Dynamics of the Unseen: Surfaces and Their Environments as Dynamic Landscapes

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Abstract

This paper presents a structural interpretation of the figure of epigenetic landscape in theoretical biology, introduced since the end of the 1930s by the embryologist and theoretical biologist Conrad Hal Waddington, in order to comprehend developmental morphogenesis. On the basis of this interpretation, a research and innovation program on morphogenesis and morphodynamics, DYNLAN, is run at ENSAD, Ecole Nationale Supérieure des Arts Décoratifs, Paris.

Introduction

In every day language the term "landscape" has several acceptations. The most obvious are perhaps the ones referring to landscape as an expanse of scenery that can be seen in a single view: a desert landscape, for example, or a picture, or an artistic representation depicting this expanse of scenery. One also speaks, in this sense, of landscape architecture, of landscape ecology, and so on.

In this paper, however, I'm using another acceptation of landscape, emerging from theoretical biology. It is not a material landscape, but an abstract one; nevertheless it also concerns vision: it is a mental picture offering a theoretical view on developmental morphogenesis. The expression "theoretical view" is a pleonasm, in the light of the etymology of "theory" [13]. I would like indeed to stress that the figure of epigenetic landscape conveys the attention of the mind's eye on sophisticated relational aspects of morphogenesis - as comprehended by Conrad Hal Waddington – which would perhaps not so clearly emerge if expressed by natural language, without the help of images.

Before considering these images in section 2, I first discuss some aspects of morphogenesis between natural sciences and arts.

[13] From *Theoria* "contemplation, speculation, a looking at, things looked at," from *theorein* "to consider, speculate, look at," from *theoros* "spectator," from *thea* "a view" + *horan* "to see."

1. Morphogenesis between natural sciences and arts

The variety of natural forms is a recurrent source of inspiration in urbanism and architectural conception and, more extensively, in art. Far from being a purely formal research, this attention to natural forms is often accompanied by a quest for the construction principles that regulate the genesis of these forms. Morphogenesis seems *d'emblée* committed to structural aspects.

This is an essential assumption in the fascinating work on morphogenesis, both in the animated and unanimated world, of the well known Scottish morphologist D'Arcy Wentworth Thompson.

His book, *On Growth and Form,* first published in 1917 [19], has influenced generations of researchers from the most various fields: biologists, architects, artists, mathematicians, and human scientists [1]. Thompson, without advocating an abandon of Darwinism, suggests in his book that evolution has been overemphasized by biologists as the determinant of the form of living organisms, and the roles of mechanics and physics have been underestimated. Structural transformations, determined by forces, are advocated instead of natural selection, in order to explain these forms.

Martin Kemp [7,8] has extensively studied the influences on the arts of Thompson and thompsonisms (carried by other morphologists belonging to the same tradition, for example Peter Medawar and Conrad Hal Waddington). Beside the intrinsic interest of appreciating the impact of scientific imagery in art, Kemp indicates another main interest of his research perspective: the discerning of fundamental qualities of structure and process in nature as shared enterprises of art and science, as witnessed, for example, by the words of the sculptor Peter Randall-Page, whose stone sculptures are evocative of the organic geometries expounded by students of phyllotaxis, without representing specific botanical forms "Altough my work is firmly rooted in observation, I try to achieve… rightness of form through a kinship with, rather than a facsimile of nature" [11].

In this paper I will consider the work of Conrad Hall Waddington (1905-1975) on morphogenesis, in particular his notion of "epigenetic landscape". Extremely known in the world of biology as the eclectic embryologist and promoter of theoretical biology who introduced in the 1942 the term "epigenetics", Conrad Hal Waddington has been an extremely curious academic, with a particularly wide range of interests. Theoretically influenced by Alfred North Whitehead's process philosophy, he also was found of art and he was acquainted with a significant number of artists and creators of his time, for example John and Mary Myfawny Piper, Henry Moore, Ben Nicholson, Alexander Calder, Laslo Moholy-Nagy, and Walter Gropius.

Witnessing his exceptional investment in "boundary investigations", his 1969 book *Behind Appearance: A Study of the relations between Painting and the Natural Sciences in this Century*. As the title explicitly indicates, Waddington analyses the reciprocal exchanges between sciences and painting in the twentieth century. Curiously, among the variety of possible objects at the interface between science and art, he does not consider in his book his own figure of epigenetic landscape.

