Geometry and morphogenesis

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Abstract

We explore the analogy between field theories of contemporary physics and the concept of morphogenetic field in biology. Their common basis is the geometrical approach.

The richness and diversity of organic forms is one of the most exciting biological phenomena. The quest for order behind diversity is a great intellectual challenge. D'Arcy Thompson [4] quotes Nehemiah Grew (in 1682) saying that "..from the contemplation of Plants men might first be invited to Mathematical Enquirys". Clearly, the contemplation of organic forms raises geometrical questions. However, the geometry we need, should not be confined to the ordinary geometry of outer form, the latter being only a projection of the inner geometrical relationships. Here instead, geometry should be taken in a broadened sense: the study of possible arrangements and interrelationships of loci mutually communicating in space. The space itself should be taken in a more general sense. It is not emptiness to be filled with arbitrary objects. It is rather a *structured potentiality space*: the space of possibilities of emergence or construction of a class of forms imposing its own characteristic constraints. In Euclidean geometry for instance, the fact that the three medians of a triangle meet in a unique point is a property of Euclidean space itself rather than a property of triangles: when constructing the centroid of a triangle, two medians suffice and we need not to bother about the third: the third one is *constrained* to pass through the same point. Nevertheless, the potentiality space limits the possibilities of forms. Such geometrical constraints are not to be viewed as 'fetters': they are exploited by the organism in a creative manner: they enable it to form mechanisms or automatisms to be relied upon.

From this perspective, a living being constitutes a very richly structured inner space whose geometry is anything but Euclidean. Historically, the study of such a *biospace* is linked to the concept of morphogenetic field. Not in the sense of a system of physical, chemical, or even some 'biological forces' yet unknown, but rather as a *geometric ordering principle* behind the synchronization and coordination of these forces. This parallels Gurwitsch's theory (see [2]), who introduced the notion of morphogenic field, stressing its geometrical nature: he distinguishes the actual course of morphogenesis and the physical medium in which it is realized. Today we might reword it: the same medium can support several morphogenetic programs. Another aspect of morphogenetic field is its *wholeness*. No part of it can be changed without influencing the rest, the structure of every part reflecting the structure of the whole.

This geometrical notion of morphogenetic field parallels well the development of field conceptions in physics. Indeed, through the line Faraday $\rightarrow$ Maxwell $\rightarrow$ Einstein the concept of field underwent successive demechanization, dematerialization and desubstantialization. As conceived today, the physical field is pure geometry. A similar approach might be applied in the study of morphogenetic field. Indeed, such an inspiration is apparent for example in Cummings [1] or Webster & Goodwin [5].

These last authors introduce generative paradigm of biology as opposed to the neodarwinian one. The latter rests on the assumption of the key role of genes in the formation of morphological structures. The generative paradigm, on the other hand, views morphological structures as products of a generative process defined by field equations. A particular morphogenetic process is regarded as a solution of these equations which put constraints on the resulting form. The field equations being non-linear admit many different solutions: the result of a generative process is determined both by its parameters (encoded as genes) and by environmental influences. The evolution is viewed as an exploration of the 'parameter space' of a single generative process.

An analogous situation, where related forms are accessible via a simply structured parameter space, is well- known from mathematics. For example, all conics are described by a simple (quadratic) equation. A computer program for drawing a conic (generative process) produces a variety of forms through a mere change of parameters, the generative equation remaining the same. The best-known example are, of course, fractals: the great abundance of their complex forms is generated by a surprisingly simple process with few parameters.

For mathematical study of biospace and morphogenetic field, the concept of differentiable analytic manifold equipped with scalar, vector or generally tensor fields suggests itself. This concept conveys both topological and geometrical properties of the space. The underlying structure of manifold involves local coordinates and determines the topology of the space, its system of neighbourhoods and connectivity. Tensor fields confer to each point of a manifold its local 'flavour': the space looks differently in different places and different directions. Nevertheless, when these tensor fields are analytic, the local diversity is supplemented by the global unity and wholeness of the space. Analytic functions being determined by their values in arbitrarily small regions, analytic manifolds can be reconstructed from their arbitrarily small fragments: the structure of each part reflects the structure of the whole. Here, the spirit of the 19th century mathematics with its interest in the wholeness of the geometrical structures of complex analysis is highly inspiring. Concepts such as holomorphic, meromorphic or automorphic functions betray the preoccupation with form. Maybe, the same spirit led to the concept of morphogenetic field.

Like in the physical field theories, the tensor field of a biospace must be constrained by tensor identities leading to a system of differential equations. We suggest that the biological laws of morphogenesis might be formulated in these lines.

Distinguished geometrical structures are Riemannian manifolds, i.e. manifolds equipped with metric tensor fields. Among them, the best-known Riemannian manifolds are two-dimensional surfaces immersed into three-dimensional Euclidean space, such as sphere or torus. The metric tensor field allows us to measure distances, lengths and angles, and compute from them such characteristics as inner curvature of the space. Here, the fundamental concept is the *geodesic* - a curve which does not change its direction as, for instance, main circles on the sphere or straight lines in the plane.

