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Some remarks on the compatibility between determinism and unpredictability

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ABSTRACT

Determinism and unpredictability are compatible since deterministic flows can produce, if sensitive to initial conditions, unpredictable behaviors. Within this perspective, the notion of scenario to chaos transition offers a new form of predictability for the behavior of sensitive to initial condition systems under the variation of a control parameter. In this paper I first shed light on the genesis of this notion, based on a dynamical systems approach and on considerations of structural stability. I then suggest a link to the figure of epigenetic landscape, partially inspired by a dynamical systems perspective, and offering a theoretical framework to apprehend developmental noise.

1. Introduction

In the laplacian view, the knowledge of the evolution laws of a deterministic system should guarantee, to an ideal intelligence able enough in analysis, to predict the future state of the system. However, since the work of Poincaré on the three-body problem (Poincaré, 1908; Barrow-Green, 1997; Béguin, 2006), we know that this view is not any longer defendable. Predictability is not, in general, guaranteed by the knowledge of the deterministic evolution laws of a system. The unavoidable uncertainty in the initial conditions implies that one can make long-time predictions only if the evolution law does not amplify the initial uncertainty too rapidly. Limits of predictability on the trajectories of systems presenting the property of sensitivity to initial conditions do exist.

In front of these limitations on the knowledge of the particular trajectory of a system, dynamic systems theory (qualitative theory of differential equations) offers the possibility of gaining a global knowledge on all the possible trajectories of the system, studying their asymptotic behavior in phase space.

For this kind of systems, the research work of several groups of physicists led, during the 1970's, to the notion of scenario to chaos transition.

What is a scenario to chaos transition? Roughly it can be defined as a generic series of bifurcations leading a system from a steady state to a chaotic regime. In the light of a general study of dynamical systems, a scenario to chaos transition allows for a new kind of prediction – of probabilistic nature -– about the qualitative behaviors of a dynamical system under the variation of an external control parameter (Eckmann, 1981).

In this paper I will first provide a short overview of the modifications in the relationship between determinism and predictability that the acknowledgment of the property of sensitivity to initial conditions introduced in the history of classical mechanics. I will then shed light on the genesis of the notion of scenario to chaos transition, and on the kind of predictions, of probabilistic nature, this notion allows. I will in particularly show that a notion from the history of dynamical systems theory, structural stability, plays a crucial role for the pertinence of the adoption of a dynamical systems point of view for the study of the behavior of physical systems. I will then suggest a link to the figure of epigenetic landscape, partially inspired by a dynamical systems perspective, and offering a theoretical framework to apprehend developmental noise.

A preliminary remark: it is usual to contrast the term "deterministic" with "stochastic", or "probabilistic". In this paper I implicitly use this distinction, too, but in a sense that need to be specified. I call "deterministic" a system if the equations representing its dynamics are deterministic, in the sense that they do not contain stochastic or probabilistic terms. In my use of the term "determinism", I will not assume – as it was assumed in the laplacian vision that dominated physics until the work of Poincaré – that determinism implies predictability. In what follows, I will employ the term "deterministic" only when referring to the deterministic character of a mathematical model, as one can see it by looking at its defining equations. As we will see in details in the next section, this property does not imply the predictability of the trajectories of the system: a deterministic system can produce an erratic behavior, very difficult to distinguish from the behavior

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produced by a stochastic system.[2] In other words, predictability cannot be taken as a discriminating criterion between deterministic and non-deterministic (stochastic) systems.

2. Determinism and limits in predictability

The term "determinism" has entered the German academic world through the school of Christian von Wolff, who introduced it to refer to the theory of his master Leibniz. Even if Leibniz himself did not use explicitly this term, he distinguishes between "necessity" of logical truths and "determination" of events: one has properly to speak of "determination" about moral and physical truths. The rational principle that, following Leibniz, operates here is the principle of "sufficient reason" or "determining reason". It would be too long here to retrace the history of the term "determinism", and of the diffusion of this term outside the wolffian school. The reader can refer on this topic to Gayon (1998a, 184–188). Laplacian determinism, as en epistemic vision, is grounded both on an ontological (cosmological) and a metaphysical vision (Gayon, 1998a; Popper (1982), 1995). Curiously, Pierre Simon de Laplace did not use the term either. What is important for us is that, in the laplacian conception, determinism is not only connoted as an expression of a principle of causality (Laplace referring explicitly in this text to Leibniz's "sufficient reason"), but it is also intimately connected to predictability.