Nevertheless, something in the appearance of this powerful figure calls for an excursion behind appearance. It is what I'm trying and showing in next sections.

2. Things You Can Tell Just by Looking at Landscapes

Images of landscapes played and play an important role in the development of biology, in very diverse fields, from population genetics and evolutionary theory to embryology and epigenetics.

Fig. 1. Sewall Wright's 1932 adaptive landscape [25]

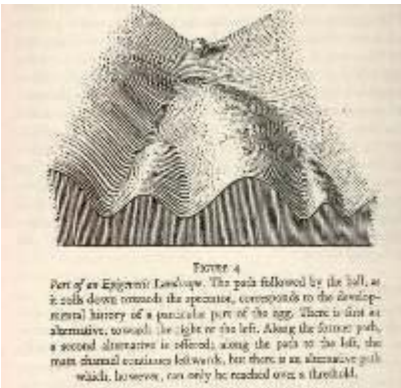

Fig. 2. C.H. Waddington's 1957 epigenetic landscape [23 p.29]

Fig. 1 represents Sewall Wright's first explicit illustration of the idea of an adaptive surface, or adaptive landscape [25] : "Diagrammatic representation of the field of gene combinations in two dimensions instead of many thousands. Dotted lines represent contours with respect adaptiveness" (from the original caption). In the framework of the modern synthesis, which found in Sewall Wright one of its founders, the dynamics of mendelian populations on this surface is expected to go towards local maxima of fitness.

Conrad Hall Waddington introduced the first image of an "epigenetic landscape" in

1940, in the frontespiece of his *Organisers and Genes* [21]. He invented himself the neologism “epigenetics” in 1942 [22], as the “the interactions of genes with their environment that bring the phenotype into being.”
Waddington’s epigenetic landscape is a metaphor for how gene interactions modulate cellular differentiation during development. One is asked to imagine a number of marbles rolling down a hill towards a wall that come to rest at the lowest points. These points represent the eventual cell fates, that is, tissue types. This idea was actually based on experiments: Waddington found that one effect of mutation (which could modulate the epigenetic landscape) was to affect how cells differentiated. Some of these experiments are discussed in *Organisers and Genes*. Notions introduced by Conrad Hal Waddington in the 1940s and 1950s, such as canalisation and genetic assimilation, have been recently reconsidered in a molecular framework, for example within the work by Rutherford and Lindquist on the Drosophila heatshock protein HSP90 [13,10]. Without contesting the importance of Waddington’s experimental activities, I do not think of them as the unique source in Waddington’s work leading to the genesis of landscape images. Another important source of inspiration comes from his theoretical interest in a possible mathematization of biological processes in terms of non-linear equations.

Questions about the status of landscapes in theoretical biology, their heuristic role, historical and conceptual relationships between fitness, adaptive, and epigenetic landscapes are debated in philosophical literature (for example [9], [12], [6]).

Despite the different acceptations of the images of landscape following the different subfields of biology, their characteristic shape defined by peaks, pits, and cols, seems to present an evocative analogy with the images of potential or energy landscapes for dissipative systems in mathematical and physical literature.

If in the case of Waddington's epigenetic landscape, especially in its 1957s' version (cf. Fig.2), the visual analogy with potential or energy landscape is evident, in the sense that the motion is meant to develop in the sense of a – local- minimisation of the potential, for fitness and adaptive landscapes one needs to take into account an inversion of polarity in the motion of the individuals or of the mendelian populations: moving, in this case, from a certain region towards a fitness maximum – local, again.

This visual analogy could encourage the mathematical minded reader towards a mathematical interpretation of landscapes in theoretical biology in terms of potential landscapes. However this clearcut interpretation seems to be absent in the establishment of this image in the history of twenty century evolutionary theory, at least in Sewall Wright's seminal papers of the 30's on population genetics, where he introduces his adaptive landscape.

The philosopher of science Jean Gayon, in his beautiful study on the figures of landscapes in biology [6], argues that it seems pertinent to think that Sewall Wright was aware of this possible interpretation, at least that he could not ignore it, in the light of his correspondence with Ronald Fisher. However, points Jean Gayon, Wright himself affirmed years later that he did not meant to give this mathematical interpretation. He was indeed interested in suggesting a visual metaphor and in using its rhetorical power in order to make his theory more understandable by non mathematics trained biologists.

