \begin{pmatrix} \frac{c_y \gamma_2}{2\gamma_1 + \gamma_2} \\ \frac{2c_y \gamma_1}{2\gamma_1 + \gamma_2} \end{pmatrix}$$

and now have as a solution to the IVP (2.25)

$$\begin{aligned} \mathbf{y}(t) &= \mathbf{\Psi}(t) \begin{pmatrix} \frac{c_y \gamma_2}{2\gamma_1 + \gamma_2} \\ \frac{2c_y \gamma_1}{2\gamma_1 + \gamma_2} \end{pmatrix} \\ &= \begin{pmatrix} 1 & -\frac{\gamma_2}{2\gamma_1} e^{-t(\frac{\alpha}{\gamma_1} + \frac{2\alpha}{\gamma_2})} \\ 1 & e^{-t(\frac{\alpha}{\gamma_1} + \frac{2\alpha}{\gamma_2})} \end{pmatrix} \begin{pmatrix} \frac{c_y \gamma_2}{2\gamma_1 + \gamma_2} \\ \frac{2c_y \gamma_1}{2\gamma_1 + \gamma_2} \end{pmatrix} \\ &= \begin{pmatrix} \frac{c_y \gamma_2}{2\gamma_1 + \gamma_2} - \frac{c_y \gamma_2}{2\gamma_1 + \gamma_2} e^{-t(\frac{\alpha}{\gamma_1} + \frac{2\alpha}{\gamma_2})} \\ \frac{c_y \gamma_2}{2\gamma_1 + \gamma_2} + \frac{2c_y \gamma_1}{2\gamma_1 + \gamma_2} e^{-t(\frac{\alpha}{\gamma_1} + \frac{2\alpha}{\gamma_2})} \end{pmatrix}. \end{aligned}$$

The proposed solution then to (2.23) is given by

$$y_1(t) = \frac{c_y \gamma_2}{2\gamma_1 + \gamma_2} - \frac{c_y \gamma_2}{2\gamma_1 + \gamma_2} e^{-t(\frac{\alpha}{\gamma_1} + \frac{2\alpha}{\gamma_2})}, \quad (2.26)$$

$$y_2(t) = \frac{c_y \gamma_2}{2\gamma_1 + \gamma_2} - \frac{c_y \gamma_2}{2\gamma_1 + \gamma_2} e^{-t(\frac{\alpha}{\gamma_1} + \frac{2\alpha}{\gamma_2})}, \quad (2.27)$$

$$y_c(t) = \frac{c_y \gamma_2}{2\gamma_1 + \gamma_2} + \frac{2c_y \gamma_1}{2\gamma_1 + \gamma_2} e^{-t(\frac{\alpha}{\gamma_1} + \frac{2\alpha}{\gamma_2})}. \quad (2.28)$$

Note that these equations are identical to those found on page 38. From the work above it is clear that these satisfy the IVP (2.23). At this point we would like to suggest that the solutions in (2.26-2.28) must be identical to $\tilde{y}_1(t)$, $\tilde{y}_2(t)$, and $\tilde{y}_c(t)$, respectively. But this may not be accurate as there would be no guarantee that these functions put into (2.24) leave it a system that has a solution. The difficulty is in the systems being coupled. As it is, systems (2.24) and (2.23) are by themselves underdetermined, and for that reason need not have a unique solution or even any solution at all. What is encouraging, however, (2.26-2.28) satisfy (2.23) with no regard for g at all. We hope that something similar occurs in finding a possible solution to (2.24). Observe how these y -component equations (2.26-2.28), being the same as the solution found in regime one, were shown to conserve the center of drag. Now we use this principle to inform the guess at a solution to (2.24).

As before a guess is made in which the x -components of the solution relate to each other in a certain way which allows the system to be reduced. As was seen earlier (page 12)

$$\frac{\gamma_1 x_1(t) + \gamma_1 x_2(t) + \gamma_2 x_c(t)}{2\gamma_1 + \gamma_2} = \frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2}. \quad (2.29)$$

To this end, assume (2.29) and so then

$$x_1 + x_2 = l + \frac{\gamma_2}{\gamma_1}(x_c(0) - x_c)$$

substituting this into the last equation of (2.24) achieves

$$\begin{aligned}\gamma_2 \dot{x}_c &= \alpha \left(l + \frac{\gamma_2}{\gamma_1} (x_c(0) - x_c) - 2x_c \right) \\ &= -\alpha \left(\frac{\gamma_2}{\gamma_1} + 2 \right) x_c + \alpha \left(l + \frac{\gamma_2}{\gamma_1} x_c(0) \right).\end{aligned}$$

This is an equation purely in \mathbf{x}_c and may be solved through elementary methods, to obtain a very familiar

$$x_c = \frac{2x_c(0)\gamma_1 - l\gamma_1}{2\gamma_1 + \gamma_2} e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t} + \frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2}.$$

Notice this is the same as the \mathbf{x}_c solution found on page 38 and that the initial condition for x_c is satisfied (that is $x_c(0) = x_c(0)$ as desired). Under the assumption of (2.29) x_c has been solved and \mathbf{x}_2 may be eliminated by writing it in terms of x_1 as follows

$$x_2 = l - x_1 + \frac{\gamma_2}{\gamma_1} (x_c(0) - x_c).$$

Notice with this assumption x_2 satisfy its initial condition ($x_2(0) = l$) provided $x_1(0) = 0$. Now, consider the first and second equations of (2.24), both of which may be written in term of a single differential equation in x_1 . If there exists a solution $x_1(t)$ that satisfies both of these equations then it will admit a solution for x_2 and these together with the above formulation of x_c will constitute a solution to (2.24).

We start with the second equation of (2.24).

$$\begin{aligned}
\gamma_1 \frac{d}{dt}(x_2(x_1)) &= g(x_1, x_2(x_1), y_1, y_2)(x_2(x_1) - x_1) + \alpha(x_c - x_2(x_1)) \\
\Leftrightarrow -\gamma_1 \dot{x}_1 - \gamma_2 \dot{x}_c &= g(x_1, x_2(x_1), y_1, y_2)(x_2(x_1) - x_1) + \alpha(x_c - x_2(x_1)) \\
\Leftrightarrow -\gamma_1 \dot{x}_1 &= g(x_1, x_2(x_1), y_1, y_2)(x_2(x_1) - x_1) + \alpha(x_c - x_2(x_1)) + \gamma_2 \dot{x}_c \\
\Leftrightarrow -\gamma_1 \dot{x}_1 &= g(x_1, x_2(x_1), y_1, y_2)(x_2(x_1) - x_1) + \alpha \left(x_c - l + x_1 - \frac{\gamma_2}{\gamma_1} (x_c(0) - x_c) \right) \\
&\quad - \alpha \left(\frac{\gamma_2}{\gamma_1} + 2 \right) x_c + \alpha \left(l + \frac{\gamma_2}{\gamma_1} x_c(0) \right) \\
\Leftrightarrow -\gamma_1 \dot{x}_1 &= g(x_1, x_2(x_1), y_1, y_2)(x_2(x_1) - x_1) + \alpha(x_1 - x_c) \\
&\quad + \alpha \left(\frac{\gamma_2}{\gamma_1} + 2 \right) x_c + \alpha \left(-l - \frac{\gamma_2}{\gamma_1} x_c(0) \right) \\
&\quad - \alpha \left(\frac{\gamma_2}{\gamma_1} + 2 \right) x_c + \alpha \left(l + \frac{\gamma_2}{\gamma_1} x_c(0) \right) \\
\Leftrightarrow \gamma_1 \dot{x}_1 &= g(x_1, x_2(x_1), y_1, y_2)(x_1 - x_2(x_1)) + \alpha(x_c - x_1)
\end{aligned}$$

This shows that any x_1 that is a solution to the first equation of (2.24), with the appropriate substitution of x_2 in terms of x_1 and initial condition, shown here:

$$\gamma_1 \dot{x}_1 = g(x_1, x_2(x_1), y_1, y_2)(x_1 - x_2(x_1)) + \alpha(x_c - x_1), \quad x_1(0) = 0 \quad (2.30)$$

will also solve the second equation (again with x_2 in terms of x_1). Which means that if there is a solution to (2.30), then that x_1 , the so generated x_2 and the already formulated x_c constitute a solution to (2.24). That (2.30) has a unique solution may be seen from a straightforward application of the techniques used to prove Theorem 1.3.8 and Theorem 1.3.9.

Notice that the solutions x_1 , x_2 , and x_c are valid for any $g(x_1, x_2(x_1), y_1, y_2)$ that provides (2.30) with a unique solution. We now take all six of the proposed solutions and investigate whether they, together satisfy (2.22). Already it has been shown that the y -direction equations of system (2.22) will be satisfied by (2.26-2.28) regardless of g and its arguments. Likewise, the x -direction equations will be satisfied with the above formulated x_1 , x_2 , and x_c , provided, y_1 and y_2 when in the argument of g admit a solution to (2.30). This we will

now investigate.

Equation (2.30) can be simplified quite a bit by recalling that throughout the entire evolution of the system $y_2(t) = y_1(t)$. We start by unpacking g

$$\begin{aligned} g(x_1, y_1(t), x_2, y_2(t)) &= \frac{f(\|\mathbf{x}_2 - \mathbf{x}_1\|)}{\|\mathbf{x}_2 - \mathbf{x}_1\|} \\ &= \frac{f(\sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2})}{\sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2}} \\ &= \frac{f(|x_2 - x_1|)}{|x_2 - x_1|}. \end{aligned}$$

So, (2.30) becomes

$$\gamma_1 \dot{x}_1 = \frac{f(|x_2 - x_1|)}{|x_2 - x_1|} (x_1 - x_2) + \alpha(x_c - x_1). \quad (2.31)$$

Now, again, since $y_2 = y_1$ it must be the case that $x_2(t) \geq x_1(t)$ for all $t \geq 0$. This is because if at $t = 0$ $x_2(0) = l > 0 = x_1(0)$ since the solutions x_1 and x_2 are continuous if $x_2(t) = x_1(t)$ at any time t then $\mathbf{x}_1(t) = \mathbf{x}_2(t)$ which is impossible, since Lemma 1.3.4 assures us that the difference of the components of a solution is bounded away from zero. Hence $-(x_1 - x_2) = |x_2 - x_1|$ and (2.31) becomes

$$\gamma_1 \dot{x}_1 = -f(x_2 - x_1) + \alpha(x_c - x_1). \quad (2.32)$$

Now to write out $x_2 - x_1$

$$\begin{aligned} x_2 - x_1 &= \left(l - x_1 + \frac{\gamma_2}{\gamma_1} (x_c(0) - x_c(t)) \right) - x_1 \\ &= l + \frac{\gamma_2}{\gamma_1} (x_c(0) - x_c(t)) - 2x_1 \\ &= l + \frac{\gamma_2}{\gamma_1} \left(x_c(0) - \left(\frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} + \frac{2x_c(0)\gamma_1 - l\gamma_1}{2\gamma_1 + \gamma_2} e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t} \right) \right) - 2x_1 \\ &= l + \frac{\gamma_2}{\gamma_1} \left(\frac{2x_c(0)\gamma_1 - l\gamma_1}{2\gamma_1 + \gamma_2} - \frac{2x_c(0)\gamma_1 - l\gamma_1}{2\gamma_1 + \gamma_2} e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t} \right) - 2x_1 \\ &= l + \frac{2x_c(0)\gamma_2 - l\gamma_2}{2\gamma_1 + \gamma_2} \left(1 - e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t} \right) - 2x_1. \end{aligned}$$

With this in hand, along with the above definition for x_c (2.32) becomes

$$\begin{aligned} \gamma_1 \dot{x}_1 = & -f \left(l + \frac{2x_c(0)\gamma_2 - l\gamma_2}{2\gamma_1 + \gamma_2} \left(1 - e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t} \right) - 2x_1 \right) \\ & + \alpha \left(\frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} + \frac{2x_c(0)\gamma_1 - l\gamma_1}{2\gamma_1 + \gamma_2} e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t} - x_1 \right). \end{aligned}$$

This will have a unique solution.

