2.1. Theoretical biology models of development

Even if some of the authors cited in the previous section were involved in theoretical research (for example Waddington, Needham and others founded the "Theoretical Biology Club" in 1930), most of the production was provided by "classical" biologists. In the following sections, we will present a state of the art of the theoretical studies in developmental biology.

En vrac

Jacobson, A.G. & Gordon, R., 1976. Changes in the shape of the developing vertebrate nervous system analyzed experimentally, mathematically and by computer simulation. Journal of Experimental Zoology, 197(2), pp.191–246. [88]: mathematical model of "the formation of the neural plate based on different autonomous, preprogrammed schedules of shape changes for different regions of the neural ectoderm."

Review

- Oates, A.C. et al., 2009. Quantitative approaches in developmental biology. Nature Reviews Genetics, [135]
- Lewis, J., 2008. From signals to patterns: space, time, and mathematics in developmental biology. Science, 322(5900), pp.399–403. [107]
- Tomlin, C.J. & Axelrod, J.D., 2007. Biology by numbers: mathematical modelling in developmental biology. Nature Reviews Genetics, 8(5), pp.331–340. [189]
- Reeves, G.T. et al., 2006. Quantitative Models of Developmental Pattern Formation. Developmental cell, 11(3), pp.289–300. [152]
- Morelli, L.G. et al., 2012. Computational approaches to developmental patterning. Science, 336(6078), pp.187–191. [121]

[149][30][151][150]

Reaction-diffusion

- Turing, A.M., 1952. The chemical basis of morphogenesis. Philosophical transactions of the Royal Society of London Series B, Biological sciences, 237(641), pp.37–72. [192]
  : coupling diffusion of chemical signals (the *morphogens*) between cells and local chemical reactions involving these agents within the cells is sufficient to generate complex spatial patterns.
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- Gierer, A. & Meinhardt, H., 1972. A theory of biological pattern formation. Biological Cybernetics, 12(1), pp.30–39. [64] and later Meinhardt, H. & Gierer, A., 1974. Applications of a theory of biological pattern formation based on lateral inhibition. Journal of Cell Science, 15(2), pp.321–346. [115] were able to reproduce various morphogenetic patterns by adding the concept of activation and inhibition interaction between morphogens.
- PCP signalling, Amonlirdviman, K. et al., 2005. Mathematical modeling of planar cell polarity to understand domineering nonautonomy. Science [1] : a reaction-diffusion model to establish that the *Drosophila melanogaster* epithelium is polarized with the PCP pathway in a non-autonomous manner.
- excellent review: Kondo, S. & Miura, T., 2010. Reaction-diffusion model as a framework for understanding biological pattern formation. Science, 329(5999), pp.1616–1620. [105]

Morphogens gradient formation and function

- Wolpert, L., 1969. Positional information and the spatial pattern of cellular differentiation. Journal of Theoretical Biology, 25(1), p.1. [204]
  introduces the theory of "positional information".
- review de wolpert Wolpert, L., 1996. One hundred years of positional information. Trends in genetics : TIG, 12(9), pp.359–364. [205]
- Shape and dynamics of the morphogen gradient
- Precision of the morphogen gradient

Epithelial cell shape and their division pattern.

- Gibson MC, Patel AB, Nagpal R, Perrimon N (2006) The emergence of geometric order in proliferating metazoan epithelia. Nature 442: 1038–1041. [62] used a *Markov chain model* to explain the evolution of the distribution of cell shape in a *Drosophila* epithelium. The authors propose that cell proliferation, and not cell packing, is responsible for the shaping of cells in monolayered epithelia. The model is compared with various organisms data. (for [135], an example of a "top-down" model: no parameters are needed.)
- Farhadifar R, Ro¨per JC, Aigouy B, Eaton S, Julicher F (2007) The influence of cell mechanics, cell-cell interactions, and proliferation on epithelia packing. CurrBiol 17: 2095–2104. [47]. defends that physical forces, in addition to cell division, are required to explain epithelial cell shape in the wing disc of *Drosophila*. A vertex based model is used where each vertex represents the junction. Forces are derived from an energy function which takes into account cell elasticity, cortical tension and inter cell adhesion. The model is tested with laser ablation experimental data.
- Patel AB, Gibson WT, Gibson MC, Nagpal R (2009) Modeling and inferring cleavage patterns in proliferating epithelia. PLoS Comp Biol 5: e1000412. [143]. investigates two factors in cell proliferation : the heritage of the cleavage plane orientation between mother and daugthter cells, and symmetry of the division. It concludes that strong symmetry is the dominant factor explaining the distribution of shapes observed experimentally.
- Sahlin P, Jonsson H (2010) A modeling study on how cell division affects properties of epithelial tissues under isotropic growth. PLoS ONE 5: e11750. [164]. study the division pattern in the shoot apical meristem epithelium of Arabidopsis. The particularity of this tissue is that an isotropic tension stretches it. The results are similar to the previous ones: symmetric division favors the simalution of observed cell shape distribution. This model used vertex based cell junction and growth rate and division of the cell

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is control by its local mechanical stretching.

