A Biomechanical Imitative Model for Pulsatile Morphogenesis

L.V. Beloussov and V.I. Grabovsky

Faculty of Biology, Moscow State University, 119992, Moscow, Russia
lbelous@soil.msu.ru

Abstract. We propose a model which imitates the morphogenesis of several species of the hydroid polyps and permits the derivation of the geometry (surface curvature) of each developmental stage from that of a preceding stage. The model is based upon two experimentally verified assumptions. First, neighboring cells are assumed to compress each other laterally in a regular and species-specific pulsatile manner. It is this pressure, and/or an active cell reaction to it, which changes the curvature of a cell layer. Secondly, cell layers are assumed to have quasi-elastic properties tending to smooth out their curvature. With our model, the different pulsatile patterns of cell-cell pressure are reproduced and the elasticity parameters are modulated. The main principles of the model can also be used for interpreting the morphogenesis of other groups of animals. A suggested model emphasizes the self-organizing properties of a "stressed geometry" of embryonic rudiments.

1 Introduction

The aim of this work is to suggest, by means of an imitative modeling, some "rules of morphogenesis", that is, more or less universal algorithms permitting the derivation of each next stage embryonic shape from a preceded one. Contrary to many up to now developed models (e.g. [1]) we use the approach which can be called geometro-mechanical. This means, that we use the formative properties of the mechanically stressed bodies of a definite geometry (curvature of a surface). Such an approach is supported by the existence of the regularly arranged and stage-dependent mechanical stresses, both tensile and pressure ones, within embryonic tissues [2]. In this paper, a geometro-mechanical approach is used for interpreting the formation of buds in several species of lower invertebrate animals called hydroid polyps, or hydroids. Hydroids buds start their development from very simple geometrical shapes which become complicated later on in a quite monotonous manner, by changing nothing more than their local curvatures. Their shapes specificity is provided by quite regular temporal patterns of so called growth pulsations (GP), that is, the periodical (taking place each several minutes) extensions-retractions of the growing tip. At the extension GP phase a lateral cell-cell pressure of a turgor origin is substantially increased. At the retraction GP phase which always follows the extension phase the intracellular turgor pressure is diminished and so does the lateral cell-cell pressure [3].

We imitate the development of three hydroids species: *Dynamena pumila.*, *Obelia loveni* and *Campanulina lacerata*. In all the mentioned species the shapes of

just initiated buds can be roughly approximated by a hemispherical surface adjoining a cylindrical stem. The growing buds increase their transversal diameters to a different extent. This increase is the greatest in *Dynamena* samples, not so great in *Obelia* and almost absent in *Campanulina* whose buds remain quite narrow. As observed in a longitudinal projection, the buds always take a trefoiled (tripartite) shapes, with one central and two lateral protuberances. While in *Obelia* and *Campanulina* samples the lateral protuberances are not so pronounced and contribute to nothing more than tentacles, in *Dynamena* samples they develop to a much greater extent, deviate from a central lobe and produce new hydranths.

GP specificity is expressed in the duration ratios of the extension/retraction phases [4]. This ratio is the greatest in *Dynamena* samples, takes smaller values in *Obelia* colonies and is the smallest in *Campanulina* (Fig. 1). Correspondingly, we define the *Dynamena* GP as broad ones, those typical for *Obelia* as intermediate and those exhibited by *Campanulina* as narrow. The GP patterns correlate in a simple manner with the shape of the arisen buds: the broader are GP, the greater the rudiments are transversely extended, and vice versa. One of the main aims of our model will be to reproduce these correlations.

Fig. 1. A correlation between shapes of the *Campanulina* and *Obelia* hydranths (A, B) and *Dynamena* growing tip (C) on one hand and the patterns of their GP on the other. Left figures show transversal/longitudinal diameters ratios of the corresponding rudiments. Figures above GP graphs give the ratios of the hatched squares to the rectangular ones. This is a rough measure of a "broadness" of GP.

