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Interaction of morphogens with geometry

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Abstract

Morphogen patterns are viewed as being affected by epithelial sheet geometry in early development. As the total area of the (closed) sheet changes, the changing geometry acts back in turn to change the morphogen pattern. A number of constraints are given on the functional form of the Gauss and Mean curvatures, considered as functions of the morphogen concentrations and their derivatives. It is shown that the constraints are sufficient to motivate a convincing dependence of the two curvatures on the morphogen concentrations.

1. Introduction

The present work is based on several assumptions. There is a patterning mechanism that provides spatial and temporal information to the genes of multicellular animals. It is considered an important aspect of early development that the geometry of the folding epithelial sheets is not only affected or directed by these morphogen concentrations, but also that the resultant geometry acts in turn to direct the morphogen patterning, and thus the genes. The morphogen concentrations vary along a closed middle epithelial surface with two coordinates, u and v. Such a coupled model system is proposed and discussed.

In particular, the geometry of thick epithelial sheets is discussed with the specific goal of motivating a functional form of the dependence of the Gauss (K) and Mean

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(H) curvatures of the middle epithelial surface on the morphogen concentrations and their first derivatives. The simplest case of constant sheet thickness 'h' is considered at present, although in general, the sheet thickness should also be considered a function of the morphogen concentrations and their derivatives. This latter and important aspect will be the focus of future work.

A striking illustration of shape affecting morphogen patterning was given by Murray [1,2], who showed the changing Turing patterns on animal tails as the radius of the (prescribed as conical) tail changed. It is the goal here to emphasize, given the Greek root of the term 'morphogens', how the geometry is in turn changed by the morphogen concentrations.

2. Geometry of epithelial sheets

It has been shown previously that the Gauss (K) and Mean (H) curvatures of a thick sheet can be expressed in terms of three variables 'A', 'B' and thickness 'h' [3]. These three are considered to be appropriate variables in place of the two principal radii of curvature R_1 and R_2, in terms of which the two curvatures needed to uniquely specify a thin surface are usually defined. These definitions giving the curvatures of the middle surface are $K = 1/(R_1 R_2)$ and $H = (1/2)(1/R_1 + 1/R_2)$. The radii of curvature are not the most transparent variables for the discussion at hand, where intracellular molecules coded for by genes are the more immediate agents of change of the surface geometry. Rather, the dimensionless apical area 'A', the basal area 'B', and the sheet thickness 'h' are more appropriate local variables. These three, A, B and h, are considered to be functions of the morphogen concentrations, which are of course themselves products of complex genetic interactions.

Begin by assuming that the middle surface is covered by small squares each of size (area) A_{m}, whose size varies over the surface. We have in mind more precisely that A_{m} be vanishingly small in the limit. Then 'A' and 'B' are defined as the dimensionless 'areas'

$$A = A_{\mathrm{a}}/A_{\mathrm{m}}, \quad B = A_{\mathrm{b}}/A_{\mathrm{m}} . \tag{2.1}$$

The 'A' and 'B' are the apical and basal areas divided by their corresponding (square) middle areas (Fig. 1). In terms of 'A', 'B' and 'h', the Gauss and Mean curvatures are given by (Appendix A, or Ref. [3])

$$K = \left(\frac{2}{h}\right)^2 \left(\frac{A+B}{2} - 1\right), \quad \text{and} \quad H = \left(\frac{2}{h}\right)\left(\frac{A-B}{4}\right) . \tag{2.2}$$

Equivalently we may write

$$A = 1 + hH + (h/2)^2 K, \quad \text{and} \quad B = 1 - hH + (h/2)^2 K . \tag{2.3}$$

An important constraint on the variables A, B is found from the fact that, by definition, the quantities K and H satisfy the inequality

$$K \leqslant H^2 . \tag{2.4}$$