- Sandersius, S. et al., 2011. Correlating Cell Behavior with Tissue Topology in Embryonic Epithelia. PLoS ONE, 6(4), p.e18081. [166]. Study epithelium pattern before and during the primitive streak formation in chick embyro. 1. They deny the relevancy of non-spatial markov model to explain the histogram of neighbor number in proliferating only epithelium (as Gibson 2006 does). Argument that any attempt to improve biological plausibility of this model (3 sided cells, asynchronous division) induces a deviation from the "universal" histogram. "We conclude from these results that attempts to improve the non-spatial model by adding biological realism are futile, and that the excellent agreement of the GPNP model with experimental data appears to be serendipitous"(!!!). 2. They show that their geometrical epithelium model (with ScEM) predict the histogram with the only sensible parameter being growth rate. 3. However, a surprising result is that they observe that their non-spatial markov model fits histogram from proliferation epithelium with cell motility (broader histogram).
- Escudero, L.M. et al., 2011. Epithelial organisation revealed by a network of cellular contacts. Nature communications, 2, p.526. [45]. introduces complex network topological measure in addition to the aformentionned article's geometrical measures. The new measures allow to discriminate the epithelia belonging to different species or different stage of development or between genetic variants of the same species. The observed data are classified with statistical methods, allowing to reveal the "signature" of an epithelium. (intersting for the measure tools but no explanatory value.)
- Gibson, W.T. et al., 2011. Control of the mitotic cleavage plane by local epithelial topology. Cell, 144(3), pp.427–438. [63]: study the interplay between the cell shape and the cleavage-plane orientation

Potts history 

- CPM is cell-oriented, as opposed to a continuum or pointillistic model. CBO given : cells stick to each other, move actively up and down gradients in their external environment, secrete and absorb materials, differentiate, grow, divide and die. Continuum models ignore cells and treat tissues as continuous materials with specific mechanical properties, completely ignoring the division of tissues into cells. Pointillistic models treat biological tissues as collections of point-like cells, ignoring many cell characteristics that are important to biological behaviors, such as cell geometry and the adhesive interactions between cells at their membranes.
- James A. Glazier, Ariel Balter, Nikodem J. Poplawski. Magnetization to Morphogenesis: A Brief History of the Glazier-Graner-Hogeweg Model. [68]
- Historical origins of CPM : Ising model (1920, Wilhelm Lenz, spin of atoms and hamiltonian to explain ferromagnetism/paramagnetism transistion), Potts model (Renfrey B. Potts, 1952, multiple values of the spin), Ashkin and Teller add dynamics with a Monte-Carlo method (1943), Glazier and Graner use the Metropolis algorithm for quasi deterministic kinetics.
- Athanasius F.M. Marée, Veronica A. Grieneisen, Paulien Hogeweg. The Cellular Potts Model and Biophysical Properties of Cells, Tissues and Morphogenesis. [113]
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Potts papers

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- Harrison, N.C., Diez Del Corral, R. & Vasiev, B., 2011. Coordination of Cell Differentiation and Migration in Mathematical Models of Caudal Embryonic Axis Extension. PLoS ONE, 6(7), p.e22700. [77]
- Zhang, Y. et al., 2011. Computer Simulations of Cell Sorting Due to Differential Adhesion. PLoS ONE, 6(10), p.e24999. [210]
- Hester, S.D. et al., 2011. A Multi-cell, Multi-scale Model of Vertebrate Segmentation and Somite Formation. PLoS Computational Biology, 7(10), p.e1002155. [79]

Cell sorting, Differential Adhesion Hypothesis

DAH, steinberg papers:

- Steinberg, M.S., 1962c. On the mechanism of tissue reconstruction by dissociated cells. I. Population kinetics, differential adhesiveness. and the absence of directed migration. Proceedings of the National Academy of Sciences of the United States of America, 48, pp.1577–1582. [182]
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- Steinberg, M.S., 1963. Reconstruction of tissues by dissociated cells. Some morphogenetic tissue movements and the sorting out of embryonic cells may have a common explanation. Science, 141(3579), pp.401–408. [183]
  - the observation of the behavior of once dissociated and then mixed together embryonic cells resemble the one of mixed immiscible fluids. Different phase tends to cluster together to finally form two clusters, one often engulfing the other. Similarly to

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these fluids, Steinberg hypothesized that the cells should also minimize their surface area and this process is modulated by differences in cell-cell adhesion.