2.3 SUMMARY AND CONCLUSION OF THE CELL SYSTEM WITH TWO CELLS AND ONE C-SITE

This gives a way for determining explicitly a solution \mathbf{x} to the original system (2.1):

- $x_1(t)$ satisfies the differential equation:

$$\begin{aligned} \gamma_1 \dot{x}_1 = & -f \left(l + \frac{2x_c(0)\gamma_2 - l\gamma_2}{2\gamma_1 + \gamma_2} \left(1 - e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t} \right) - 2x_1 \right) \\ & + \alpha \left(\frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} + \frac{2x_c(0)\gamma_1 - l\gamma_1}{2\gamma_1 + \gamma_2} e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t} - x_1 \right) \end{aligned}$$

with $x_1(0) = 0$.

- $x_2 = l - x_1 + \frac{\gamma_2}{\gamma_1}(x_c(0) - x_c(t))$
- $y_1(t) = \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} - \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t}$
- $y_2(t) = \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} - \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t}$
- $x_c(t) = \frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} + \frac{2x_c(0)\gamma_1 - l\gamma_1}{2\gamma_1 + \gamma_2} e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t}$
- $y_c(t) = \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} + \frac{2y_c(0)\gamma_1}{2\gamma_1 + \gamma_2} e^{-\alpha(\gamma_1^{-1} + 2\gamma_2^{-1})t}$

The equilibrium associated with system (2.1) may also be written explicitly as

$$\lim_{t \rightarrow \infty} \mathbf{x}(t) = \begin{pmatrix} \frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} - \frac{r_0}{2} \\ \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} \\ \frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} + \frac{r_0}{2} \\ \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} \\ \frac{x_c(0)\gamma_2 + l\gamma_1}{2\gamma_1 + \gamma_2} \\ \frac{y_c(0)\gamma_2}{2\gamma_1 + \gamma_2} \end{pmatrix}.$$

CHAPTER 3. MULTIPLE C-SITES BETWEEN PAIRS OF CELLS

It is sometimes the case that a pair of cells may be attached by more than one c-site. Hookean cell systems of type 1 have c-sites of identical parameters, meaning, they all share the same drag coefficient and pseudopodia spring constant. In this chapter we explore Hookean cell system of type 1 analogous to that occurrence. This will be very useful in our eventual study of cell systems in much more generality. We begin by considering Hookean cell system of type 1 with two cells and m c-sites, where m is some positive integer. Principally, it would be good to know if this system can be simplified and perhaps become suitable to applying the results of Chapter Two.

A main result in this chapter is the general c-site reduction theorem which roughly states that given a Hookean cell system of type 2 \mathfrak{H} in which two cells are connected by some number of c-sites there, exists an analogous Hookean cell system also of type 2 \mathfrak{H}' with the same number of cells but with only one c-site between each pair, provided that pair already had at least one c-site between them in \mathfrak{H} . The c-sites in \mathfrak{H}' have drag coefficients and locations that may be determined along with their pseudopodia spring constant. In \mathfrak{H}' the behavior of the cell centers is identical to that of \mathfrak{H} . So, when only the behavior of the cell centers is desired this theorem allows the system to be simplified considerably.

We begin our study of reducing c-sites with the case of only two cells.

3.1 C-SITE REDUCTION THEOREM

In order to state the theorem more concisely we define a specific projection transformation: let $P_{n,m} : \mathbb{R}^{2n+2m} \rightarrow \mathbb{R}^{2n}$ be defined for $\mathbf{x} = (\mathbf{x}_1, \mathbf{x}_2, \dots, \mathbf{x}_n, \mathbf{c}_1, \mathbf{c}_2, \dots, \mathbf{c}_m)^T \in \mathbb{R}^{2n+2m}$ as

$$P_{n,m}(\mathbf{x}) = (\mathbf{x}_1, \mathbf{x}_2, \dots, \mathbf{x}_n)^T.$$

This projection truncates any information about the c-sites and returns only the locations of the cells. Also, in the following it is handy to use the aforementioned Global Existence

and Uniqueness for Hookean Cell System Models of Type 2 (Theorem 1.3.9).

Now we state the theorem.

Theorem 3.1.1 (c-Site Reduction Theorem). *Let \mathfrak{H} be a Hookean cell system model of type 1 with two cells and m c-sites, $\mathbf{x}^0 \in \Theta_n \times \mathbb{R}^{2m}$, and $\mathbf{x}(t)$ be the solution to $\mathfrak{H}(0, \mathbf{x}^0)$, Then there exist a Hookean cell system model of type 2, \mathfrak{H}' , with two cells and one c-site, such that if $\mathbf{y}(t)$ is a solution to \mathfrak{H}' ,*

$$P_{2,m}(\mathbf{x}(t)) = P_{2,1}(\mathbf{y}(t)) \quad \text{for all } t \in [0, \infty).$$

Furthermore, the drag coefficient of the c-site is $m\gamma_2$, the pseudopodia spring constants are $m\alpha$ and the location of the center of the c-site is

$$\mathbf{c}(t) = \frac{1}{m} \sum_{i=1}^m \mathbf{c}_i(t).$$

A picture illustrating Theorem 3.1.1 is given in Figure 3.1.

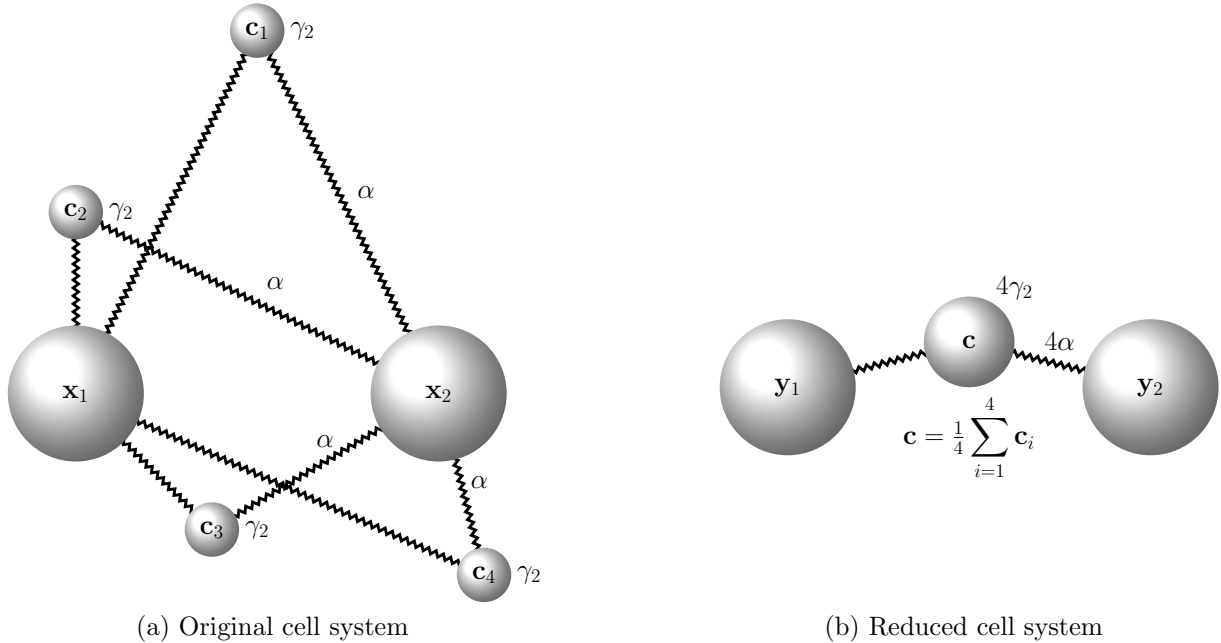


Figure 3.1: Here is a depiction of a cell system with two cells and four c-sites (Figure 3.1a) that is reduced to a system with a single c-site (Figure 3.1b)

Whereas in Figure 3.1a the drag coefficients of each c-site is γ_2 , in Figure 3.1b the drag

coefficient of the single c-site is $4\gamma_2$. The pseudopodia spring constants of Figure 3.1a have likewise been summed together to make the spring constant of the reduced cell system. And the location of the c-sites in Figure 3.1a have been averaged to supply the location of the single c-site in Figure 3.1b. This can be done to the system as a whole. Above is shown a particular instance in time but this is only for illustrative purposes.

Proof. As in the hypothesis of the theorem let $\mathbf{x}(t)$ be the solution to $\mathfrak{H}(0, \mathbf{x}^0)$. This means, since \mathfrak{H} is of type 1, $\mathbf{x}(t)$ satisfies the following IVP

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_1 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_1 - \mathbf{x}_2}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \sum_{i=1}^m \alpha(\mathbf{c}_i - \mathbf{x}_1) \\ \gamma_1 \dot{\mathbf{x}}_2 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_2 - \mathbf{x}_1}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \sum_{i=1}^m \alpha(\mathbf{c}_i - \mathbf{x}_2) \\ \gamma_2 \dot{\mathbf{c}}_1 = \alpha(\mathbf{x}_1 - \mathbf{c}_1) + \alpha(\mathbf{x}_2 - \mathbf{c}_1) \\ \vdots \\ \gamma_2 \dot{\mathbf{c}}_m = \alpha(\mathbf{x}_1 - \mathbf{c}_m) + \alpha(\mathbf{x}_2 - \mathbf{c}_m) \\ \mathbf{x}(0) = \mathbf{x}^0. \end{array} \right. \quad (3.1)$$

Consider what would become of this system if the last m equations (the c-site equations) were added together and a new system was formed as follows:

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_1 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_1 - \mathbf{x}_2}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \sum_{i=1}^m \alpha(\mathbf{c}_i - \mathbf{x}_1) \\ \gamma_1 \dot{\mathbf{x}}_2 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_2 - \mathbf{x}_1}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \sum_{i=1}^m \alpha(\mathbf{c}_i - \mathbf{x}_2) \\ \sum_{i=1}^m \gamma_2 \dot{\mathbf{c}}_i = \sum_{i=1}^m (\alpha(\mathbf{x}_1 - \mathbf{c}_i) + \alpha(\mathbf{x}_2 - \mathbf{c}_i)). \end{array} \right. \quad (3.2)$$

Certainly, \mathbf{x} satisfies (3.2). Now, splitting up sums and rearranging terms slightly, system

(3.2) becomes

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_1 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_1 - \mathbf{x}_2}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha \left(\sum_{i=1}^m \mathbf{c}_i - \sum_{i=1}^m \mathbf{x}_1 \right) \\ \gamma_1 \dot{\mathbf{x}}_2 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_2 - \mathbf{x}_1}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha \left(\sum_{i=1}^m \mathbf{c}_i - \sum_{i=1}^m \mathbf{x}_2 \right) \\ \gamma_2 \sum_{i=1}^m \dot{\mathbf{c}}_i = \alpha \left(\sum_{i=1}^m \mathbf{x}_1 - \sum_{i=1}^m \mathbf{c}_i \right) + \alpha \left(\sum_{i=1}^m \mathbf{x}_2 - \sum_{i=1}^m \mathbf{c}_i \right) \end{array} \right.$$

and then

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_1 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_1 - \mathbf{x}_2}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha m \left(\left(\frac{1}{m} \sum_{i=1}^m \mathbf{c}_i \right) - \mathbf{x}_1 \right) \\ \gamma_1 \dot{\mathbf{x}}_2 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_2 - \mathbf{x}_1}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \alpha m \left(\left(\frac{1}{m} \sum_{i=1}^m \mathbf{c}_i \right) - \mathbf{x}_2 \right) \\ \gamma_2 m \left(\frac{1}{m} \sum_{i=1}^m \dot{\mathbf{c}}_i \right) = \alpha m \left(\mathbf{x}_1 - \frac{1}{m} \sum_{i=1}^m \mathbf{c}_i \right) + \alpha m \left(\mathbf{x}_2 - \frac{1}{m} \sum_{i=1}^m \mathbf{c}_i \right). \end{array} \right. \quad (3.3)$$

Again, observe that \mathbf{x} is a solution to (3.3) but it is not unique, in fact here there are a variety of solutions.