> "Nous devons donc envisager l'état présent de l'univers, comme l'effet de son état antérieur, et comme la cause de celui qui va suivre. Une intelligence qui pour un instant donné, connaîtrait toutes les forces dont la nature est animée, et la situation respective des êtres qui la composent, si d'ailleurs elle était assez vaste pour soumettre ces données à l'analyse, embrasserait dans la même formule, les mouvements des plus grands corps de l'univers et ceux du plus léger atome: rien ne serait incertain pour elle, et l'avenir comme le passé, serait présent à ses yeux" (Laplace (1814), 1840, 4).

This often quoted passage, that constitutes the manifesto of scientific determinism, states clearly that an intelligence that knew the laws of evolution of the universe and its initial conditions, and that was able enough in analysis, could predict its state at any time.

We know today that this optimism is unjustified. Due to sensitivity to initial conditions, the trajectories of certain deterministic systems exponentially diverge at a certain time, and become unpredictable.

The consequences on the unpredictability of trajectories, due to the impossibility of knowing initial conditions with an infinite precision, were already clear to Poincaré, as well this passage from the chapter on chance from Science et Méthode indicates:

> "Une cause très petite, qui nous échappe, détermine un effet considérable que nous ne pouvons pas ne pas voir, et alors nous disons que cet effet est dû au hasard. Si nous connaissions exactement les lois de la nature et la situation de l'univers à l'instant initial, nous pourrions prédire exactement la situation de ce même univers à un instant ultérieur. Mais, lors même que les lois naturelles n'auraient plus de secret pour nous, nous ne pourrons connaître la situation initiale qu'*approximativement*. Si cela nous permet de prévoir la situation ultérieure avec la même *approximation*, c'est tout ce qu'il nous faut, nous disons que le phénomène a été prévu, qu'il est régi par des lois; mais il n'en est pas toujours ainsi, il peut arriver que de petites différence dans les conditions initiales en engendrent de très grands dans les phénomènes finaux; une petite erreur sur les premières produirait une erreur énorme sur les derniers. La prédiction devient impossible et nous avons le phénomène fortuit" (Poincaré (1908), 1999, 62).

At the time of Poincaré, another French *savant-philosophe*, Duhem (1906) wrote about the limitations of predictability in a mathematical model of the geodesics on a surface of negative curvature presented by the mathematician Hadamard (1898). On the basis of an analogy between geodesics and trajectories of point-masses on the surface, defined by similar differential equations, Hadamard's work can be relevant both for geometry and for mechanics. Duhem points out that the impossibility of using this kind of mathematical models – presenting sensitivity to initial conditions – for making predictions on physical systems depends on the impossibility, for a physical measure, to be made with infinite precision.

Today we know that for "sensitive to initial conditions" – or hyperbolic – systems, temporal limitations on their predictability can be quantified thanks to indicators measuring the rate of error growth produced by the dynamical system, such as Lyapunov exponents and Kolmogorov–Sinai entropy (Boffetta et al., 2002).

However, despite these limitations, dynamical systems theory offers a global approach carrying the possibility of treating in a rigorous, even if qualitative way, the study of the behavior of hyperbolic systems.

David Ruelle, one of the main contributors to chaos theory in the 1970's (namely to the study of transition to weak turbulence) speaks of a change in idealization in physics: thanks to dynamical systems theory, a mathematically rigorous approach to the study of non-linear systems has become possible (Ruelle, 1988). The idea is not any longer to report oneself to the properties of linear or linearized systems, but to study the global properties of all the possible trajectories of the system in phase space.