Waddington himself, in his 1957 book *The Strategy of the genes* [23], qualifies his epigenetic landscape as a mental image, a representation by a diagram of the developmental system of an embryo:

"Although the epigenetic landscape only provides a rough and ready picture of the developing embryo, and cannot be interpreted rigorously, it has certain merits for those who, like myself, find it comforting to have some mental picture, however vague, for what they are trying to think about" [23, p.30].

Let us consider the 1957 version of the epigenetic landscape again (cf. Fig. 2). A ball, lying on the top of an undulating landscape, is ready to move along one of the paths opened in front of it. The undulated surface represents the fertilized egg. The path followed by the ball represents the developmental history of a particular part of the egg. As Waddington emphasizes it in the original caption, there is first an alternative, towards the right or the left. Along the former path, a second alternative is offered; along the path to the left, the main channel continues leftwards, but there is an alternative path which, however, can only be reached over a threshold.

This image is completed by a “hidden” part, underlying the epigenetic surface, and giving an explicit and mysterious at a time interpretation of the constitution of the surface itself (Fig. 3): “the complex system of interaction underlying the epigenetic landscape. The pegs in the ground of the figure represent genes; the strings leading from them the chemical tendencies which the genes produce. The modelling of the epigenetic landscape […] is controlled by the pull of these numerous guy-rops which are ultimately anchored to the genes” (from the original caption).

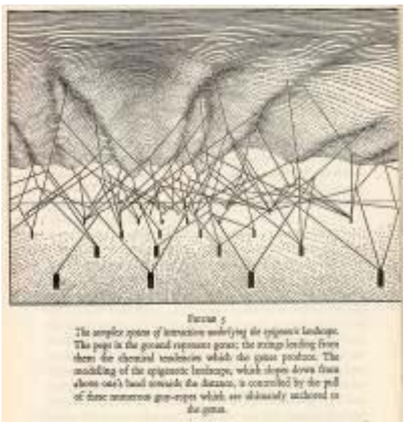

Fig. 3 The underlying part of the epigenetics landscape [23]

Insofar, if seriously taken, this “mental picture”, says quite clearly at least two things:

- the development of the embryo is canalized along defined pathways
- the undulating surface on which pathways, or channels, are defined, is moulded by the underlying network of genes interactions.

It thus conveys a non reductionist position *vis-à-vis* single gene action. Waddington writes “it is not necessary, in fact, to await a full understanding of the chemistry of single genes before trying to form some theoretical picture of how gene-systems produce integrated patterns of developmental change”. [23, p. 9]

I will leave the reader forge his own opinion from literature (for example [3], [2]) of the innovative and iconoclastic character of Waddington’s vision, namely with regard to his integrated representation of (epi)genetic actions and of embryological development, in the context of epistemological cultures dominating biological research of his time.

Here I rather wish to shed light on structural thinking inscribed in Waddington’s images. Since the first occurrence and illustration of the notion of epigenetic landscape, as the frontispiece of his 1940 *Organisers and genes* [Fig. 4], Waddington presents the landscape from a holistic point of view, even if not yet so explicitly as in the 1957 representations.

Fig. 4. from a drawing by the painter John Piper. Original caption: "Looking down the main valley toward the sea. As the river flows away into the mountains it passes a hanging valley, and then the two branch valleys, on its left bank". [21]

The following passage form a book of 1939, *An introduction to modern genetics* [20, pp.180-4] seems to indicate that Waddington had already a structural image of the process of constitution of the landscape:

"If we want to consider the whole set of reactions concerned in a developmental process such as pigment formation, we therefore have to replace the single time-effect curve by a branching system of lines which symbolizes all the possible ways of development controlled by different genes. Moreover we have to remember that each branch curve is affected not only by the gene whose branch it is but by the whole genotype. We can include this point if we symbolize the developmental reactions not by branching lines on a plane but by branching valleys on a surface. The line followed by the process, *i.e.* the actual time-effect curve, is now the bottom of the valley, and we can think of the sides of the valley as symbolizing all the other genes which co-operate to fix the course of the time-effect curve; some of these genes will belong to one side of the valley, tending to push the curve in one direction, while others will belong to the other side and will have an antagonistic effect. One might roughly say that all these genes correspond to the geological structure which moulds the form of the valley."