Now, consider the IVP

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{y}}_1 = f(\|\mathbf{y}_1 - \mathbf{y}_2\|) \frac{\mathbf{y}_1 - \mathbf{y}_2}{\|\mathbf{y}_1 - \mathbf{y}_2\|} + \tilde{\alpha}(\mathbf{c} - \mathbf{y}_1) \\ \gamma_1 \dot{\mathbf{y}}_2 = f(\|\mathbf{y}_1 - \mathbf{y}_2\|) \frac{\mathbf{y}_2 - \mathbf{y}_1}{\|\mathbf{y}_1 - \mathbf{y}_2\|} + \tilde{\alpha}(\mathbf{c} - \mathbf{y}_2) \\ \gamma \dot{\mathbf{c}} = \tilde{\alpha}(\mathbf{y}_1 - \mathbf{c}) + \tilde{\alpha}(\mathbf{y}_2 - \mathbf{c}) \\ \mathbf{y}(0) = \mathbf{y}_0 = (\mathbf{x}_1(0), \mathbf{x}_2(0), \frac{1}{m} \sum_{i=1}^m \mathbf{c}_i(0))^T \end{array} \right. \quad (3.4)$$

where $\gamma = \gamma_2 m$, and $\tilde{\alpha} = \alpha m$. Notice that this is a Hookean cell system model of type 2;

label this \mathfrak{H}' . Theorem 1.3.9 guarantees a unique solution $\mathbf{y}(t)$ on $[0, \infty)$ to \mathfrak{H}' . however

$$\tilde{\mathbf{x}} = \begin{pmatrix} \mathbf{x}_1 \\ \mathbf{x}_2 \\ \frac{1}{m} \sum_{i=1}^m \mathbf{c}_i \end{pmatrix}$$

is a solution to \mathfrak{H}' by the uniqueness of solutions to \mathfrak{H}' , it must be that $\mathbf{y}(t) = \tilde{\mathbf{x}}(t)$ on $[0, \infty)$ and so,

$$P_{2,m}(\mathbf{x}(t)) = P_{2,1}(\tilde{\mathbf{x}}(t)) = P_{2,1}(\mathbf{y}(t)) \quad \text{for all } t \in [0, \infty).$$

Observe above from \mathfrak{H}' the parameters of the c-site \mathbf{c} are as promised in the theorem. \square

So, in fact $\mathbf{x}_1(t)$ and $\mathbf{x}_2(t)$ in the solution to \mathfrak{H} move as if there were only one c-site attached to them this c-site having drag coefficient $\gamma_2 m$, spring constant αm and location $\frac{1}{m} \sum_{i=1}^m \mathbf{c}_i(t)$.

3.1.1 Behavior of Multiple c-sites in a Hookean Cell System of Type 1 with

Two Cells. We know that the c-sites may be “combined” into a single average c-site. The work done in Chapter 2 gives the exact steady state solution for a Hookean cell system model of type 2 with two cells and one c-site for any positive values of α and γ_2 . So, a system of many c-sites can easily be solved with an application of Theorem 3.1.1. An interesting question however, is how do the different c-sites move? It is shown that their center of drag moves in the path of a line, but how do the individual c-sites move?

Consider a given Hookean cell system of type 1, \mathfrak{H} . For convenience this is written out

explicitly below

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_1 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_1 - \mathbf{x}_2}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \sum_{i=1}^m \alpha(\mathbf{c}_i - \mathbf{x}_1) \\ \gamma_1 \dot{\mathbf{x}}_2 = f(\|\mathbf{x}_1 - \mathbf{x}_2\|) \frac{\mathbf{x}_2 - \mathbf{x}_1}{\|\mathbf{x}_1 - \mathbf{x}_2\|} + \sum_{i=1}^m \alpha(\mathbf{c}_i - \mathbf{x}_2) \\ \gamma_2 \dot{\mathbf{c}}_1 = \alpha(\mathbf{x}_1 - \mathbf{c}_1) + \alpha(\mathbf{x}_2 - \mathbf{c}_1) \\ \vdots \\ \gamma_2 \dot{\mathbf{c}}_m = \alpha(\mathbf{x}_1 - \mathbf{c}_m) + \alpha(\mathbf{x}_2 - \mathbf{c}_m) \\ \mathbf{x}(0) = ((0, 0), (l, 0), \mathbf{c}_1(0), \mathbf{c}_2(0), \dots, \mathbf{c}_m(0))^T = \mathbf{x}^0. \end{array} \right. \quad (3.5)$$

Proposition 1.3.1 showed that the center of drag of \mathfrak{H} is constant so

$$\frac{\gamma_1(\mathbf{x}_1 + \mathbf{x}_2) + \gamma_2(\mathbf{c}_1 + \dots + \mathbf{c}_m)}{2\gamma_1 + m\gamma_2} = \frac{\gamma_1(\mathbf{x}_1(0) + \mathbf{x}_2(0)) + \gamma_2(\mathbf{c}_1(0) + \dots + \mathbf{c}_m(0))}{2\gamma_1 + m\gamma_2}$$

or rather (since $\mathbf{x}_1(0) = \mathbf{0}$)

$$\mathbf{x}_1 + \mathbf{x}_2 = \mathbf{x}_2(0) + \frac{\gamma_2}{\gamma_1}(\mathbf{c}_1(0) + \dots + \mathbf{c}_m(0) - \mathbf{c}_1 - \dots - \mathbf{c}_m).$$

Now each c-site equations may be written as

$$\gamma_2 \dot{\mathbf{c}}_i = \alpha(\mathbf{x}_1 + \mathbf{x}_2 - 2\mathbf{c}_i)$$

and using the above substitution, can be written as

$$\gamma_2 \dot{\mathbf{c}}_i = \alpha \left(\mathbf{x}_2(0) + \frac{\gamma_2}{\gamma_1}(\mathbf{c}_1(0) + \dots + \mathbf{c}_m(0) - \mathbf{c}_1 - \dots - \mathbf{c}_m) - 2\mathbf{c}_i \right)$$

or better yet,

$$\dot{\mathbf{c}}_i = \frac{\alpha}{\gamma_2} \mathbf{x}_2(0) + \frac{\alpha}{\gamma_1}(\mathbf{c}_1(0) + \dots + \mathbf{c}_m(0) - \mathbf{c}_1 - \dots - \mathbf{c}_m) - \frac{2\alpha}{\gamma_2} \mathbf{c}_i.$$

So, the c -site equations are now uncoupled with the cell equations. The c -site equations form the following system:

$$\left\{ \begin{array}{l} \dot{\mathbf{c}}_1 = -\left(\frac{\alpha}{\gamma_1} - \frac{2\alpha}{\gamma_2}\right)\mathbf{c}_1 - \frac{\alpha}{\gamma_1}\mathbf{c}_2 - \cdots - \frac{\alpha}{\gamma_1}\mathbf{c}_m + \mathbf{k} \\ \dot{\mathbf{c}}_2 = -\frac{\alpha}{\gamma_1}\mathbf{c}_1 - \left(\frac{\alpha}{\gamma_1} - \frac{2\alpha}{\gamma_2}\right)\mathbf{c}_2 - \cdots - \frac{\alpha}{\gamma_1}\mathbf{c}_m + \mathbf{k} \\ \vdots \\ \dot{\mathbf{c}}_m = -\frac{\alpha}{\gamma_1}\mathbf{c}_1 - \frac{\alpha}{\gamma_1}\mathbf{c}_2 - \cdots - \left(\frac{\alpha}{\gamma_1} - \frac{2\alpha}{\gamma_2}\right)\mathbf{c}_m + \mathbf{k} \end{array} \right. \quad (3.6)$$

where $\mathbf{k} = \frac{\alpha}{\gamma_2}\mathbf{x}_2(0) + \frac{\alpha}{\gamma_1}(\mathbf{c}_1(0) + \cdots + \mathbf{c}_m(0))$. Now notice that the x -coordinate equations and the y -coordinate equations are completely uncoupled. This means we can study each set separately. To that end, let

$$\mathbf{c} = \begin{pmatrix} \mathbf{c}_1 \\ \mathbf{c}_2 \\ \vdots \\ \mathbf{c}_m \end{pmatrix}, \quad \mathbf{c}_x = \begin{pmatrix} x_{c1} \\ x_{c2} \\ \vdots \\ x_{cm} \end{pmatrix}, \quad \text{and} \quad \mathbf{c}_y = \begin{pmatrix} y_{c1} \\ y_{c2} \\ \vdots \\ y_{cm} \end{pmatrix}$$

(recall $\mathbf{c}_i = (x_{ci}, y_{ci})$). Similarly let

$$\mathbf{k} = \begin{pmatrix} \mathbf{k} \\ \mathbf{k} \\ \vdots \\ \mathbf{k} \end{pmatrix}, \quad \mathbf{k}_x = \begin{pmatrix} x_k \\ x_k \\ \vdots \\ x_k \end{pmatrix}, \quad \text{and} \quad \mathbf{k}_y = \begin{pmatrix} y_k \\ y_k \\ \vdots \\ y_k \end{pmatrix}$$

where, as would be expected, $\mathbf{k} = (x_k, y_k)$ so

$$x_k = \frac{\alpha l}{\gamma_2} + \frac{\alpha}{\gamma_1}(x_{c1}(0) + \cdots + x_{cm}(0)),$$

$$y_k = \frac{\alpha}{\gamma_1}(y_{c1}(0) + \cdots + y_{cm}(0)).$$

With this in hand, the two uncoupled systems may be written as follows:

$$\left\{ \begin{array}{l} \dot{x}_{c1} = -\left(\frac{\alpha}{\gamma_1} - \frac{2\alpha}{\gamma_2}\right)x_{c1} - \frac{\alpha}{\gamma_1}x_{c2} - \cdots - \frac{\alpha}{\gamma_1}x_{cm} + x_k \\ \dot{x}_{c2} = -\frac{\alpha}{\gamma_1}x_{c1} - \left(\frac{\alpha}{\gamma_1} - \frac{2\alpha}{\gamma_2}\right)x_{c2} - \cdots - \frac{\alpha}{\gamma_1}x_{cm} + x_k \\ \vdots \\ \dot{x}_{cm} = -\frac{\alpha}{\gamma_1}x_{c1} - \frac{\alpha}{\gamma_1}x_{c2} - \cdots - \left(\frac{\alpha}{\gamma_1} - \frac{2\alpha}{\gamma_2}\right)x_{cm} + x_k \end{array} \right. \quad (3.7)$$

$$\left\{ \begin{array}{l} \dot{y}_{c1} = -\left(\frac{\alpha}{\gamma_1} - \frac{2\alpha}{\gamma_2}\right)y_{c1} - \frac{\alpha}{\gamma_1}y_{c2} - \cdots - \frac{\alpha}{\gamma_1}y_{cm} + y_k \\ \dot{y}_{c2} = -\frac{\alpha}{\gamma_1}y_{c1} - \left(\frac{\alpha}{\gamma_1} - \frac{2\alpha}{\gamma_2}\right)y_{c2} - \cdots - \frac{\alpha}{\gamma_1}y_{cm} + y_k \\ \vdots \\ \dot{y}_{cm} = -\frac{\alpha}{\gamma_1}y_{c1} - \frac{\alpha}{\gamma_1}y_{c2} - \cdots - \left(\frac{\alpha}{\gamma_1} - \frac{2\alpha}{\gamma_2}\right)y_{cm} + y_k \end{array} \right. \quad (3.8)$$

These are both initial value problems as each variable was assumed to have a fixed value in \mathbb{R} at $t = 0$. Now, if

$$A = \begin{pmatrix} -\left(\frac{\alpha}{\gamma_1} + \frac{2\alpha}{\gamma_2}\right) & -\frac{\alpha}{\gamma_1} & \cdots & -\frac{\alpha}{\gamma_1} \\ -\frac{\alpha}{\gamma_1} & -\left(\frac{\alpha}{\gamma_1} + \frac{2\alpha}{\gamma_2}\right) & \cdots & -\frac{\alpha}{\gamma_1} \\ \vdots & \vdots & \ddots & \vdots \\ -\frac{\alpha}{\gamma_1} & -\frac{\alpha}{\gamma_1} & \cdots & -\left(\frac{\alpha}{\gamma_1} + \frac{2\alpha}{\gamma_2}\right) \end{pmatrix}$$

then the systems (3.7) and (3.8) may be written in matrix form as

$$\dot{\mathbf{c}}_x = A\mathbf{c}_x + \mathbf{k}_x \quad \text{and} \quad \dot{\mathbf{c}}_y = A\mathbf{c}_y + \mathbf{k}_y,$$

respectively.

