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A 2-DIMENSIONAL MECHANICAL MODEL OF THE FORMATION OF A SOMITE

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Abstract. The mechanochemical model proposed in 1983 by G. Oster, J. D. Murray and A. K. Harris has been deployed to describe various morphological phenomena in biology, such as feather bud formation [17] and angiogenesis and vasculogenesis [10, 13]. In this article, we apply a mechanochemical model to the formation of a somite to better understand the role that the mechanical aspects of the cells and the extracellular matrix (ECM) play in somitogensis. In particular, our focus lies in the effect of the contractile forces generated by the cells, which are exerted onto the surrounding ECM. Our approach involves the linear stability analysis and a study of asymptotic behavior of the cell density based on a priori estimates. The full model considered in 2 dimensional space is numerically simulated to show that the traction force of the cells alone can generate a pattern.

Key words. somites, somitogenesis, mechano-chemical model, traction, linear stability analysis, numerical analysis

1. Introduction

Somites are spherical blocks of the mesodermal cells in vertebrate embryos aligning alongside the notochord, which longitudinally extends underneath the neural tube. In later development, they are the precursors to various organs such as ribs, limbs and dorsal skins [25]. Somitogenesis is the formation of these somites and involves a wide range of mechanisms which are spatially and temporally intertwined [1].

At an early developmental stage, the cells in the bilateral bands of the presomitic mesoderm (PSM) express a variety of adhesive molecules on their surfaces depending on their positions. Particularly, those located at the far anterior end of the mesoderm show higher adhesion than those at the posterior end [25]. Consequently, the cells at the anterior end undergo drastic increase in the density and become compacted to much rounder shape, and eventually they separate themselves into a somite at regular time intervals. Throughout the process of somitogenessis, new cells are added in the posterior end of the PSM due to the cell division and the cells entering from Hensen's node, keeping each band of the PSM approximately constant.

The formation of somites are highly regulated in terms of space and time. Each somite is periodically formed in pair on both sides of the notochord from the anterior end to the posterior end of the PSM [24, 25]. For example, the amount of time required for one somite to form is approximately 30 minutes in case of zebrafish and, for the chick embryo 90 minutes and for the mouse embryo 120 minutes. Furthermore, the total number of somites is characteristic to species: 30, 50 and 65 somites for Zebrafish, chick and mouse embryo, respectively, [8, 24]

There have been several models proposed to explain the formation of somites, among which are the clock and wavefront model first proposed by Cookee and Zeeman [3] and later revised by Pourquié et al. [5, 6], the wave/cell polarization

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model proposed by Polezhaev [19, 20], the Reaction-diffusion model proposed by Meinhardt [12], and the cell-cycle model proposed by Stern et al.[21, 22] and later mathematically formulated by Colliers and his co-workers [2, 11]. The model which we choose to study in this paper is the mechanochemical model, applied to somitogenesis. This model was first introduced by J. D. Murray, G. F. Oster and A. K. Harris in 1983, see [17], and there have been various applications of this model to morphogenetic pattern formation [10, 14, 15, 17, 18, 23]. Compared to the other models mentioned earlier, this model focuses on the mechanical aspects of the cells and their surrounding environment and relies on the measurable quantities such as tissue deformation properties, cell densities and forces [15, 16, 17].

This article is organized as follows. In Section 2, we give a brief overview of the mechanical properties of the mesodermal cells and the ECM and that of their mechanical interaction, followed by the introduction of a mechanochemical model in the context of somitogenesis along with the short explanation of its construction. Then, in Section 3, the linear stability analysis is performed and asymptotic behavior of the cell density is analyzed via linearization of the system and a priori estimates. Finally, in Section 4, we show the discretization of the system and the results of our numerical simulation.

2. Mechanochemical model

The fibroblast cells live and crawl within the fibrous tissue composed of the extracellular matrix (ECM). Their interaction with the surrounding environment can lead to a morphogenic pattern formation in an embryo at an early developmental stage. The characteristic features which enable the cells to move within the fibrous surroundings are broad and flat protrusions, called lamellipodia, and long finger-like protrusions, called filopodia, which extend from the lamellipodia. The filopodia are often assumed to sense the surface of the environment to look for guidance cues. However, since the precise functionalities of the two remain elusive, we will not make distinction between the roles each one takes upon locomotion of the cells. The filopodia (lamellipodia) can attach themselves to the surrounding adhesive sites which include the ECM material points and the surfaces of other cells and then, contract. Since the filopodia extend to all the opposing directions, the resulting situation is just like a tug-of-war and so, the cell migrates in the direction of the net contractile (traction) force. In accordance to the translocation of the cells, the ECM provides further geometric guidance cues directing the cells' movement.

This intricately coordinated mechanical interaction between the cells and the viscoelastic ECM is encapsulated in the mechano-chemical model [17]. In this paper, we will make use of this framework to find out whether the mechanical interaction of the cells with their surrounding environment alone can lead to the formation of a somite. To be more precise, we will numerically experiment to see if the traction forces exerted by the cells onto the ECM are enough to generate a somite.

Now let us introduce the mechanochemical model. Let $\Omega = (0, L_1) \times (0, L_2)$ where L_1, $L_2 > 0$. For each $\mathbf{x} = (x, y) \in \Omega$ and $t > 0$, we define the three variables

$$
\begin{aligned}
n = n(\mathbf{x}, t) &= \text{ the density of cells (cells/cm}^3\text{)}, \\
\rho = \rho(\mathbf{x}, t) &= \text{ the density of ECM (mg /cm}^3\text{)}, \\
\mathbf{u} = \mathbf{u}(\mathbf{x}, t) &= \text{ the displacement vector of the ECM.}
\end{aligned}
\tag{1}
$$