Waddington's comparison of the of genetic actions on the whole to the geological structure moulding the valleys of the landscape leads us to think to the epigenetic surface as a generic emergent process.

The question of a possible interpretation of the epigenetic landscape in terms of a dynamical systems approach is not only based on historiographical considerations on its genesis, in the context of the use of non-linear equations, and the study of attractors in phase-space, in other fields of theoretical biology (such as epidemiology and population dynamics: Waddington knows and quote the work of Lotka and Kostizin).

In fact, several authors have theoretically interpreted Waddington images from this perspective (for example Jonathan Slack [17] and Peter Saunders [14], [15]).

Perhaps the first has been the mathematician René Thom, who in the 1960's elaborated his catastrophe theory, as a mathematical theory of morphogenesis, inspired, as he wrote himself, by embryology and in particular by Waddington's notions.

The possible interpretation of the epigenetic landscape in terms of catastrophe theory has animated a famous correspondence between Conrad Hal Waddington and René Thom in the late 1960's and in the 1970's [18]. I've already written on this correspondence, showing their misunderstandings on the notions of stability that can be associated to the figure of the epigenetic landscape [4], [5].

Here I just remind an aspect of their misunderstandings, in order to show that their partial mutual incomprehension is interesting, since it gives an example of the power of images to catch theoretical questions, difficult to express in mathematical terms.

3. A "generative" misunderstanding? Towards an image of dynamic landscapes

Waddington speaks of two kinds of stability: on one hand homeostasis, that means stability towards a final steady state (different tissues, different organs); on the other hand, homeorhesis, one of his neologisms, as the stability of the process of development itself. This second acceptation of stability is a dynamical one, the stability of a pathway, not of a final state. This is important to Waddington, since it explains why development stays on track, despite external aggressions. On the model of epigenetic landscape, this is represented by the slope of the valleys -or channels-, avoiding that a perturbed trajectory of the ball escapes the valley itself, unless the perturbation is important enough. In this case, the ball would jump in another valley, *i.e.* in another canalized path.

Thom bases his catastrophe theory on structural stability, as a property of observable objects (living or not). In his opinion homeorhesis should be implied as a property of a structurally stable process.

One can ask the question: what is the reason of the misunderstanding between the two savants?

A first interpretation of this lack of agreement between the two scientists can be based on taking into account of their cultural differences. To use the expression introduced by Evelyn Fox Keller in *Making Sense of Life* [3], they do not share the same "epistemological culture" and they do not have the same explanatory needs.
René Thom himself introduces this correspondence as an example of the difficulties in communication between a mathematician and a biologist because of the differences in their exigencies of mathematical rigour. However, following some of Waddington's remarks on the peculiarity of the variable "time" in biology, I suggest another interpretation of their disagreement, based on Waddington's unsatisfied need of representing, thanks to the metaphor of epigenetic landscape, different spatio-temporal scales in the process of the organism development.

Waddington's landscape implies different variables and parameters depending on the spatio-temporal scale (morphogenesis of tissues/organs; morphogenesis of the landscape itself).
Thom's catastrophe theory gives a general description of the variations of the form, but it does not consider a temporal dynamics.

I called this misunderstanding "generative", since it puts on the table a set of desiderata defining epigenetic landscape as a dynamical landscape that synthetically captures several essential questions for the modelling of complex systems.

What are the nature and the evolution of equilibria that characterise the landscape? How is their stability characterised? And their robustness? What is the effect on a landscape of different kinds of disturbances or interactions with the environment? At what spatio-temporal scale is it suitable to situate such analyses and investigations? What are the variables that are represented by the landscape? In what space do they live?

We took this set of questions as an agenda four our research program DYNLAN, on the conception and realization of dynamic landscapes, that begun in October 2009, in collaboration with my colleague at ENSAD Yves Mahieu, architect. The program implies two students/researchers: Chengliang Wang, artist and Jonas Ranft, PhD student in theoretical biophysics.

In the following section, I will shortly present a first pedagogical experience based on this approach to landscapes that took place in May 2008 at ENSAD. It deals with the conception and realization of a dynamic surface in relation with its environment.