The eigenvalues of A for $m \geq 2$ are $-2\frac{\alpha}{\gamma_2}$ with multiplicity $m - 1$ and $-2\frac{\alpha}{\gamma_2} - m\frac{\alpha}{\gamma_1}$ with multiplicity 1. The eigenvector associated with $\lambda_m = -2\frac{\alpha}{\gamma_2} - m\frac{\alpha}{\gamma_1}$ is $\boldsymbol{\xi}_m = (1, 1, \dots, 1)^T \in \mathbb{R}^m$

and the eigenvectors associated with $\lambda_1 = -2\frac{\alpha}{\gamma_2}$ are

$$\boldsymbol{\xi}_1 = \begin{pmatrix} -1 \\ 1 \\ 0 \\ 0 \\ \vdots \\ 0 \end{pmatrix}, \boldsymbol{\xi}_2 = \begin{pmatrix} -1 \\ 0 \\ 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix}, \dots, \boldsymbol{\xi}_{m-1} = \begin{pmatrix} -1 \\ 0 \\ 0 \\ \vdots \\ 0 \\ 1 \end{pmatrix}.$$

Notice these eigenvectors are all linearly independent. So, to solve systems (3.7) and (3.8) we first specify that because they are fundamentally the same they will be treated simultaneously as

$$\dot{\mathbf{c}}_\iota = A\mathbf{c}_\iota + \mathbf{k}_\iota \quad (3.9)$$

for $\iota = x, y$. The approach will be to find the complementary solution to (3.9) and then add to it the particular solution $\hat{\mathbf{c}}_\iota = -A^{-1}\mathbf{k}_\iota$. Notice that $\mathbf{k}_\iota = \iota_k \boldsymbol{\xi}_m$ and recall that a matrix has the same eigenvectors as its inverse but the associated eigenvalues are reciprocals (multiplicative inverses) meaning

$$\hat{\mathbf{c}}_\iota = -A^{-1}\mathbf{k}_\iota = -A^{-1}(\iota_k \boldsymbol{\xi}_m) = -\iota_k A^{-1}\boldsymbol{\xi}_m = -\frac{\iota_k}{\lambda_m} \boldsymbol{\xi}_m = -\frac{1}{\lambda_m} \mathbf{k}_\iota.$$

Now these define a particular¹ solution $\hat{\mathbf{c}}_\iota$ of system (3.7) or (3.8) according to which variable, x or y , to which ι refers. Now, we seek the complementary solution.

¹The word ‘‘particular’’ is used in a technical sense to mean any solution to a nonhomogeneous system (see [8]).

So, the fundamental matrix to the solution (3.9) yields

$$\mathbf{\Psi}(t) = \begin{pmatrix} -e^{-2\frac{\alpha}{\gamma_2}t} & -e^{-2\frac{\alpha}{\gamma_2}t} & -e^{-2\frac{\alpha}{\gamma_2}t} & \dots & -e^{-2\frac{\alpha}{\gamma_2}t} & e^{-(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1})t} \\ e^{-2\frac{\alpha}{\gamma_2}t} & 0 & 0 & \dots & 0 & e^{-(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1})t} \\ 0 & e^{-2\frac{\alpha}{\gamma_2}t} & 0 & \dots & 0 & e^{-(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1})t} \\ 0 & 0 & e^{-2\frac{\alpha}{\gamma_2}t} & \dots & 0 & e^{-(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1})t} \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & e^{-2\frac{\alpha}{\gamma_2}t} & e^{-(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1})t} \end{pmatrix}.$$

Now to find the vector $\mathbf{l}_i \in \mathbb{R}^m$ such that $\mathbf{c}_i(0) = \mathbf{\Psi}(0)\mathbf{l}_i + \hat{\mathbf{c}}_i$. Solving for \mathbf{l}_i , it is found that $\mathbf{l}_i = \mathbf{\Psi}(0)^{-1}(\mathbf{c}_i(0) + A^{-1}\mathbf{k}_i) = \mathbf{\Psi}(0)^{-1}\mathbf{c}_i(0) + \mathbf{\Psi}(0)^{-1}A^{-1}\mathbf{k}_i$. We will construct this vector in parts. First, consider the inverse matrix of $\mathbf{\Psi}(0)$, shown here

$$\mathbf{\Psi}(0)^{-1} = \frac{1}{m} \begin{pmatrix} -1 & m-1 & -1 & -1 & \dots & -1 \\ -1 & -1 & m-1 & -1 & \dots & -1 \\ -1 & -1 & -1 & m-1 & \dots & -1 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ -1 & -1 & -1 & -1 & \dots & m-1 \\ 1 & 1 & 1 & 1 & \dots & 1 \end{pmatrix}.$$

So, to get the first part we multiply by $\mathbf{c}_\iota(0)$

$$\begin{aligned} \Psi(0)^{-1}\mathbf{c}_\iota(0) &= \frac{1}{m} \begin{pmatrix} -\iota_{c1}(0) + (m-1)\iota_{c2}(0) - \iota_{c3}(0) - \iota_{c4}(0) - \dots - \iota_{cm}(0) \\ -\iota_{c1}(0) - \iota_{c2}(0) + (m-1)\iota_{c3}(0) - \iota_{c4}(0) - \dots - \iota_{cm}(0) \\ \vdots \\ -\iota_{c1}(0) - \iota_{c2}(0) - \iota_{c3}(0) - \iota_{c4}(0) - \dots + (m-1)\iota_{cm}(0) \\ \iota_{c1}(0) + \iota_{c2}(0) + \iota_{c3}(0) + \iota_{c4}(0) + \dots + \iota_{cm}(0) \end{pmatrix} \\ &= \frac{1}{m} \begin{pmatrix} m\iota_{c2}(0) - \sum_{i=1}^m \iota_{ci}(0) \\ m\iota_{c3}(0) - \sum_{i=1}^m \iota_{ci}(0) \\ \vdots \\ m\iota_{cm}(0) - \sum_{i=1}^m \iota_{ci}(0) \\ \sum_{i=1}^m \iota_{ci}(0) \end{pmatrix}. \end{aligned}$$

For the other part $\Psi(0)^{-1}A^{-1}\mathbf{k}_\iota$, the vector $A^{-1}\mathbf{k}_\iota$ has already been computed. So, we now just multiply:

$$\Psi(0)^{-1}A^{-1}\mathbf{k}_\iota = \Psi(0)^{-1} \begin{pmatrix} \iota_k \\ \lambda_m \boldsymbol{\xi}_m \end{pmatrix} = \frac{\iota_k}{\lambda_m} \Psi(0)^{-1}\boldsymbol{\xi} = \frac{\iota_k}{\lambda_m} \begin{pmatrix} 0 \\ \vdots \\ 0 \\ 1 \end{pmatrix} = \begin{pmatrix} 0 \\ \vdots \\ 0 \\ \frac{-\iota_k \gamma_1 \gamma_2}{\alpha(m\gamma_2 + 2\gamma_1)} \end{pmatrix}.$$

Now, the assignment of ι becomes important in simplifying the last component of $\Psi(0)^{-1}A^{-1}\mathbf{k}_\iota$,

so for $\iota = x$

$$\begin{aligned}
\frac{-x_k \gamma_1 \gamma_2}{\alpha(m\gamma_2 + 2\gamma_1)} &= \frac{-\gamma_1 \gamma_2}{\alpha(m\gamma_2 + 2\gamma_1)} \left(\frac{\alpha l}{\gamma_2} + \frac{\alpha}{\gamma_1} (x_{c1}(0) + x_{c1}(0) + \cdots + x_{cm}(0)) \right) \\
&= -\frac{1}{\alpha(m\gamma_2 + 2\gamma_1)} (\alpha\gamma_1 l + \alpha\gamma_2 (x_{c1}(0) + x_{c2}(0) + \cdots + x_{cm}(0))) \\
&= -\frac{1}{m\gamma_2 + 2\gamma_1} \left(\gamma_1 l + \gamma_2 \sum_{i=1}^m x_{ci}(0) \right),
\end{aligned}$$

and for $\iota = y$

$$\begin{aligned}
\frac{-y_k \gamma_1 \gamma_2}{\alpha(m\gamma_2 + 2\gamma_1)} &= \frac{-\gamma_1 \gamma_2}{\alpha(m\gamma_2 + 2\gamma_1)} \left(\frac{\alpha}{\gamma_1} (y_{c1}(0) + y_{c2}(0) + \cdots + y_{cm}(0)) \right) \\
&= -\frac{\gamma_2}{m\gamma_2 + 2\gamma_1} \sum_{i=1}^m y_{ci}(0).
\end{aligned}$$

Now putting these together, we find

$$\begin{aligned}
\mathbf{l}_x &= \mathbf{\Psi}(0)^{-1} \mathbf{c}_x(0) + \mathbf{\Psi}(0)^{-1} A^{-1} \mathbf{k}_x \\
&= \frac{1}{m} \begin{pmatrix} mx_{c2}(0) - \sum_{i=1}^m x_{ci}(0) \\ mx_{c3}(0) - \sum_{i=1}^m x_{ci}(0) \\ \vdots \\ mx_{cm}(0) - \sum_{i=1}^m x_{ci}(0) \\ \sum_{i=1}^m x_{ci}(0) \end{pmatrix} + \begin{pmatrix} 0 \\ 0 \\ \vdots \\ 0 \\ -\frac{1}{m\gamma_2+2\gamma_1} \left(\gamma_1 l + \gamma_2 \sum_{i=1}^m x_{ci}(0) \right) \end{pmatrix} \\
&= \begin{pmatrix} x_{c2}(0) - \frac{1}{m} \sum_{i=1}^m x_{ci}(0) \\ x_{c3}(0) - \frac{1}{m} \sum_{i=1}^m x_{ci}(0) \\ \vdots \\ x_{cm}(0) - \frac{1}{m} \sum_{i=1}^m x_{ci}(0) \\ -\frac{\gamma_1 l}{m\gamma_2+2\gamma_1} + \frac{2\gamma_1}{m(m\gamma_2+2\gamma_1)} \sum_{i=1}^m x_{ci}(0) \end{pmatrix},
\end{aligned}$$

and

$$\begin{aligned}
\mathbf{l}_y &= \mathbf{\Psi}(0)^{-1} \mathbf{c}_y(0) + \mathbf{\Psi}(0)^{-1} A^{-1} \mathbf{k}_y \\
&= \begin{pmatrix} y_{c2}(0) - \frac{1}{m} \sum_{i=1}^m y_{ci}(0) \\ y_{c3}(0) - \frac{1}{m} \sum_{i=1}^m y_{ci}(0) \\ \vdots \\ y_{cm}(0) - \frac{1}{m} \sum_{i=1}^m y_{ci}(0) \\ \frac{2\gamma_1}{m(m\gamma_2+2\gamma_1)} \sum_{i=1}^m y_{ci}(0) \end{pmatrix}.
\end{aligned}$$