Before considering the genesis of the notion of scenario to chaos transition, bound to this change in perspective, it will be useful to consider a notion of stability emerged in the development of dynamical systems theory, and playing a crucial role in establishing a link between this high abstract branch of mathematics and the study of physical systems.

3. Structural stability: is a model a good model?

Looking at the genesis of the notion of scenario to chaos transition, a striking feature is the shift, in dynamical systems theory, from the study of the properties of a given dynamical system, to the study of the properties of classes of systems, defined on the basis of their structural stability. It is the structural stability of a system that provides a justification for applying the – mathematical – qualitative theory of differential equations to the study of the behavior of particular dynamical systems in the physical world. From the point of view of structural stability, what it counts are not the details of a dynamical system, for example as expressed by its equations. On the contrary, one is interested in the invariance of some topological properties of the system under the variation of one of the parameters of its defining equations. The idea is that a function F is structurally stable if, for a small perturbation of the function, the perturbed function has the same topological properties of the previous one.

The notion of structural stability has been introduced in dynamical systems theory by Aleksander Andronov and Lev Pontryagin in 1937 (Andronov and Pontrjagin, 1937). However they did not use this expression that has been introduced later in the first English translation overseen by Solomon Lefschetz. They used the

[2] See the contribution of Eric Bertin, this volume. See also the discussion about determinism and undeterminism in a mathematical model by Adrien Douady (1992).

expression "rough systems" or "coarse systems" to indicate what we call today "structurally stable" systems. The notion has extensively been used in oscillations theory and plays an important role to analyze oscillating physical systems in the book of 1937 by the same Andronov, Vitt, and Kahikin (Andronov et al. (1937), 1966). Structural stability emerges thus, inside dynamical systems theory, as an essential feature that a dynamical system (in the sense of a mathematical model) should present in order to correspond to a real system (in the sense of being observable in the physical world). It is difficult to express the idea clearly than in the following passage, taken from the book Theory of oscillators, co-authored by A.A. Andronov:

> "What properties must dynamic systems (models) possess to correspond to physical systems? In setting out the differential equations we cannot take account of all the factors that influence in some manner or other the behavior of the physical system. On the other hand, none of the factors taken into account can remain absolutely constant during a motion of the system […]. A certain number of parameters corresponding to physical parameters of the problem occur in the functions P and Q of our system equations, so these functions are never known exactly. Small variations of these parameters must leave unchanged the qualitative structure of the phase portrait. Therefore, if certain qualitative features appear for well-determined quantitative relations between the parameters but vanish for an arbitrarily small variation of the parameters, then it is clear that such qualitative features are not, generally speaking, observed in real systems. It is natural, therefore, to separate the class of dynamic systems whose topological structure of the phase paths does not vary for small variations of the differential equations. We call such systems «*coarse*» or *structurally stable* […]". (Andronov et al. (1937), 1966, 374–375)

The notion of structural stability expresses an ambition peculiar of this branch of mathematics, developed inside one of the schools pioneering the field of auto-oscillations and of control theory: the use of mathematical criteria to evaluate the pertinence of mathematical models.

This methodological perspective has been consolidated during the 1960's by a theorem of global analysis proved by a student of S. Lefschetz, Mauricio Peixoto (1962). However it has been shown by Stephen Smale that Peixoto theorem does not generalize for dimensions higher than two.[3] Despite this formal result and other considerations that determined, following Guckenheimer and Holmes ((1983), 1996, 259) in their influential book on dynamical systems, a wakening of the "structural stability dogma", considerations of structural stability played a crucial role in establishing the pertinence of the use of dynamical systems theory for the study of the behavior of physical systems. This role is particularly evident in the work of René Thom, father of catastrophes theory, a mathematical theory of morphogenesis based on topology and differential geometry. Structural stability is for Thom the natural and indispensable attribute of every identifiable form (Thom, 1968).

The work of David Ruelle on the study of transition to weak turbulence, one of the contributions to the genesis of the notion of scenario to chaos transition, has been inspired by Thom's perspective.