2 Description of the Model

2.1 Main Assumptions

The model is based upon the following suggestions derived from the biological data:

1. A surface of a rudiment consists of a finite number N of kinematically independent units, each of them corresponding to a group of 2 – 4 cells of a real rudiment. We take this value because it fits the smallest diameters of the morphological elements (protuberances, invaginations) produced during morphogenesis of the given species (see also Results).
2. Any element i is compressed laterally by its neighbors, $i-1$ and $i+1$. In the case of a non-zero local curvature, the pressure force applied to i acquires a radial component directed towards increasing the local curvature. Therefore, i should be shifted centrifugally. Correspondingly, we introduce either a purely passive, or the passive-active centrifugal force f_k . (Fig. 2A).
3. We assume that f_k is increased during the GP extension phase and is decreased (up to negative values) during the retraction phase. We express this effect by introducing a coefficient K of a force f_k . We also schematize GP patterns by dividing each model GP into 5 steps and ascribing to each step the different K values. We explore separately the effects of a constant (non-pulsating) regime and of three above mentioned types of pulsations: broad, intermediate and narrow. They were approximated by the following sets of K values:

Constant regime	1;1;1;1;1;
Broad pulsations	(in most cases) 1;-0,2;1;1
Intermediate pulsations	-0,2;0,3;0,8;1;0,7
Narrow pulsations	-0,2;0;0,2;1;0

Fig. 2. The forces which increase and smooth out the curvature. A: a curvature-increasing force F_k acting upon a cell i due to the lateral pressure exerted by the neighboring cells $i-1$ and $i+1$. B: a quasi-elastic force F_w acting to any cell of a layer independently of its neighbors.

4. At the same time, we assume that a quasi-elastic force f_w exists which is constantly (in a non-pulsating manner) applied to an entire cell layer and directed towards the diminishment of a local curvature (Fig. 2 B).
5. Due to a high viscosity (friction) of the rudiments' tissues there are no accelerations within a system and the forces are taken proportional to the linear shifts Δ of the elements per time unit:

$$\Delta_i = f(f_k, f_w)$$

where Δ_i is the resulted shift of an element i and f is the function connecting the value of Δ_i with those of the forces f_k and f_w .

2.2 Technical Description of the Model

The model is based upon a 2-dimensional set, its dimensionality taken as $[2, No^*]$, where No is a number of kinematically independent units within a model rudiment. Each element of a set $[a, b]$ contains a coordinate a (x or y) of an element i . For example, an element $[1, 12]$ contains an X-axis coordinate of an element No12 within an euclidean space, while an element $[2, 12]$ contains an Y-coordinate of the same element.

We take two initial configurations (arrangement of elements), both of them 2-dimensional (as exemplifying medial longitudinal sections through the rudiments' bodies), which we call cylindrical (Fig. 3A) and curved (Fig. 3B). In the both cases a first 1/3 of the elements' set is used for constructing a "left" wall of a rudiment. The second 1/3 creates a "cap", namely, a semi-circle, its beginning being joined with the end of a "left" wall while its end being joined with the beginning of a right wall. The last 1/3 contributes to the right wall itself. In the case of a cylindrical configuration the both walls are straight lines.

Fig. 3. Cylindrical (A) and curved (B) initial rudiments

In the case of a curved rudiment the left wall is an arch of a radius $R_l = R + D$, where D is a diameter of a "cap". Usually we take $R : D = 4$.

Then, according to the model algorithm we are transforming the coordinates of each element. The algorithm includes three following steps:

1. Change of an element's coordinate according to: (a) its momentary coordinate; (b) the coordinates of two neighboring elements, and (c) the value of K coefficient given as a parameter;
2. Correction of the newly obtained coordinates in relation to: (a) the coordinates of an average position of the given element and the two neighboring ones; (b) the value of a W coefficient given as a parameter;
3. Rearrangement of the obtained coordinates for avoiding the distances between neighboring points to override the limits of an initially taken interval. This is a condition limiting the mutual cells shifts within a real rudiment.

When thus obtained new set of coordinates of a given element replaces the initial one, the first step of a GP (out of 5) is fulfilled. Then the program returns back to point 1 for fulfilling the second step of GP, etc. After performing all the 5 steps, the program may be either stopped or starting a new GP. The number of GP can be set automatically installing a parameter *No of steps*.