And so $\mathbf{c}_i = \Psi(t)\mathbf{l}_i + \hat{\mathbf{c}}_i$,

$$\begin{aligned}
\mathbf{c}_x &= \begin{pmatrix} -e^{-2\frac{\alpha}{\gamma_2}t} & -e^{-2\frac{\alpha}{\gamma_2}t} & -e^{-2\frac{\alpha}{\gamma_2}t} & \dots & -e^{-2\frac{\alpha}{\gamma_2}t} & e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} \\ e^{-2\frac{\alpha}{\gamma_2}t} & 0 & 0 & \dots & 0 & e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} \\ 0 & e^{-2\frac{\alpha}{\gamma_2}t} & 0 & \dots & 0 & e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} \\ 0 & 0 & e^{-2\frac{\alpha}{\gamma_2}t} & \dots & 0 & e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & e^{-2\frac{\alpha}{\gamma_2}t} & e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} \end{pmatrix} \begin{pmatrix} \sum_{i=1}^m x_{ci}(0) \\ \sum_{i=1}^m x_{ci}(0) \\ \vdots \\ \sum_{i=1}^m x_{ci}(0) \\ -\frac{\gamma_1 l}{m\gamma_2+2\gamma_1} + \frac{(m-1)\gamma_2+2\gamma_1}{m\gamma_2+2\gamma_1} \sum_{i=1}^m x_{ci}(0) \end{pmatrix} + \hat{\mathbf{c}}_x \\
&= \begin{pmatrix} \left(x_{c1}(0) - \frac{1}{m} \sum_{i=1}^m x_{ci}(0) \right) e^{-2\frac{\alpha}{\gamma_2}t} + \left(-\frac{\gamma_1 l}{m\gamma_2+2\gamma_1} + \frac{2\gamma_1}{m(m\gamma_2+2\gamma_1)} \sum_{i=1}^m x_{ci}(0) \right) e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} \\ \left(x_{c2}(0) - \frac{1}{m} \sum_{i=1}^m x_{ci}(0) \right) e^{-2\frac{\alpha}{\gamma_2}t} + \left(-\frac{\gamma_1 l}{m\gamma_2+2\gamma_1} + \frac{2\gamma_1}{m(m\gamma_2+2\gamma_1)} \sum_{i=1}^m x_{ci}(0) \right) e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} \\ \left(x_{c3}(0) - \frac{1}{m} \sum_{i=1}^m x_{ci}(0) \right) e^{-2\frac{\alpha}{\gamma_2}t} + \left(-\frac{\gamma_1 l}{m\gamma_2+2\gamma_1} + \frac{2\gamma_1}{m(m\gamma_2+2\gamma_1)} \sum_{i=1}^m x_{ci}(0) \right) e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} \\ \vdots \\ \left(x_{cm}(0) - \frac{1}{m} \sum_{i=1}^m x_{ci}(0) \right) e^{-2\frac{\alpha}{\gamma_2}t} + \left(-\frac{\gamma_1 l}{m\gamma_2+2\gamma_1} + \frac{2\gamma_1}{m(m\gamma_2+2\gamma_1)} \sum_{i=1}^m x_{ci}(0) \right) e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} \end{pmatrix} \\
&= \begin{pmatrix} \left(x_{c1}(0) - \frac{1}{m} \sum_{i=1}^m x_{ci}(0) \right) \left(\gamma_1 l + \gamma_2 \sum_{i=1}^m x_{ci}(0) \right) \\ \left(x_{c2}(0) - \frac{1}{m} \sum_{i=1}^m x_{ci}(0) \right) \left(\gamma_1 l + \gamma_2 \sum_{i=1}^m x_{ci}(0) \right) \\ \left(x_{c3}(0) - \frac{1}{m} \sum_{i=1}^m x_{ci}(0) \right) \left(\gamma_1 l + \gamma_2 \sum_{i=1}^m x_{ci}(0) \right) \\ \vdots \\ \left(x_{cm}(0) - \frac{1}{m} \sum_{i=1}^m x_{ci}(0) \right) \left(\gamma_1 l + \gamma_2 \sum_{i=1}^m x_{ci}(0) \right) \end{pmatrix}
\end{aligned}$$

Similarly,

$$\mathbf{c}_y = \begin{pmatrix} \left(y_{c1}(0) - \frac{1}{m} \sum_{i=1}^m y_{ci}(0) \right) e^{-2\frac{\alpha}{\gamma_2}t} + \left(\frac{2\gamma_1}{m(m\gamma_2+2\gamma_1)} \sum_{i=1}^m y_{ci}(0) \right) e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} + \frac{\gamma_2}{m\gamma_2+2\gamma_1} \sum_{i=1}^m y_{ci}(0) \\ \left(y_{c2}(0) - \frac{1}{m} \sum_{i=1}^m y_{ci}(0) \right) e^{-2\frac{\alpha}{\gamma_2}t} + \left(\frac{2\gamma_1}{m(m\gamma_2+2\gamma_1)} \sum_{i=1}^m y_{ci}(0) \right) e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} + \frac{\gamma_2}{m\gamma_2+2\gamma_1} \sum_{i=1}^m y_{ci}(0) \\ \left(y_{c3}(0) - \frac{1}{m} \sum_{i=1}^m y_{ci}(0) \right) e^{-2\frac{\alpha}{\gamma_2}t} + \left(\frac{2\gamma_1}{m(m\gamma_2+2\gamma_1)} \sum_{i=1}^m y_{ci}(0) \right) e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} + \frac{\gamma_2}{m\gamma_2+2\gamma_1} \sum_{i=1}^m y_{ci}(0) \\ \vdots \\ \left(y_{cm}(0) - \frac{1}{m} \sum_{i=1}^m y_{ci}(0) \right) e^{-2\frac{\alpha}{\gamma_2}t} + \left(\frac{2\gamma_1}{m(m\gamma_2+2\gamma_1)} \sum_{i=1}^m y_{ci}(0) \right) e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} + \frac{\gamma_2}{m\gamma_2+2\gamma_1} \sum_{i=1}^m y_{ci}(0) \end{pmatrix}.$$

And so,

$$\mathbf{c}_j(t) = \begin{pmatrix} \left(x_{cj}(0) - \frac{1}{m} \sum_{i=1}^m x_{ci}(0) \right) e^{-2\frac{\alpha}{\gamma_2}t} + \left(-\frac{\gamma_1 l}{m\gamma_2+2\gamma_1} + \frac{2\gamma_1}{m(m\gamma_2+2\gamma_1)} \sum_{i=1}^m x_{ci}(0) \right) e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} + \frac{1}{m\gamma_2+2\gamma_1} \left(\gamma_1 l + \gamma_2 \sum_{i=1}^m x_{ci}(0) \right) \\ \left(y_{cj}(0) - \frac{1}{m} \sum_{i=1}^m y_{ci}(0) \right) e^{-2\frac{\alpha}{\gamma_2}t} + \left(\frac{2\gamma_1}{m(m\gamma_2+2\gamma_1)} \sum_{i=1}^m y_{ci}(0) \right) e^{-\left(2\frac{\alpha}{\gamma_2}+m\frac{\alpha}{\gamma_1}\right)t} + \frac{\gamma_2}{m\gamma_2+2\gamma_1} \sum_{i=1}^m y_{ci}(0) \end{pmatrix} \quad (3.10)$$

notice that, for each $j = 1, 2, \dots, m$, $\mathbf{c}_j(0) = (x_{cj}(0), y_{cj}(0))$.

Observe that if $m = 1$ (3.10) agrees with (2.10) and (2.11). Now we seek to verify that the center of drag is constant at least until the system enters the support of f for the above solutions. So, summing the x -coordinates of the solution gives

$$\sum_{j=1}^m x_{cj}(t) = \frac{-m\gamma_1 l + 2\gamma_1 \sum_{i=1}^m x_{ci}(0)}{m\gamma_2 + 2\gamma_1} e^{-(2\frac{\alpha}{\gamma_2} + m\frac{\alpha}{\gamma_1})t} + \frac{lm\gamma_1 + m\gamma_2 \sum_{i=1}^m x_{ci}(0)}{m\gamma_2 + 2\gamma_1}. \quad (3.11)$$

Now, by the c-site reduction theorem the solutions for the x -coordinates are

$$x_1(t) = \frac{l\gamma_1 + \gamma_2 \sum_{i=1}^m x_{ci}(0)}{2\gamma_1 + m\gamma_2} - \frac{l}{2} e^{-\frac{m\alpha t}{\gamma_1}} + \frac{lm\gamma_2 - 2\gamma_2 \sum_{i=1}^m x_{ci}(0)}{2(2\gamma_1 + m\gamma_2)} e^{-(2\frac{\alpha}{\gamma_2} + m\frac{\alpha}{\gamma_1})t}, \quad (3.12)$$

$$x_2(t) = \frac{l\gamma_1 + \gamma_2 \sum_{i=1}^m x_{ci}(0)}{2\gamma_1 + m\gamma_2} + \frac{l}{2} e^{-\frac{m\alpha t}{\gamma_1}} + \frac{lm\gamma_2 - 2\gamma_2 \sum_{i=1}^m x_{ci}(0)}{2(2\gamma_1 + m\gamma_2)} e^{-(2\frac{\alpha}{\gamma_2} + m\frac{\alpha}{\gamma_1})t}, \quad (3.13)$$

and

$$x_1(t) + x_2(t) = \frac{2l\gamma_1 + 2\gamma_2 \sum_{i=1}^m x_{ci}(0)}{2\gamma_1 + m\gamma_2} + \frac{lm\gamma_2 - 2\gamma_2 \sum_{i=1}^m x_{ci}(0)}{2\gamma_1 + m\gamma_2} e^{-(2\frac{\alpha}{\gamma_2} + m\frac{\alpha}{\gamma_1})t}.$$

So,

$$\begin{aligned} & \gamma_2 \sum_{j=1}^m x_{cj}(t) + \gamma_1 (x_1(t) + x_2(t)) \\ &= \gamma_2 \left(\frac{-1m\gamma_1 + 2\gamma_1 \sum_{i=1}^m x_{ci}(0)}{m\gamma_2 + 2\gamma_1} e^{-(2\frac{\alpha}{\gamma_2} + m\frac{\alpha}{\gamma_1})t} + \frac{lm\gamma_1 + m\gamma_2 \sum_{i=1}^m x_{ci}(0)}{m\gamma_2 + 2\gamma_1} \right) \\ & \quad + \gamma_1 \left(\frac{2l\gamma_1 + 2\gamma_2 \sum_{i=1}^m x_{ci}(0)}{2\gamma_1 + m\gamma_2} + \frac{lm\gamma_2 - 2\gamma_2 \sum_{i=1}^m x_{ci}(0)}{2\gamma_1 + m\gamma_2} e^{-(2\frac{\alpha}{\gamma_2} + m\frac{\alpha}{\gamma_1})t} \right) \\ &= \frac{lm\gamma_1\gamma_2 + m\gamma_2^2 \sum_{i=1}^m x_{ci}(0)}{m\gamma_2 + 2\gamma_1} + \frac{2l\gamma_1^2 + 2\gamma_1\gamma_2 \sum_{i=1}^m x_{ci}(0)}{2\gamma_1 + m\gamma_2} \\ &= \frac{m\gamma_2 (l\gamma_1 + \gamma_2 \sum_{i=1}^m x_{ci}(0)) + 2\gamma_1 (l\gamma_1 + \gamma_2 \sum_{i=1}^m x_{ci}(0))}{2\gamma_1 + m\gamma_2} \\ &= l\gamma_1 + \gamma_2 \sum_{i=1}^m x_{ci}(0). \end{aligned}$$

Similarly for y -coordinates since,

$$\sum_{j=1}^m y_{cj}(t) = \frac{2\gamma_1 \sum_{i=1}^m y_{ci}(0)}{m\gamma_2 + 2\gamma_1} e^{-(2\frac{\alpha}{\gamma_2} + m\frac{\alpha}{\gamma_1})t} + \frac{m\gamma_2 \sum_{i=1}^m y_{ci}(0)}{m\gamma_2 + 2\gamma_1} \quad (3.14)$$

and

$$y_1(t) + y_2(t) = \frac{2\gamma_2 \sum_{i=1}^m y_{ci}(0)}{2\gamma_1 + m\gamma_2} + \frac{-2\gamma_2 \sum_{i=1}^m y_{ci}(0)}{2\gamma_1 + m\gamma_2} e^{-(2\frac{\alpha}{\gamma_2} + m\frac{\alpha}{\gamma_1})t},$$

$$\gamma_2 \sum_{j=1}^m y_{cj}(t) + \gamma_1 (y_1(t) + y_2(t)) = \gamma_2 \sum_{i=1}^m y_{ci}(0).$$

Now, using the theorem just proven, the cell centers' behavior in system (3.5) on page 72 is the same as how the cell centers behave in the system with a single c-site of drag coefficient $m\gamma_2$, spring constant $m\alpha$, and residing at the point $\frac{1}{m} \sum_{i=1}^m \mathbf{c}_i$.