[3] For a discussion on structural stability see Smale (1980), Chaperon (2007). The importance of structural stability in explanatory arguments in contemporary statistical physics has been acknowledged by the philosopher of physics Robert Batterman (2002).

4. Scenarios to chaos transition: a new form of predictability?

4.1. The genesis of the notion of scenario to chaos transition

At the origin of this notion, David Ruelle and Floris Takens wrote a seminal paper, published in 1971, "On the Nature of Turbulence", that modified considerably the approach to this difficult problem of fluid mechanics and of mathematical physics (Ruelle and Takens, 1971).

The problem of understanding how a viscous incompressible fluid in a stationary state can evolve, under the effect of an external stress,[4] to a turbulent state, was first considered by Landau (1944) and Hopf (1948) in the 1940's. In scientific literature one speaks of Landau–Hopf road to turbulence, even if, historically, the two scientists independently obtained their results. They both adopted a perturbative approach, studying the successive destabilizations (in the linear approximation) of the fluid beginning with the steady state and proceeding to the turbulent state. The turbulent state is seen as the superposition of an infinite number of quasi-periodic movements, that is, as the superposition of an infinite number of independent frequencies ("the independent modes"). Each independent frequency can be seen as a new degree of freedom of the system. Thus, within this picture, a turbulent transition is only possible for a system with an infinite number of degrees of freedom.

The problem of the transition to turbulence in a viscous incompressible fluid submitted to a steady external action, expressed by a control parameter μ, is completely reconsidered from a dynamical systems perspective by David Ruelle and Floris Takens. Ruelle and Takens ask the question of the variation of the behavior of the system under the variation of the control parameter μ. When $\mu = 0$ the fluid is at rest, in equilibrium. For $\mu > 0$ one obtains first a steady state, i.e., the physical parameters (velocity, temperature, etc.) describing the fluid at any point are constant in time, but the fluid is no longer in equilibrium. For further increases of μ various new phenomena may occur: the fluid motion may remain steady but change its symmetry pattern; the fluid motion may become periodic in time; for sufficiently large μ, the fluid motion may become very complicated, irregular and chaotic (it is in the turbulent state).

Instead of considering a particular dynamical system, Ruelle and Takens deal with a one-parameter family of dynamical systems:

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \boldsymbol{X}_\mu(V);\ V(t = 0) = v_0$$

Where $X_\mu : H \to H$ is a vectorial field defined on an infinite dimensional vector space H and μ is the experimental control parameter, which can be varied. Because of dissipation, a reduction to a small number of degrees of freedom is possible. Hence Ruelle and Takens replace H by a finite dimensional manifold.

Assumed that the control parameter μ remains fixed during the whole duration of an experiment (physical or numerical), they are interested in the changes of the *attractors*[5] as μ is varied. The values of μ for which the attractor changes are the *bifurcation* points, which correspond to a local loss of the *structural stability* of the system.

[4] A control parameter, typically the Reynolds or the Rayleigh number, gives a measure of the external stress.

[5] To define an attractor, one has to define a non-wandering set. A point x belongs to the non-wandering set (i.e. is non-wandering) if for every neighborhood U of x and every T *0* one can find t T such that $D_{x,t}(U) \cap U \neq 0$, where D_x is the integral of the vector field X. A closed subset A of the non-wandering set is an attractor if it has a neighborhood U such that $\cap_{t0} D_{x,t}(U) = A$.

Ruelle and Takens criticize the Landau–Hopf's conclusions, arguing that the Landau–Hopf road is not *generic*. The definition of genericity they refer to comes from Smale (1967): a property is generic if it holds on a countable intersection of dense open sets (called a residual set).[6] Genericity can be considered as a minimal way to judge if something is likely. Thus the lack of genericity of the Landau–Hopf road to turbulence means that a transition following this road is not likely. Moreover, Ruelle and Takens claim that a generic transition to turbulence may occur after a small number of bifurcations and that, in phase space, the turbulent behavior is associated with a non-trivial attractor (a *strange* attractor), defined as the product of a two dimensional manifold by a Cantor set. Thus, the continuous frequency spectrum associated with turbulence is no longer interpreted as the superposition of an infinity of independent frequencies, as in the Landau–Hopf picture, but as the consequence of sensitivity to initial conditions, showed by the presence of a strange attractor. In other words, if a system undergoes three Hopf bifurcations, starting from a stationary solution, as the parameter is varied, then it is likely that the system possess a strange attractor after the third bifurcation.