At each step of the program, the transformations of the coordinates obey the following formalisms (Fig. 4A).

Step 1 can be generally expressed as

$$(i)'_{x,y} = f_i\{(i)_{x,y}; (i-1)_{x,y}; (i+1)_{x,y}; K_n\}$$

where

$(i)_{x,y}$ are coordinates of an element i ($i = 1, 2, 3, \dots, No$);

K_n is the parameter of each step of a pulsation ($n = 1, 2, \dots, 5$);

f_i is the function connecting the values;

In our model we take the function f_i as

$$(i)'_{x,y} = (i)_{x,y} - S \cdot K_n \left\{ \frac{(i-1)_{x,y} + (i+1)_{x,y}}{2} - (i)_{x,y} \right\}$$

Where

$$S = \frac{[i-1, i+1]}{[i-1, i] + [i, i+1]}$$

(in square brackets the euclidean distances between the points are given).

The parameter S is introduced for avoiding too sharp bending of a rudiments' surface. As one can see, under slight bending it is close to 1 while under increased bending it approaches zero.

After fulfilling this step, the initial elements' coordinates (i) are exchanged by the new ones $(i)'$. This step imitates the main model assumption, namely, the passive-

active movement of each element of a rudiment's surface towards the local curvature increase.

Step 2: corrections of the new coordinates $(i)'$ according to the value of W parameter and the initial coordinates of the point i and its nearest neighbors $(i-1)$ and $(i+1)$. Formally the corresponding transformations of the coordinates can be expressed as

$$(i)''_{x,y} = f_2[(i)'_{x,y}; (i)_{x,y}; (i-1)_{x,y}; (i+1)_{x,y}; W]$$

The function f_2 looks like

$$(i)''_{xy} = (i)'_{xy} - W \cdot ((i)'_{xy} - (\overline{XY}))$$

where $\overline{XY}$ are the averaged coordinates of all the three points: i , $i-1$ and $i+1$ (the corresponding point is denoted by a triangle, Fig. 6B). This step imitates the mechanical elasticity of a rudiment expressed by W parameter. The greater be its value, the more elastic should be the rudiment's tissue (Fig. 4B).

Step 3. Now the distances between the neighboring elements are tested and if they do not correspond to the formal limits the coordinates are rearranged.

The program language is Visual Basic 6.0. The program was implemented on IBM PC.

Fig. 4. A working scheme for producing a curvature-increasing (A) and a smoothing (B) component of the cell shifts.

3 Results

Fig. 4 exemplifies a generalized scheme of shape formation under different W values and different pulsatile regimes. Firstly, one can distinguish two different regimes with respect to the effect of the W values on the shapes produced. With low W values the trajectories of the imaging points cross each other, so that the points rapidly converge into dense "spots" (Fig. 5 C, G, L). This corresponds to the early developmental

stages of some embryos, but not to those which morphogenesis we aim to model. On the other hand, under very high elasticity values the initial shapes always gradually unfold towards a stationary state of a slightly concave line (Fig. 5H), or give a “sand-glass” shape (Fig. 5M) which again has little or no relation to the real morphogenesis. There are the intermediate zones of W values (correlated with pulsatile patterns) into which the required shapes are fairly well reproduced. We call them the “morphogenetic zones”, MZ (densely outlined in Fig. 5). The shapes reproduced within MZ, are rather sensitive to the pulsatile patterns, and this sensitivity fits the empirical data (4). The shapes produced under constant regime (Fig. 5A,B) are rather poor and non-realistic. Those employing “broad” pulsations possess the apically extending rudiments (Fig. 5 D, E) and wide stems which are straight even if emerged from the curved rudiments (Fig. 5 F). This is typical for *Dynamena*. The “intermediate” pulsations give the rudiments without an apical extension (Fig. 5 J) and having S-shaped stems (Fig. 5 K). Those are features characteristic for *Obelia*. Lastly, under “narrow” pulsations we get quite narrow shapes (Fig. 5 N, N₁) which are straight even if produced by curved rudiments (Fig. 5 O). It is remarkable, that the shapes emerged from the axi-symmetrical initial rudiments rapidly (after a restricted number of iterations) come to the stationary states (this is illustrated by thin contours of the frames D, E, I, J, N₁). On the other hand, the shapes produced by the curved rudiments exhibit more prolonged “growth” (frames B, F, K, O) which is just typical for the stems of hydroid polyps. Some more details of the shapes formation under different pulsatorial regimes are given in Fig. 6. As one can see, the resulted shapes are quite sensitive to the changes in the pulsatorial regimes, especially, to the changes in the amplitude of “troughs”: surprisingly, an increase or a decrease of a single trough within GP can produce rather global shape transformations. Meanwhile, the modeled shapes are biologically realistic.