3.2 GENERAL REDUCTION THEOREM

Consider now a more general cell system with n cells and between the cell centers \mathbf{x}_i and \mathbf{x}_j ($i \neq j$) there are $n_{i,j}$ c-sites. An example of such is depicted in Figure 3.2.

The question is: can the c-site reduction theorem be applied to a pair of cells connected in a larger cell system? Consider the Hookean cell system model of type 1, \mathfrak{H} (again displayed below for convenience)

We now state the theorem:

Theorem 3.2.1 (General c-Site Reduction Theorem). *Let \mathfrak{H} be a Hookean cell system model of type 1 with n cells and m c-sites, $\mathbf{x}^0 \in \Theta_n \times \mathbb{R}^{2m}$, and $\mathbf{x}(t)$ be the solution to $\mathfrak{H}(0, \mathbf{x}^0)$. Then there exists a Hookean cell system model of type 2, \mathfrak{H}' , with n cells and $m' = \sum_{i < j} m_{i,j}$*

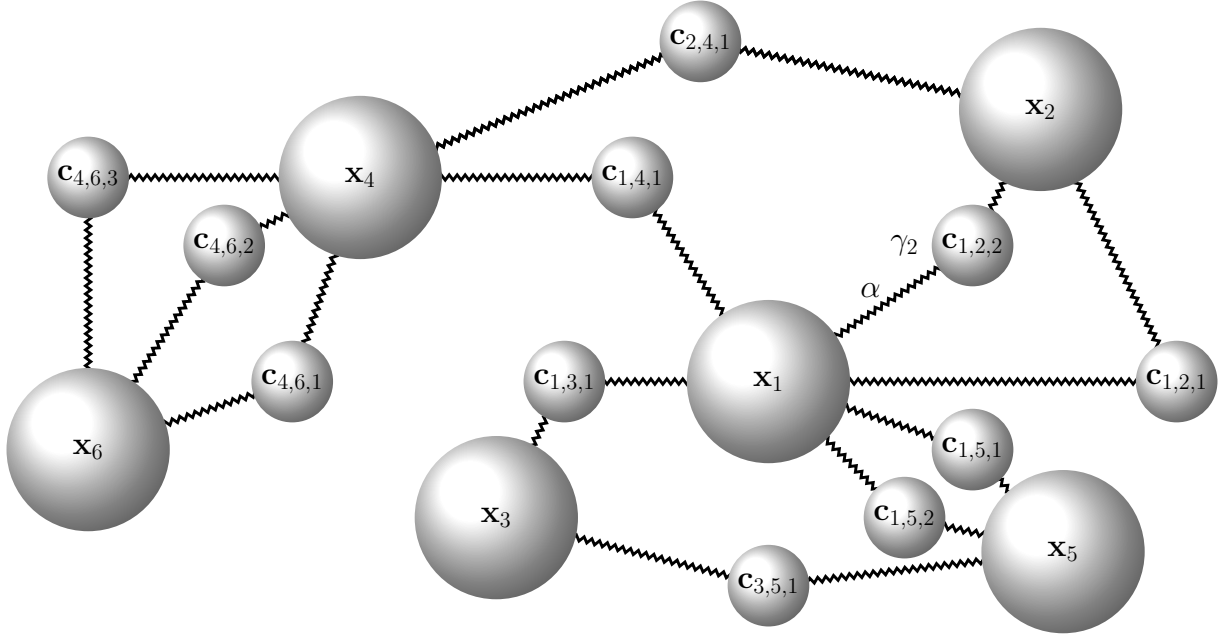


Figure 3.2: The cell system with six cells and with eleven c-sites. This is a Hookean cell system of type 1, note that each c-site has the same drag coefficient of γ_2 and pseudopodia spring constants of α

c-sites, such that if $\mathbf{y}(t)$ is a solution to \mathfrak{H}' ,

$$P_{n,m}(\mathbf{x}(t)) = P_{n,m'}(\mathbf{y}(t)) \quad \text{for all } t \in [0, \infty).$$

In the cell system which generates \mathfrak{H}' , each of the m' *c*-sites connects a unique pair of cells \mathbf{x}_i and \mathbf{x}_j ; this *c*-site will be referred to as $\mathbf{c}_{i,j}$. The drag coefficient $\gamma_{i,j}$ of $\mathbf{c}_{i,j}$ is $n_{i,j}\gamma_2$, the pseudopodia spring constants are $\alpha_{i,j} = n_{i,j}\alpha$ and the location of the center of the *c*-site is

$$\mathbf{c}_{i,j}(t) = \frac{1}{n_{i,j}} \sum_{k=1}^{n_{i,j}} \mathbf{c}_{i,j,k}(t).$$

The theorem is constructive, and shows there exists at least one such cell system with the properties of \mathfrak{H}' , from the statement of the theorem, this we call the *c-site-reduced cell system* of \mathfrak{H} . So, the cell system depicted in Figure 3.2 may be reduced to the cell system with six cells and only seven *c*-sites show in Figure 3.3.

Proof. Let \mathbf{x} be the solution to $\mathfrak{H}(0, \mathbf{x}^0)$. So, if f is the generating function² of the force

²Recall definition on page 11

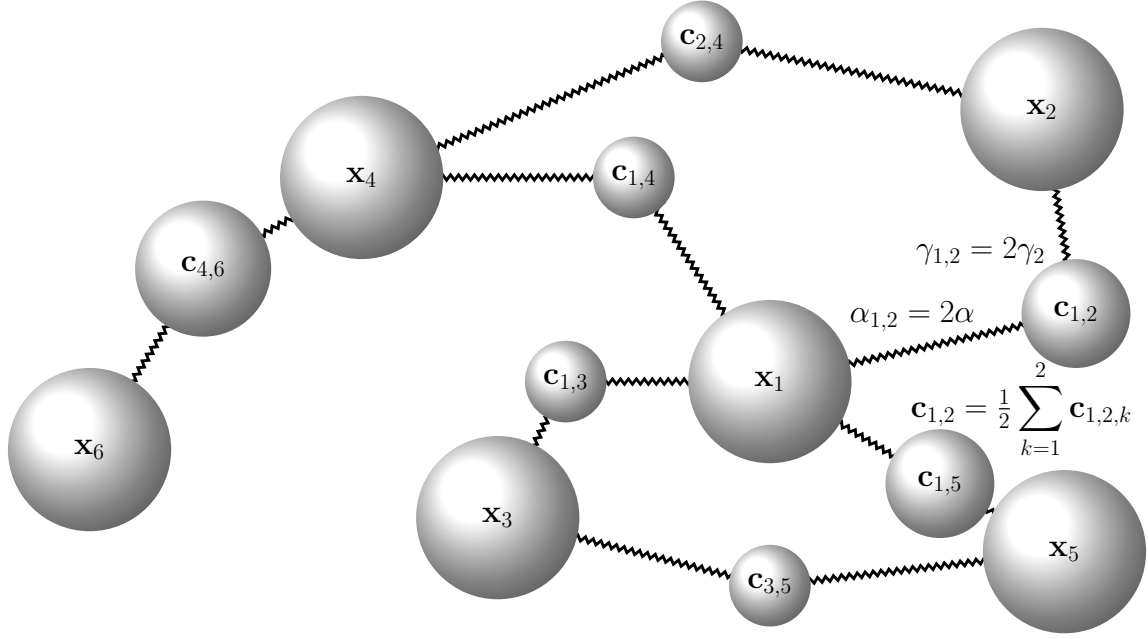


Figure 3.3: Here is the reduced cell system of Figure 3.2. Notice the c-sites attached to the same pair of cells are combined into one c-site with different parameters. In this figure we see that c-sites $\mathbf{c}_{1,2,1}$ and $\mathbf{c}_{1,2,2}$ from Figure 3.2 are substituted for $\mathbf{c}_{1,2}$ this new c-site has drag coefficient $\gamma_{1,2} = 2\gamma_2$, pseudopodia spring constant $\alpha_{1,2} = 2\alpha$, and locations $\mathbf{c}_{1,2} = \frac{1}{2} \sum_{k=1}^2 \mathbf{c}_{1,2,k}$.

function of \mathfrak{H} then $\mathfrak{H}(0, \mathbf{x}^0)$ may be written explicitly as

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_j = \sum_{\substack{i=1 \\ i \neq j}}^n f(\|\mathbf{x}_j - \mathbf{x}_i\|) \frac{\mathbf{x}_j - \mathbf{x}_i}{\|\mathbf{x}_j - \mathbf{x}_i\|} + \sum_{i=1}^n \left(\sum_{k=1}^{n_{i,j}} \alpha(\mathbf{c}_{i,j,k} - \mathbf{x}_j) \right) \\ \gamma_2 \dot{\mathbf{c}}_{i,j,k} = \alpha(\mathbf{x}_i - \mathbf{c}_{i,j,k}) + \alpha(\mathbf{x}_j - \mathbf{c}_{i,j,k}) \\ \mathbf{x}^0 = (\mathbf{x}_1(0), \dots, \mathbf{x}_n(0), \dots, \mathbf{c}_{i,j,k}(0), \dots)^T. \end{array} \right.$$

Now, adding together the c-site equations associated with $\mathbf{c}_{i,j,k}$ for each $k = 1, 2, \dots, n_{i,j}$ and

each appropriate pair³ $i, j = 1, 2, \dots, n$ the following is achieved:

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_j = \sum_{\substack{i=1 \\ i \neq j}}^n f(\|\mathbf{x}_j - \mathbf{x}_i\|) \frac{\mathbf{x}_j - \mathbf{x}_i}{\|\mathbf{x}_j - \mathbf{x}_i\|} + \sum_{i=1}^n \left(\sum_{k=1}^{n_{i,j}} \alpha(\mathbf{c}_{i,j,k} - \mathbf{x}_j) \right) \\ \gamma_2 \sum_{k=1}^{n_{i,j}} \dot{\mathbf{c}}_{i,j,k} = \sum_{k=1}^{n_{i,j}} (\alpha(\mathbf{x}_i - \mathbf{c}_{i,j,k}) + \alpha(\mathbf{x}_j - \mathbf{c}_{i,j,k})) \\ \mathbf{x}^0 = (\mathbf{x}_1(0), \dots, \mathbf{x}_n(0), \dots, \mathbf{c}_{i,j,k}(0), \dots)^T. \end{array} \right.$$

which is equivalent to

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_j = \sum_{\substack{i=1 \\ i \neq j}}^n f(\|\mathbf{x}_j - \mathbf{x}_i\|) \frac{\mathbf{x}_j - \mathbf{x}_i}{\|\mathbf{x}_j - \mathbf{x}_i\|} + \sum_{i=1}^n \alpha \left(\left(\sum_{k=1}^{n_{i,j}} \mathbf{c}_{i,j,k} \right) - n_{i,j} \mathbf{x}_j \right) \\ \gamma_2 \sum_{k=1}^{n_{i,j}} \dot{\mathbf{c}}_{i,j,k} = \alpha \left(n_{i,j} \mathbf{x}_i - \sum_{k=1}^{n_{i,j}} \mathbf{c}_{i,j,k} \right) + \alpha \left(n_{i,j} \mathbf{x}_j - \sum_{k=1}^{n_{i,j}} \mathbf{c}_{i,j,k} \right) \\ \mathbf{x}^0 = (\mathbf{x}_1(0), \dots, \mathbf{x}_n(0), \dots, \mathbf{c}_{i,j,k}(0), \dots)^T. \end{array} \right. \quad (3.15)$$