The possibility of a turbulent transition after a low number of bifurcations opened up the theoretical possibility of a direct experimental test, which was difficult in the case of the preceding Landau–Hopf interpretation for the onset of turbulence, dealing with an infinite number of successive destabilizations. Between the beginning of the 1970's and the beginning of the 1980's, a large amount of research has been carried out in this direction, aimed at showing that in some systems a transition to turbulence can occur after a *low* number of bifurcations. The first positive results came from the study of Taylor–Couette instability (Gollub and Swinney, 1975), Rayleigh–Bénard instability (Bergé and Dubois, 1976; Libchaber and Maurer, 1978), chemical oscillations (Pomeau et al., 1981), or from the numerical study of the Lorenz's system (McLaughlin and Martin, 1974), or other truncations of the Navier–Stokes equations (Franceschini and Tebaldi, 1979). Both experimental and numerical results suggested that the Ruelle–Takens transition was not the only possible alternative to the Landau–Hopf transition and that other "roads to chaos" could exist, characterized by a different succession of bifurcations.[7] The fact that the Landau–Hopf transition is not generic, as Ruelle and Takens argue, does not imply that the Ruelle–Takens transition is the only possible generic alternative. Indeed, in the spirit of the dynamical systems theory, one should be able to describe the non-transient behavior of dynamical systems by a complete classification of their attractors and of the motion on them. As one is, however, far from any complete classification of attractors, or even from a canonical choice of adequate classification criteria, the notion of "scenario to chaos transition" has been created at the beginning of the 1980's. As far as I know, this term has been introduced in a paper by Jean-Pierre Eckmann (1981).

4.2. The kind of predictability allowed by scenarios to chaos transition

What is a scenario to chaos transition and what is the nature of the predictions one can make with the help of scenarios?

A scenario to chaos transition is defined as a generic sequence of bifurcations under the variation of the control parameter μ. Far from an exhaustive classification, the idea of scenario to chaos transition is, more modestly, based on an approach leading to a description of some non-trivial or strange attractors, which have the additional feature that they arise as modifications of trivial attractors (fixed points, limit cycles) as the control parameter is changed. One is then interested in the successive bifurcations of the system, and one may ask what happens when a certain sequence of bifurcations has been encountered. Even if there are in principle an infinity of further possibilities, not all of them are equally likely.

Here the mathematical sense of "likely" is again expressed in a minimal way by the property of genericity (cf. Eckmann, 1981, 645–646). Eckmann discusses three scenarios, known at the beginning of the 1980: the Ruelle–Takens scenario, the Feigenbaum period-doubling scenario (Feigenbaum, 1978) the intermittency scenario (Manneville and Pomeau, 1979; Pomeau and Manneville, 1979).[8]

Which is the nature of the prediction that can be made with the help of scenarios?

The statement of a scenario always takes the form "if… then…". More precisely: "If certain things happen to the attractor as the parameter is varied, then certain other things are likely to happen as the parameter is varied further".

It should be underlined that the classification in terms of scenarios is made on the basis of the series of bifurcations a system undergoes under the variation of the control parameter, and not *a priori* on the basis of its equations. In other words it is the history of the changes in the structural stability of the system that allows for predictions on the future of the system, and not the form of its equations. The fact that the problem of knowing the behavior of a non-linear dynamical system is not solved by the knowledge of its governing equations is, in my opinion, essential in order to understand the novelty offered by a dynamical systems approach. It is implicitly one of the elements of the mentioned "change in idealization" that David Ruelle (1988) underlined.