The Euclidean space which is a special case of a Riemannian space, might be adequate for the description of outer forms of bodies; we use it for measuring or describing the bodies or when we draw them on display. However, for the inner geometry of an organism (i.e. its hidden pattern of relationships) a communication metric (see [3]) seems more adequate. The way in which different parts of an organism communicate with each other is a principal factor influencing its inner as well as outer form. The form of an organism is closely correlated with the arrangement of its arteries, veins and nerves, or, in the global organism of a community, with the arrangement of its paths, roads, telephone lines or computer networks. The *communication distance* between two points of an organism might be defined as the effort or time necessary to transfer information or substance between them. Since different things are communicated through distinct, though interconnected networks, it is possible for the present purposes to view the organism as an analytical manifold equipped with several communication metrics and possibly other tensor fields. This allows us to understand its form as the result of the interplay between these fields and the Euclidean metric of our description.

As an example of such an approach let us consider the structure of a tree leaf. Here we have a system of veins transporting water and minerals to the whole surface and energy rich substances to the stem. Thus the stem is the centre of a communication network of a leaf.

Let us consider the backward flow. We may conjecture a communication metric in the leaf, which reflects the cost of thev transport. It is reasonable to suppose that the transport is organized efficiently, i.e. that the transported substances flow along the geodesics. Thus, the hidden structure of the communication metric determines the geodesics leading from the stem, which manifest themselves anatomically as veins. The thick veins around the stem might be interpreted as densely packed bunches of geodesics in those directions, in which the communication is cheap. Let's make another reasonable assumption: the edge of the leaf is a *geodesic circle* of the communication metric, i.e. that the points at the edge have the same communication distance from the stem. Relative to Euclidean metric, however, the edge is further away in the direction of thick veins. The system of veins (or geodesics leading from the stem) determines another geometric structure - the *communication vector field*. At each point, we define the communication vector as a tangent vector to the geodesic leading from the point to the stem. Conversely, the geodesics can be regarded as *trajectories* of this communication vector field. Since the veins collect substance and transport it to the stem, the outflow at each point should exceed inflow by a constant value. This amounts to a requirement, that the divergence of the communication vector field should be constant and positive. This requirement of constant divergence may be thought as a constraint on the leaf form.

Of course we do not claim that this contraint is the requested law of leaf shape. Our example should only illustrate principles along which the biological field theories might be build. Our considerations have been limited to the principles of economy of transport. While the constraints on effectiveness seem to be inevitable, we think that the proper morphological constraints are to be looked for on a higher level respecting though the lower one.

This seems the reason why the most simple examples based on the mere considerations of effectiveness, for which geodesics and geodesic circles can be evaluated explicitly (see Appendix), do yield interesting and biologically suggestive forms (Fig. 1). One of them (c) resembles the heraldic coat-of-arms of the South Bohemian medieval house of Rosenberg.

Appendix

We consider a region of Euclidean two-dimensional space in a neighborhood of a distinguished point (stem). We use polar coordinates (r, φ) with the origin at the stem, so the components of the Euclidean metric tensor are $g_{rr} = 1,\ g_{r\varphi} = 0,\ g_{\varphi\varphi} = r^2,\ g^{rr} = 1,\ g^{r\varphi} = 0,\ g^{\varphi\varphi} = r^{-2}$. We consider another metric tensor $d_{ij},\ d^{ij}$ with $d_{ij}d^{jk} = \delta_i^k$, which we call communication metric and which determines the flow of some substance synthetized in the leaf. Let us consider the family of geodesics of d leading from the origin:

$$r(s,\alpha)\ ,\ \varphi(s,\alpha)\ \text{ with }\ r(0,\alpha) = 0\ ;\ ,\ \varphi(0,\alpha) = \alpha \tag{1}$$

where s is the parameter of length and α is the angle of a geodesic at the origin. We suppose that except at the origin the mapping $(s,\alpha) \mapsto (r,\varphi)$ is smooth and one-to-one, so (s,α) is an alternative system of coordinates. It can be easily proved that in these coordinates

$$d_{ss} = 1 \text{ and } \frac{\partial}{\partial s} d_{s\alpha} = 0 \tag{2}$$

and conversely for any metric d with this property the curves $\alpha = const$ are geodesics and s is their length parameter. We define the communication vector field v as tangent field of this family of geodesics.

$$v^s = -1 \; , \; v^\alpha = 0, \tag{3}$$

i.e.

$$v^r = -\partial r/\partial s \; , \; v^\varphi = -\partial \varphi/\partial s \tag{4}$$

For some radius R we interpret the geodetic circle with equation $s = R$ as the edge of a leaf and the geodesics 1 as its veins. Let us now search for constraints on the metric d. We suppose that there is a substance which is synthetized in the whole surface of the leaf and transported to the origin. Moreover, let its concentration $u(s)$ depend only on its communication distance from the origin and

$$u(0) = 0 \; , \; \frac{du}{ds}(R) = 0 \tag{5}$$

We suppose that the communication metric d acts as a diffusion tensor, so that the flow vector F of the substance u might be written as

$$F^i = -d^{ij} \frac{\partial u}{\partial x^j} \tag{6}$$

and the Laplace operator Δu as

$$\Delta u = -div(F) \tag{7}$$

where the divergence is meant with respect to the Euclidean metric.