Now, let

$$\gamma_{i,j} = \gamma_2 n_{i,j} \quad \text{and} \quad \alpha_{i,j} = \alpha n_{i,j}, \quad (3.16)$$

³By appropriate we simply mean for which $n_{i,j} > 0$.

then (3.15) becomes

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_j = \sum_{\substack{i=1 \\ i \neq j}}^n f(\|\mathbf{x}_j - \mathbf{x}_i\|) \frac{\mathbf{x}_j - \mathbf{x}_i}{\|\mathbf{x}_j - \mathbf{x}_i\|} + \sum_{i=1}^n \alpha_{i,j} \left(\left(\frac{1}{n_{i,j}} \sum_{k=1}^{n_{i,j}} \mathbf{c}_{i,j,k} \right) - \mathbf{x}_j \right) \\ \gamma_{i,j} \left(\frac{1}{n_{i,j}} \sum_{k=1}^{n_{i,j}} \dot{\mathbf{c}}_{i,j,k} \right) = \alpha_{i,j} \left(\mathbf{x}_i - \frac{1}{n_{i,j}} \sum_{k=1}^{n_{i,j}} \mathbf{c}_{i,j,k} \right) + \alpha_{i,j} \left(\mathbf{x}_j - \frac{1}{n_{i,j}} \sum_{k=1}^{n_{i,j}} \mathbf{c}_{i,j,k} \right) \\ \mathbf{x}^0 = (\mathbf{x}_1(0), \dots, \mathbf{x}_n(0), \dots, \mathbf{c}_{i,j,k}(0), \dots)^T. \end{array} \right. \quad (3.17)$$

Now, (3.17) is not equivalent to $\mathfrak{H}(0, \mathbf{x}^0)$ but, clearly any solution to $\mathfrak{H}(0, \mathbf{x}^0)$ will be a solution to (3.17).

Consider the following Hookean cell system model of type 2, \mathfrak{H}' defined by

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_j = \sum_{\substack{i=1 \\ i \neq j}}^n f(\|\mathbf{x}_j - \mathbf{x}_i\|) \frac{\mathbf{x}_j - \mathbf{x}_i}{\|\mathbf{x}_j - \mathbf{x}_i\|} + \sum_{i=1}^n \alpha_{i,j} ((\mathbf{c}_{i,j} - \mathbf{x}_j)) \\ \gamma_{i,j} \dot{\mathbf{c}}_{i,j} = \alpha_{i,j} (\mathbf{x}_i - \mathbf{c}_{i,j}) + \alpha_{i,j} (\mathbf{x}_j - \mathbf{c}_{i,j}) \\ \mathbf{y}_0 = (\mathbf{x}_1(0), \dots, \mathbf{x}_n(0), \dots, \frac{1}{n_{i,j}} \sum_{k=1}^{n_{i,j}} \mathbf{c}_{i,j,k}(0), \dots)^T. \end{array} \right. \quad (3.18)$$

By Theorem 1.3.9 there exists a unique solution $\mathbf{y}(t)$. However,

$$\tilde{\mathbf{x}} = \begin{pmatrix} \mathbf{x}_1 \\ \vdots \\ \mathbf{x}_n \\ \vdots \\ \frac{1}{n_{i,j}} \sum_{k=1}^{n_{i,j}} \mathbf{c}_{i,j,k} \\ \vdots \end{pmatrix} \in C(\mathbb{R}, \mathbb{R}^{2n+2m'}) \quad (3.19)$$

is also a solution to \mathfrak{H}' since $\mathbf{x}(t)$ satisfies (3.17). By uniqueness of solutions to \mathfrak{H}' we conclude $\mathbf{y}(t) = \tilde{\mathbf{x}}(t)$ on $[0, \infty)$ and so,

$$P_{n,m}(\mathbf{x}(t)) = P_{n,m'}(\tilde{\mathbf{x}}(t)) = P_{n,m'}(\mathbf{y}(t)) \quad \text{for all } t \in [0, \infty).$$

Then (3.16) and (3.19) justify the remaining claims of the theorem. □

3.3 CONCLUSION

It has been shown that Hookean cell systems of type 1 possessing a multiplicity of c-sites for a pair of cells may be reduced to a simple⁴ system of type 2. Theorems of greater generality may also be shown such as one reducing systems already of type 2 to a simple system of type 2. One difference in that result would probably be that the resultant $\mathbf{c}_{i,j}$ would be a weighted average, weighted according to the various drag coefficients $\gamma_{i,j,k}$. The drag coefficient and pseudopodia spring constant would also have to be modified accordingly. It is likely, then, that the result may be extended to all Hookean cell systems and have a proof similar to the one presented here. A more general result would warrant a different method of proof as that above requires linearity in the $\mathbf{a}_{i,j,k,l}$.

⁴Recall Definition 7 on page 12.

CHAPTER 4. CONCLUSION AND FUTURE WORK

In chapter one we developed language and perspectives that proved to be useful in analyzing in great detail the motion of deterministic¹ cell systems. This included a version of the existence and uniqueness theorem for initial value problems, which was necessary to the results of Chapter Two and Chapter Three. It is certain that these theorems will continue to be helpful in the solving of systems of several cells.

In chapters two we provided an explicit solution to the Hookean cell system model of two cells and a single c-site. This included a discussion of the stability of the equilibria by determining and analyzing the center manifold of an arbitrary equilibrium.

Chapter Three provided a way to extend the work of Chapter Two to cell systems of two cells but several c-sites and explicit solutions were presented for the motion of each of the c-sites. This was accomplished by means of the c-site reduction theorem. The c-site reduction theorem was then generalized to arbitrary Hookean cell systems of type 1. Explicit solutions to Hookean cell system models of type 1 and type 2 of two cells.

4.1 FUTURE WORK

There is tremendous room to expand these results to systems of several cells. To follow, we provide an approach with a few conjectures that may be helpful to that end. The main question this work provides for deals with the Hookean cell system of several cells and c-sites. Such a system can be reduced and studied more readily. Some questions of interest to us are:

1. What are the equilibria of a Hookean cell system of n cells?
2. What is the behavior of the system at that equilibria?
3. What is the next step in modifying the model to make it a closer approximation of the motion of a slug?

¹Here deterministic is used as opposed to a stochastic based cell systems.

4. How can stochastics be introduced to such a frame work?

4.1.1 What are the equilibria of a Hookean cell system of n cells?. Thanks to Theorem 1.3.9 the motion of the cell centers in a Hookean cell system of type 1 may be studied by choosing a particular cell system of type 2 in which there is at most a single c-site connecting any pair of cell centers (recall these are referred to as simple cell systems). This simplifies its corresponding system model because it may have much fewer equations in the IVP. For this discussion it will be helpful to recall (from page 5) that an adjacency graph of a cell system \mathfrak{G} with n cells was the graph G whose adjacency matrix is the $n \times n$ matrix $N = [n_{i,j}]$ and that the reduced adjacency graph for \mathfrak{G} was the simple graph G' whose adjacency matrix was $M = [m_{i,j}]$. Notice that if \mathfrak{G} is a Hookean cell system of type 1 and \mathfrak{G}' its c-site-reduced cell system, then the adjacency graph of the cell system generating \mathfrak{G}' is equal to the reduced adjacency graph of \mathfrak{G} .

To clarify the adjacency graphs are not the same as the graphs in the definition of the cell system.

Let \mathfrak{H} be a Hookean cell system model of type 1, and let \mathfrak{H}' be its c-site-reduced cell model of type 2. Let \mathbf{f} be the force function of \mathfrak{H}' . The following discussion, as in Section 2.2, deals with a cell system independent of its initial conditions. As such, consider the ordinary differential equation form \mathfrak{H}'

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}). \quad (4.1)$$

To find any equilibrium points of (4.1) we set the LHS equal to $\mathbf{0}$. Writing this out we get

$$\left\{ \begin{array}{l} \gamma_1 \dot{\mathbf{x}}_j = \sum_{\substack{i=1 \\ i \neq j}}^n f(\|\mathbf{x}_j - \mathbf{x}_i\|) \frac{\mathbf{x}_j - \mathbf{x}_i}{\|\mathbf{x}_j - \mathbf{x}_i\|} + \sum_{i=1}^n \alpha_{i,j} (\mathbf{c}_{i,j} - \mathbf{x}_j) \\ \gamma_{i,j} \dot{\mathbf{c}}_{i,j} = \alpha_{i,j} (\mathbf{x}_i - \mathbf{c}_{i,j}) + \alpha_{i,j} (\mathbf{x}_j - \mathbf{c}_{i,j}). \end{array} \right. \quad (4.2)$$

Now for each c-site equation for which $\alpha_{i,j} \neq 0$ we may solve for $\mathbf{c}_{i,j}$ achieving

$$\mathbf{c}_{i,j} = \frac{\mathbf{x}_i + \mathbf{x}_j}{2}.$$

Substituting these into the cell equations for any i and j such that $m_{i,j} = 0$ achieves

$$\begin{aligned} 0 &= \sum_{\substack{i=1 \\ i \neq j}}^n \frac{f(\|\mathbf{x}_j - \mathbf{x}_i\|)}{\|\mathbf{x}_i - \mathbf{x}_j\|} (\mathbf{x}_i - \mathbf{x}_j) + \sum_{i=1}^n \alpha_{i,j} \left(\frac{\mathbf{x}_i - \mathbf{x}_j}{2} \right) \\ &= \sum_{\substack{i=1 \\ i \neq j}}^n \left(\frac{f(\|\mathbf{x}_i - \mathbf{x}_j\|)}{\|\mathbf{x}_i - \mathbf{x}_j\|} - \frac{m_{i,j} \alpha_{i,j}}{2} \right) (\mathbf{x}_j - \mathbf{x}_i). \end{aligned}$$

Let

$$\beta_{i,j} := \frac{f(\|\mathbf{x}_i - \mathbf{x}_j\|)}{\|\mathbf{x}_i - \mathbf{x}_j\|} - \frac{m_{i,j} \alpha_{i,j}}{2}$$

and simply define $\beta_{i,j} = 0$. Notice, $\beta_{i,j} = \beta_{j,i}$. So, our equations become for any $j = 1, 2, \dots, n$

$$\begin{aligned} 0 &= \sum_{i=1}^n \beta_{i,j} (\mathbf{x}_j - \mathbf{x}_i) \\ &= \sum_{i=1}^n \beta_{i,j} \mathbf{x}_j - \sum_{i=1}^n \beta_{i,j} \mathbf{x}_i \\ &= \beta_{1,j} \mathbf{x}_1 + \beta_{2,j} \mathbf{x}_2 + \dots + \beta_{j-1,j} \mathbf{x}_{j-1} - \sum_{i=1}^n \beta_{i,j} \mathbf{x}_j + \beta_{j+1,j} \mathbf{x}_{j+1} + \beta_{n,j} \mathbf{x}_n \end{aligned}$$

this gives us the system

$$\left\{ \begin{array}{l} 0 = -\sum_{i=1}^n \beta_{i,1} \mathbf{x}_1 + \beta_{2,1} \mathbf{x}_2 + \beta_{3,1} \mathbf{x}_3 + \dots + \beta_{n,1} \mathbf{x}_n \\ 0 = \beta_{1,2} \mathbf{x}_1 - \sum_{i=1}^n \beta_{i,2} \mathbf{x}_2 + \beta_{3,1} \mathbf{x}_3 + \dots + \beta_{n,2} \mathbf{x}_n \\ 0 = \beta_{1,3} \mathbf{x}_1 + \beta_{2,3} \mathbf{x}_2 - \sum_{i=1}^n \beta_{i,3} \mathbf{x}_3 + \dots + \beta_{n,3} \mathbf{x}_n \\ \vdots \\ 0 = \beta_{1,n} \mathbf{x}_1 + \beta_{2,n} \mathbf{x}_2 + \beta_{3,n} \mathbf{x}_3 + \dots - \sum_{i=1}^n \beta_{i,n} \mathbf{x}_n \end{array} \right. \quad (4.3)$$