Eckmann also stresses that several scenarios may evolve concurrently in different regions of phase space, depending on how the initial state of the system is prepared. In addition, the relevant parameter ranges may overlap, and while the basins of attraction for different scenarios must be disjoint, they may be interlaced. An important property, implicit in the notion of scenario to chaos transition, is that it does not describe its domain of applicability.

> "We have already stated that a scenario consists of an "if" part and a "then" part, which should be a statement that something is likely to happen. But there is no attempt being made to say how the "if" part is; such statements must be found by other, maybe more specific, theories". (Eckmann, 1981, 646)

Thus, if the hypotheses of a scenario to chaos transition do not apply, no prediction is being made. Furthermore, no claim is made that this is the only way to find turbulence!

4.3. On observability and repeatability in physical and numerical experiments

What does, following Eckmann, "likely" mean in a physical (and experimental) context? Several elements are to be considered:

- One never knows exactly which equation is relevant for the description of a given physical system.
- When an experiment is repeated, the equations representing the situation may have slightly changed.
- The equation under investigation is one among several, all of which are very close to each other. If among these equations

[6] An introduction to the notion of genericity in dynamical systems theory can be found in Yoccoz (1992). For a discussion of the polysemy of this notion, see Chenciner (1988).

[7] For an historical account of these researches, see Franceschelli (2001).

[8] For a study on the genesis of the scenario of intermittency, see Franceschelli (2001, 2007).

there are many which satisfy the conclusion of the scenario, then one seems allowed to say that he's performing an actual experiment, and that it will be probable that the conclusions of the scenario apply (cf. Eckmann, 1981, 646).

In order to understand these considerations it is worthwhile to stress that experimental observations are not, properly speaking, repeatable when a system is sensitive to initial conditions. Every experiment/observation is indeed unique: instability is the experimental mark of sensitivity to initial conditions. About this aspect, the following quotation from a paper of Pierre Bergé, one of the leading experimenters involved in the study of transition to turbulence, refers to experimental observations on a Rayleigh-Bénard cell[9]:

> "Even more confusing situations are the following experimental results:
>
> Two identical twin cells (small boxes) filled with the same fluid and inserted between the same massive copper plates (then submitted to the same R_a number with the same thermal history) are generally exactly under the same convective regime.
>
> Sometimes however, we have found the following situation: One may be oscillating, the other being either turbulent or stationary!
>
> These confusing behaviours are just mentioned to emphasize – for the last time – the fact that any behaviour cannot be either predicted or understood from the only knowledge of R_a, Γ_x, Γ_y, Pr, … etc… etc. if one does not specify the actual structure which is sensitive to so small uncontrolled perturbations (even in a highly careful experiment) that they remain far away from the attention of the standard R.B. experimentalist!". (Bergé, 1979, 306–307)

If in a numerical experiment it is possible to follow the divergence of trajectories due to sensitivity to initial conditions, in physical experiments the sensitivity to initial conditions is only appreciable as instability of the actual trajectory. In physical experiences, repeatability is extremely difficult to realize: it depends on the actual convention structure, which is difficult to control.

In summary, if one wants to dress a comparison between physical experiments and numerical experiments, one realizes that in the second case only the divergence of trajectories due to sensitivity to initial conditions can be numerically «observed»: starting from two different (and close) initial conditions. In this case repeatability is guaranteed. But what do these trajectories represent with respect to real (physical) experiments (or to ideal mathematical solutions)?

Sensitivity to initial conditions poses the problem of the very relevance of numerical simulations to investigate such equations, since any rounding error will deeply affect the computed trajectory!

However, as a consequence of results of dynamical systems theory (Bowen, 1970, 1978), a "shadowing property" holds: one can show that, for hyperbolic systems, any computed trajectory in fact is "shadowed" by a continue trajectory of the system and it is thus relevant, at least in a statistical sense. Works of Palis and Smale (1970) and of other dynamical systems theorists aim at showing the connection between the properties of shadowing and of structural stability (for an accessible discussion, see Yoccoz, 1992, 2007). The reader can find an extensive bibliography and a technical treatment of these aspects in the framework of the analysis of topological properties of hyperbolic sets in Katok and Hasselblatt (1995, 566–574) and Katok and Hasselblatt (2002, 244–245).