Let us make an additional assumption about the metric d:

$$d_{\alpha s} = 0 \tag{8}$$

so that

$$d^{ss} = 1 \; , \; d^{s\alpha} = 0 \; , \; d^{\alpha\alpha} = 1/d_{\alpha\alpha} \tag{9}$$

Then we have

$$F = \frac{du}{ds} v \text{ and } \Delta u = \frac{d^2 u}{ds^2} - div(v) \frac{du}{ds} \tag{10}$$

Since the stationary distribution of the substance should satisfy a reaction-diffusion equation $\Delta u + h(u) = 0$, where h is a function expressing the local dynamics of u, we get by differentiating with respect to α

$$\frac{\partial}{\partial \alpha} div(v) = 0 \tag{11}$$

In this way we obtain a kind of differential constraint on the metric d. To obtain interesting examples, we adopt a stronger constraint of constant divergence

$$div(v) = c \tag{12}$$

and proceed as follows: We start with a communication vector field v singular at the origin, and solve the system of differential equation 4 to obtain the family of its trajectories $r(s,\alpha)$, $\varphi(s,\alpha)$ satisfying 1. These functions then determine the equation of geodesic circle. The determination of communication metric is not necessary for this procedure, however any metric d for which $d_{ss} = 1$, $d_{s\alpha} = 0$ is compatible with the communication vector field v.

A simple class of communication vector fields, for which this procedure is feasible is

$$v^r = \frac{1}{2}(r - \frac{1}{r})(c - p'(\varphi)) \ , \ v^\varphi = p(\varphi) \tag{13}$$

with constant divergence

$$div(v) = \frac{\partial v^r}{\partial r} + \frac{\partial v^\varphi}{\partial \varphi} + \frac{v^r}{r} = c \tag{14}$$

Here p is a periodic function with period $2\pi/k$ for some integer k such that $p(\varphi) = p(-\varphi) = -p(\frac{\pi}{k} - \varphi)$ and $p'(\varphi) < c$ for any φ. Under this assumption $v^r(r,\varphi) < 0$ for any $0 < r < 1$ and in this region the trajectories lead to the origin. The equations 4 can be integrated and we obtain explicit formulas for r and φ. Denote q a function for which $q'(\varphi) = 1/p(\varphi)$ provided $p(\varphi) \neq 0$. The function q is monotone in any interval, in which it is defined, so for any φ there is an inverse function q_φ^{-1} for which $q_\varphi^{-1}(q(\varphi)) = \varphi$. Then we obtain the equation of geodesics as

$$\varphi = q_\alpha^{-1}(q(\alpha) - s) \ , \ r = \sqrt{1 - \frac{p(\alpha)}{p(\varphi)} e^{-cs}} \tag{15}$$

Eliminating from this equation α and substituting R for s we obtain the equation of geodesic circle.

The forms of Fig.1 were obtained using the functions

$$\begin{array}{lll} p(\varphi) = a(\cosh \frac{\pi m}{2k} - \cosh m\varphi), & -\frac{\pi}{k} < \varphi < \frac{\pi}{k}, & 0 < m, \ a > 0 \\ p(\varphi) = a(\cos m\varphi - \cos \frac{\pi m}{2k}), & -\frac{\pi}{k} < \varphi < \frac{\pi}{k}, & 0 < m < 2k, \ a > 0 \end{array} \tag{16}$$

with varying parameters m, a, R and fixed c. When R approaches 0, the form approaches a limiting form with straight geodesics like in 1a, 1b and 1d For large value of R the form approaches the Euclidean circle with (Euclidean) radius 1 and bent geodesics (1f). The articulate forms are obtained when the maximum of $p'(\varphi)$ approaches c, and less articulate with smaller values of a as in 1e. For small values of m (1d,1f) there is a negligible difference between cosh (left column) and cos (right column). The form 1b is obtained with m approaching $2k$ and the forms in the left column with large value of m

References

[1] Cummings F.W.:A Pattern Surface Interactive Model of Morphogenesis. J.Theor.Biol. 116,243-273,1985

[2] Gurwitsch A.:Die historischen Grundlagen der Biolo- gie. Gustav Fischer, Jena 1930

[3] Kůrka P.:Communication Metric and Organic Form. Differential Geometry and its Applications (J.Janyška, D.Krupka, eds,) World Scientific, London 1990

[4] Thompson D'Arcy W.:On Growth and Form, Cambridge 1942

[5] Webster C., Goodwin B.C.:Il Problema della Forma in Biologia, Roma 1988