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- Maître, J.-L. et al., 2012. Adhesion Functions in Cell Sorting by Mechanically Coupling the Cortices of Adhering Cells. Science. [112]
  reformuler le texte suivant from Mechanical control at cell–cell contacts Cell adhesion and cortex tension are known to regulate cell–cell contact formation. Heisenberg, Paluch and colleagues now analyse the contributions of cell adhesion and cortex tension in contact formation and sorting of zebrafish progenitor cells (Science http://doi.org/jcp; 2012). Building on previously published models of cell–cell adhesion and sorting, the authors developed a theoretical description of the shape of two progenitor cells adhering to each other. They then used dual micropipette aspiration assays to separate adhering progenitor cells from zebrafish embryos ex vivo and determined that cortex tension controls interfacial tension at the cell–cell contact, and thereby regulates cell–cell contact expansion. In contrast, cell adhesion was not involved in determining cell–cell contact size. Instead, the authors demonstrated that following mechanical separation of adhering cells, the linkage of cadherin to the actin cytoskeleton was crucial in limiting the mechanical resistance of adhesive bonds to pulling forces. The cytoskeletal anchoring of cadherins was further shown to be important for correct progenitor cell sorting within cell aggregates in vitro, and also during the segregation of progenitor cells in gastrulating zebrafish embryos in vivo. Thus, by combining theoretical, biophysical and live imaging experiments, the authors showed that cell adhesion is necessary to mechanically couple the cortices of adhering cells to support cell sorting.
- cite recent papers with interfacial tension, cortical tension to modulate ...

Individual/Collective Cell migration

Kabla, A.J., 2012. Collective cell migration: leadership, invasion and segregation. Journal of the Royal Society, Interface / the Royal Society, 9(77), pp.3268–3278. [92]

Somitogenesis

- Intro: from Oates, A.C., Morelli, L.G. & Ares, S., 2012. Patterning embryos with oscillations: structure, function and dynamics of the vertebrate segmentation clock. Development, 139(4), pp.625–639. [136]: The discovery of the segmentation clock, an oscillating genetic network in the pre-somitic mesoderm (PSM), leading the formation of somites in the elongating body axis of vertebrate embryo is the source of an active field of theoretical modeling. The phenomenon is conserved in various species and it illustrates the interplay of inner cell regulation and cell-cell communication. Cooke and Zeeman introduced a general mechanism called the "clock and wavefront" mechanism which has intensively been studied since its introduction in 1976 [28]. Lacking molecular grounding, it predicts the number and size of the somites from the period of the clock and the velocity of a wave travelling from the anterior to the posterior part of the axis, locking the cellular oscillators and forming a fixed periodic pattern. From then on, multiple oscillating genes, ie genes whose encoding protein and RNA follow cyclic creation and degradation, have been discovered in various species: Delta/Notch, Wnt, FGF, Hes/Her, and multiple models have been proposed to explain their interactions.
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- Jensen PB, Pedersen L, Krishna S, Jensen MH (2010) A Wnt Oscillator Model for Somitogenesis. Biophys J 98: 943–950. [89]

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- Murray, P.J., Maini, P.K. & Baker, R.E., 2011. The clock and wavefront model revisited. Journal of Theoretical Biology, 283(1), pp.227–238. [126]. In addition to the posteriorly moving molecular gradient which slows the rate of the segmantation clock oscillations, the authors propose that ocillator coupling may also induce a slowing of the oscillations. Using a continuum model of oscillators, an emergent wavefront is produced with three parameters: the clock period in the PSM, the somite length, the length of the PSM. Their model predicts the distance between moving shapes of gene expression, the number of moving stripes and the oscillating period profile along the antero-posterior axis. It also states that the ratio of coupling strength explains interspecies variability and that the period profile is conserved along the antero-posterior axis.
- Hester, S.D. et al., 2011. A Multi-cell, Multi-scale Model of Vertebrate Segmentation and Somite Formation. PLoS Computational Biology, 7(10), p.e1002155. [79]. Builds an integrative model of the clock and wavefront mechanism. Using a wide variety of accepted "submodels" as intracellular segmentation clock, coupling through the Notch-Delta signalling pathway, FGF8 determination front, delayed differentiation or a biomechanical model of cell sorting (potts with differential cell-cell adhesion), they reveal some inconsistencies between these sub-models.

Limb

- Newman, S.A. et al., 2008. Multiscale models for vertebrate limb development. Current topics in developmental biology, 81, pp.311–340. [131]
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Plants (Phyllotaxis, mechanosensing)

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- Review: Uyttewaal, M., Traas, J. & Hamant, O., 2010. Integrating physical stress, growth, and development. Current opinion in plant biology, 13(1), pp.46–52. [194]
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- Jönsson, H. et al., 2006. An auxin-driven polarized transport model for phyllotaxis. Proceedings of the National Academy of Sciences of the United States of America, 103(5), pp.1633–1638. [91] how is determined the presumptive tissue for leaf primordia in the apical meristem of *Arabidopsis thaliana*. These regions express a high concentration of auxin which is transfered from the neighboring cells. The auxin transporter, PIN1, is polarized along the auxin gradient. The authors combine ODE modeling of theses interactions with cell growth and eventually compare the simulation with live imaging.
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Biomechanical properties of living organisms

- Mechanosensing in single cells
- Mechanosensing in tissues and organisms
- Mechanical control of tissue morphogenesis
- Mechanical control of epithelial morphogenesis
- Hamant, O. et al., 2008. Developmental patterning by mechanical signals in Arabidopsis. Science, 322(5908), pp.1650–1655. [75]
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