4. « Paysages sensibles et dynamiques »: an experience

The framework of the experience has been a month of interdisciplinary work for 1st year students[14]. During the month of may, 16 students have worked on the project "Paysages sensibles et dynamiques", proposed by Yves Mahieu and myself. Three more ENSAD teachers joined us: Sophie Larger, designer; René Lesné, art historian and Xavier Miclet, set decorateur. Our already interdisciplinary team has been completed by two technical assistants: Michel Davidov and Xavier Tiret, both engineers. Moreover Carole Knibbe and Guillaume Beslon, bioinformaticians of IXXI, Rhonalpin Institute of Complex Systems, working on synthetic evolution, visited us twice, at the beginning and at the end of the experience, in the framework of a IXXI project ("Morphostructural and semantics properties of landscapes in theoretical biology").

The first day a workshop took place, in which each teacher introduced his own vision of the landscape:

[14] The 16 following ENSAD students participated to the project: Sarah Escamilla, Julien Cédolin, Victor Alvar de Biaudos de Casteja, Camille Pajot, Marie Riegert, Juliette Mallet, Anaïs Mathieu, Jennifer Pineau, Kevin Garcia, Laura Martinez, Hélène-Mahi Fofana, Nils Lacroix, Marion De Villechabrolle, Sophie Dang Vu, Matthieu Rocolle, Sarah Théron.

-my self on the epigenetic landscape and on the Thom-Waddington correspondence
-Yves Mahieu, on architecture of tensed membranes
-Carole Knibbe, on the image of fitness landscape
-Sophie Larger, on some contemporary artists that could be inspiring for the work (Ernesto Neto, Fischli & Weiss).
-René Lesné, on the figure of landscape in the history of art
-Xavier Miclet, on several materials and cloth.

Eventually Xavier Tiret presented a variety of mechanisms that could be conceived to move the landscape. Michel Davidov introduced the notion of interactivity and some electronic devices in order to realize it.

We asked students to conceive and construct a structure underlying a surface whose form can change under the variation of the parameters controlling the structure and in relation with environmental stimuli. Here you can find some pictures of the dynamic surface, generated by the interplay of motor actions on the cables and the bars connected to the composite tensed membranes.


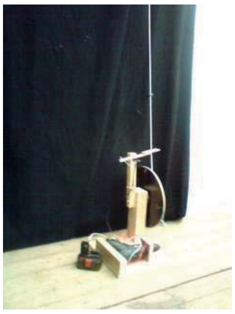
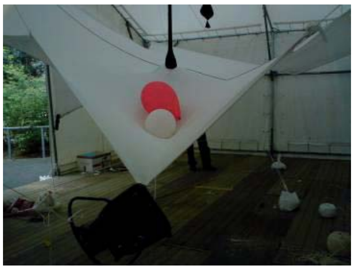

Fig. 5-6-7 First experimentations on tensed membranes. In the middle: one of the motors.



Fig. 8-9-10 On the left: a reduced 1 :10 model of the external tent. Various morphologies of the final dynamic landscape.

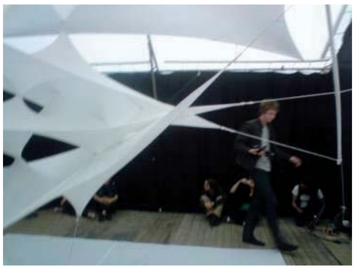

Fig. 11-12-13 Various morphologies of the final dynamic landscape.

By way of conclusion

The figure of epigenetic landscape conveys properties of complex dynamical systems that put on the table a new aspect with respect to the traditional problem of morphogenesis, *i.e.* the one of considering the action of forces on the morphogenetic process. This new aspect concerns the cartography of these possible actions - defined by the valleys of the landscape's surface. It also concerns the generation of the surface itself, as the result of its underlying tectonics, or of its epigenetics. These underlying processes, whatever their nature, may run at different spatio-temporal scales with respect to the morphogenetic events that the landscape should comprehend in its space of possibilities. In other terms, the constitution and dynamics of the landscape themselves can be seen, in a more abstract way, as a morphogenetic problem.

In the first experience of 3D realization, described here above, we concentrated on this last aspect: to generate a landscape of possibilities as emerging by an underlying tectonics. In this sense, our dynamic composite surface, moving in relation to its environment, under the integrated effect of motors and of human decisions, is intended to share some of the emerging character of other unknown dynamic landscapes.

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