Now , let $\mathbf{x}_n = P_{n,m}(\mathbf{x})$ then (4.3) may be written in matrix form if

$$B(\mathbf{x}_n) = \begin{pmatrix} -\sum_{i=1}^n \beta_{i,1} & \beta_{2,1} & \beta_{3,1} & \dots & \beta_{n,1} \\ \beta_{1,2} & -\sum_{i=1}^n \beta_{i,2} & \beta_{3,1} & \dots & \beta_{n,2} \\ \beta_{1,3} & \beta_{2,3} & -\sum_{i=1}^n \beta_{i,3} & \dots & \beta_{n,3} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \beta_{1,n} & \beta_{2,n} & \beta_{3,n} & \dots & -\sum_{i=1}^n \beta_{i,n} \end{pmatrix}$$

as

$$0 = B(\mathbf{x}_n) \mathbf{x}_n.$$

Now as before we seek only solutions for which $\mathbf{x}_n \in \Theta_{n,\epsilon}$. Solving this is equivalent to finding a vector $\mathbf{x}_n \in \Theta_{n,\epsilon}$. Such that the following condition is satisfied:

$$\mathbf{x}_n \in \mathcal{N}(B(\mathbf{x}_n)). \quad (4.4)$$

That this approach is easier than directly analyzing the original system is apparent since now, instead of $n + m$ equation of vectors in \mathbb{R}^2 we have only n . However, this approach

is yet far from easy. It will require a sophisticated understanding of how the nullspace of a matrix from a matrix-valued function changes as the input changes. Methods from fixed point theory may prove instructive in this problem. For our part, we found that there was much in our intuition that needed to be developed. The first approach we took was to recognize that \mathbf{x}_n had to be an element of Θ_n and then to ask what conditions must be on a symmetric, 0 row sum matrix in order to ensure that its nullspace intersects Θ_n . Our investigation of this problem began by asking what sort of matrices A have a nullspace that intersect Θ_n ?

First, note that $B(\mathbf{x}_n)$ is always symmetric and has 0-row sums. This implies that $B(\mathbf{x}_n)$ has a nontrivial nullspace, as the vector $(\mathbf{a}, \mathbf{a}, \dots, \mathbf{a})^T$ will always be in the nullspace for any $\mathbf{a} \in \mathbb{R}^2$. This also demonstrates that $B(\mathbf{x}_n)$ has a eigenvalue of zero.

To study this we started by building intuition using $n \times n$ matrices and dealing with real numbers (as opposed to vectors). To that end, Dr. Gary Lawlor (BYU) and I wrote a program in *Mathematica* to produce several random symmetric, 0-row sum matrices. The *Mathematica* code is provided here:

```
findMO[range_, n_] := Module[{i, j, temp, M, sum},
M = Table[RandomInteger[{-range, range}], {i, 1, n}, {j, 1, n}];
M = (M + Transpose[M]);
For[i = 1, i <= n, i++,
sum = Sum[M[[i, j]], {j, 1, n}];
M[[i, i]] -= sum];
Return[M]
]
```

This allowed us to produce $n \times n$ random matrices with integer coefficients, that are symmetric and have 0-row sum. It was then easy to check whether a matrix produced this way had a nullspace that intersected $\tilde{\Theta}_n = \{\mathbf{x} : \mathbf{x} = (x_1, x_2, \dots, x_n) \in \mathbb{R}^n \text{ and } \prod_{i \neq j} (x_i - x_j) \neq 0\}$

0}. We created the following flag to catch matrices produced by the *findMO* function (with arguments *range*= 10 and *n*= 5) whose null intersected $\tilde{\Theta}_5$:

```
If[Length[NullSpace[U]] > 1,
If[Product[
Product[NullSpace[U][[1, i]] - NullSpace[U][[1, j]], {i,
j - 1}], {j, 2, 5}] != 0, Print["Here!"]];
```

What this code does is checks that the product of the difference of every pair of components of one of the basis vectors of the nullspace is nonzero. That is, it checks whether one of the basis vectors of the nullspace is an element of $\tilde{\Theta}_5$. It is reasonable to check only one vector in the nullspace because most of the nullspaces generated this way had only two dimensions. Using this and similar criteria checks, we arrived at some conjectures which will be introduced after a few definitions.

For ease of notation let S be a set and k be a positive integer no bigger than the cardinality of S . Now let $\wp_k(S) = \{T \in \wp(S) : |T| = k\}$ (where $\wp(S)$ is the power set of S). So, $\wp_k(S)$ is simply the set of all subsets of S which have cardinality k . It will be convenient to use the notation $[n] = \{1, 2, 3, \dots, n\}$ for any positive integer n .

Now, in order to precisely state the conjectures to follow we will need to define an total order \preceq on $\wp_k([n])$. First, for each $S \in \wp_k([n])$ let $G_k(S)$ be the number generated by multiplying powers of the first k consecutive primes. The power of the first prime is the smallest element of S , the power of the second prime is the next smallest power of S and so on. For example, note $\{1, 4, 3, 6\} \in \wp_4([8])$; so,

$$G_4(\{1, 4, 3, 6\}) = 2^1 \cdot 3^3 \cdot 5^4 \cdot 7^6.$$

With this in hand for $S, T \in \wp_k([n])$ we say $S \preceq T$ if and only if $G_k(S) < G_k(T)$. This is a total order since each element of $\wp_k([n])$ is mapped uniquely to some integer (here the fundamental theorem of arithmetic is used). Now, let $\phi_{n,k} : \binom{[n]}{k} \rightarrow \wp_k([n])$ be defined in

terms of the order on the set $\wp_k([n])$; it assigns i to the i th subset in $\wp_k([n])$. Now we will state a few definitions.

Let A be an $n \times n$ matrix.

Definition 9. Let $S, T \subset [n]$ and define the $S \times T$ -submatrix $A_{S,T}$ of A to be the submatrix of A formed by deleting the i th row of A only if $i \notin S$, and by deleting the j th column only if $j \notin T$. The $S \times T$ -minor of A is the determinat of $A_{S,T}$.

Definition 10. The k -minors matrix $M_k(A)$ of a matrix A is the $\binom{n}{k} \times \binom{n}{k}$ matrix in which the i, j -entry is the $\phi_{n,k}(i) \times \phi_{n,k}(j)$ -minor of A . So,

$$(M_k(A))_{i,j} = \det(A_{\phi_{n,k}(i), \phi_{n,k}(j)}).$$

Also, for any matrix A let $\text{rref}(A)$ denote the reduced row echelon form of A .

Conjecture 4.1.1. If B is an symmetric, 0-row sum matrix, then

- (i) $\dim(\mathcal{N}(B)) \geq 2$ if and only if $M_{n-2}(B)$ has rank 1.
- (b) $\mathcal{N}(B) \cap \Theta_n \neq \emptyset$ if and only if the top right $(n-2) \times 2$ -submatrix of $\text{rref}(B)$ has no repeated numbers in a column and contains no zeros.
- (c) $\mathcal{N}(B) \cap \Theta_n \neq \emptyset$ if and only if the top row of $\text{rref}(M_{n-2}(B))$ contains no zeros.

These systems have a variety of symmetries. It has been shown that these symmetries may be used to great effect in simplifying the problem as was seen in Section 2.2.2. A few results to keep in mind are the Theorem 1.3.9 (global existence and uniqueness of the solutions of Hookean cell system models of type 2) and Proposition 1.3.1 (conservation of the center of drag).

4.1.2 What is the behavior of the system at that equilibria? To study the stability of the equilibria we have shown by an example that center manifold theory may be employed and that the set of all equilibria itself formed the center manifold. This finding

was facilitated by the fact that the set of all equilibria could be defined explicitly. It would be interesting to see if such is the case in systems with a greater number of cells.

Another approach may be to suppose that a point is an equilibria and compute the derivative matrix at that point to determine the tangent space of the center manifold (assume there is one, which is likely because there is sure to be a continuum of equilibria). This may then give information of the set of equilibria. A good result to prove might be stated as follows:

Conjecture 4.1.2. *Given a force function \mathbf{f} of some Hookean cell system model \mathfrak{H} , the set equilibria $e(\mathbf{f})$ of the system $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ is exactly the same as it's center manifold.*

4.1.3 What is the next step in modifying the model to make it a closer approximation of the motion of a slug?. After a firm understand of how these cell systems behave in a deterministic (stochastic free) scene the next step would be to include random switching times that govern the attachment and detachment of the c-sites from the cells.

4.1.4 How can stochastics be introduced to such a framework?. And let ψ be a Bernoulli random variable. The *state* of a c-site describes whether or not it is “attached” or “detached.” A c-site is said to be *attached* if it is connected to two cells and *detached* if otherwise. In the model the random variable ψ determines the state of the c-site. If $\psi = 1$ the c-site is attached to both of the cells if $\psi = 0$ the c-site is detached. With these notations in hand we may rewrite system (2.1)

$$\left\{ \begin{array}{l} \gamma_i \dot{\mathbf{x}}_i = \sum_{j=1}^n \mathbf{f}_{i,j}(\mathbf{x}_i, \mathbf{x}_j) - \sum_{j=1}^n \sum_{k=1}^{n_{i,j}} \psi_{i,j,k,1} \mathbf{a}_{i,j,k,1}(\mathbf{x}_i, \mathbf{c}_{i,j,k}) \\ \psi_{i,j,k} \gamma_{i,j,k} \dot{\mathbf{c}}_{i,j,k} = \psi_{i,j,k,1} \mathbf{a}_{i,j,k,1}(\mathbf{x}_i, \mathbf{c}_{i,j,k}) + \psi_{i,j,k,2} \mathbf{a}_{i,j,k,2}(\mathbf{x}_j, \mathbf{c}_{i,j,k}). \end{array} \right. \quad (4.5)$$

where $\psi_{i,j,k} = \max\{\psi_{i,j,k,1}, \psi_{i,j,k,2}\}$ and $\psi_{i,j,k,1} = \psi_{i,j,k,2}$. Here we would require that $\mathbf{c}_{i,j,k}$ be only sectionally, continuously differentiable. This allows for dissolution and reformation of c-sites.

4.2 CONCLUSION

The work here presented is a prime example of simplifying and reducing a problem down to a more tractable level. We began by working on the expected steady state configuration of system (4.5) but it proved to be far from tractable. Then we focused on just the deterministic behavior of a system of several cells and c-sites. Again, with our current understanding it proved to be beyond our capabilities. So, then we boiled down the problem to a deterministic system with only two cells and one c-site. We worked with that obtaining a very rich understanding of the evolution of that system as well as a system with two cells and several c-sites. The reduction theorem came out of this work; it was a thing we had not previously supposed possible. Now, with the discovery that in this small case the center manifold is the same as the set of equilibria, we have a method, far from any we previously considered, that may prove to answer our original question.

This research has been a singular experience which I have enjoyed very much. I feel this problem, though rich in challenges, now has a few sturdy tools which may be used to find what we are looking for.

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