Another important developmental parameter (not included in Fig. 5) is associated with the kinematically independent units. We found, that the morphogenesis is quite non-sensitive (robust) to the total number of such units: the initial rudiments cut from below and including slightly more than the apical hemisphere exhibit roughly the same morphogenesis as the complete rudiments.

That corresponds to the high regenerative capacities of hydroid polyps, which are able to reconstruct roughly the same shapes from little pieces of their tissue. On the other hand, the morphogenesis turned out to be very sensitive to the density of the units’ arrangement: under high density (single units are of the scale of the single cells diameters) the shape changes are going slowly, so that quite monotonous wavy patterns are produced. In the opposite, if the units are too large, all the rudiments, irrespective of the pulsatorial regimes, come to smooth spheroid shapes. We speculate, that the optimal density of the kinematically independent units (employed in our model) is partly determined by the inherent properties of a tissue, and partly self-selected within the course of morphogenesis, as providing a most rapid formation of macroscopic shapes.

We are well aware that our model is up to now very much simplified as compared with the biological reality. Obviously, a number of the control parameters should be increased. One can also assume that they are evolved during development. We suggest however that the main assumptions of the above presented model will be included in these, more perfect constructions.

Fig. 5. Generalized scheme of the main model shapes, as depending upon the pulsatorial regimes and the quasi-elasticity of tissues. Columns from left to right: constant regime, broad, intermediate and narrow growth pulsations (imaged below). Vertical axis: values of a quasi-elasticity coefficient (W). Densely outlined are the morphogenetic zones. Within MZ, the lowest frames B, F, K, O show the typical resulted shapes of the curved rudiments, while the upper shape(s) A, D, E, I, J, N, N₁ are those of cylindrical rudiments. Frames D, E, I, J, M, N₁ (shown by thin lines) give just the final configurations, all of which are stationary. On the contrary, black frames give the apposition of all the intermediate configurations.

Fig. 6. Shapes modeled within MZ under different pulsation regimes if starting from a cylindrical configuration. A: “broad” GP. Left frame: 50 iterations (=10 GP), right frame: 75 iterations (=15 GP), stationary configuration. B: “broad” GP, but trough at the 3rd step is changed from $-0,2$ to $+0,2$. C: same” trough is $+0,3$. Note the change of an arisen shape from quasi-quadrangular to quasi-triangular. These are observed in real *Dynamena* colonies. For A–C $W = 0,48$. In all the cases *Dynamena*-like shapes are obtained. D: “intermediate” GP, producing *Obelia*-like shapes. $W = 0,39$. Left frame: 5 iterations, right frame: 15 iterations, stationary configuration.

4 Conclusions

The model presented is related to one of the most fundamental biological problems, namely to the conceptual gap between genetic factors which influence shape formation and the shapes themselves. The main difficulty here is in understanding, how the genetic factors which are *per se* uniformly distributed within embryonic space, are able to control both local and holistic morphological (that is, spatially non-uniform) properties of the developing organisms. One can see, that the both main parameters used in our model (elasticity W and the pulsatile patterns) are indeed spatially uniform and may be hence directly linked with genetic factors. As to the pulsatile patterns, this is shown directly (5). Same seems to be plausible in respect to the dimensions (density) of the kinematically independent units. Meanwhile, as shown by the model, such values can largely affect numerous morphological features. We suggest therefore, that the genetic control of development can be considered as a parametric modulation of some universal morphogenetic rules.

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