Despite the failure of the mathematical program of a general classification of all dynamical systems on the basis of their properties of structural stability, more pragmatic definitions and uses of structural stability hold. The already evoked wakening of the "structural stability dogma" (Guckenheimer and Holmes, (1983), 1996, 259) can be summarized as a transition from: "Only structurally stable models are good potential models" (Andronov and Pontryagin, (1937), 1966) to: "For a good model, only structurally stable consequences of the model are reproducibly observable" (Chen et al., 1994).

The function of the notion of structural stability in guaranteeing the pertinence of the use of the qualitative approach to study a physical problem seems quite important even if, in general, still undervalued outside the specialized literature.

If one looks in details at the practices of researchers that worked during the 1970's and the 1980's on chaos physics, it is evident that considerations of structural stability played a heuristic role. To summarize these practices, the study of simple generic model has been justified through a verification of the properties of structural stability of the model or of the physical system. This has been done thanks to numerical or physical experiments: if by varying some of the parameters of the model or of the physical system the topological properties of the model or of the physical system were conserved, the model or the physical system could be considered as structurally stable.

Beyond questions of chaos transition, the shift we observed in looking at the genesis of the notion of scenario – from the study of a particular system to the study of classes of systems – has, in my opinion, a broader interest for the analysis of complex systems, since it is at the heart of several approaches from contemporary statistical physics (for example: spin glasses, renormalization group methods). In these cases as well predictability is based on properties of classes of models, regardless of the details defining a particular model.

In the next section I propose a transition, that might seem abrupt, to a notion that emerged in the 1940's (Waddington, 1940) and has developed within theoretical biology: the epigenetic landscape, a representation by diagrams of the developmental system of an embryo. The images defining an epigenetic landscape can be found in Waddington (1957, 29, 36).

The pertinence of this proposition is to be found in the possibility to look at these images from a dynamical systems point of view. This assumption, I argue, can be justified from two perspectives at least, a historiographical and a prospective one.

5. Developmental noise from an epigenetic landscape perspective

On one side, looking for the genesis of this notion in Conrad Hal Waddington's writings, one finds Waddington's need of developing an appropriate mathematical apprehension of developmental

[9] A Rayleigh–Bénard convection cell is composed of two horizontal, heat-conducting plates heated from below, between which a fluid is enclosed (walls are of insulating material). Warmer and less dense fluid, located on the bottom of the layer, will tend to ascend; *vice versa* more dense and higher located fluid will tend to descend. But this destabilizing effect, due to the temperature difference ΔT applied to the layer, is fought by the stabilizing effect of viscosity and thermal diffusivity which both tend to diminish hydrodynamic movements. The balance between stabilizing and destabilizing effects depends on a dimensionless number: the Rayleigh number R_a, which is proportional to the imposed temperature difference. Movements of fluid will appear only if the temperature difference is important enough, when the Rayleigh number reaches a certain critical number Ra_c. Below this critical value, Ra_c, the stable state of the fluid layer is the state of rest (fluid velocity = 0). Over this threshold, the resting stable state becomes unstable in favor of a new equilibrium state: the convective state. For another, higher, critical value of Rayleigh number, it is possible to observe turbulent motion, characterized by the presence of convective rolls. Another important number in a convection experience is the Prandtl number, Pr. This number fixes the (dimensionless) ratio of fluid kinematic viscosity and thermal diffusivity. It is a characteristic of the considered fluid; it depends, above all, on the fluid nature and, less, on its temperature. Γ_x and Γ_y indicate the aspect ratio of the cell along the x and the y direction.

processes. And Waddington was looking in the field of non-linear systems, of topology and of attractor analysis in phase space in order to find the good candidates for such an apprehension. He knew the importance of these branches of mathematics for the development of other fields of theoretical biology, such as epidemiology and population dynamics: Waddington quotes the work of Lotka and Kostizin. He is furthermore explicitly influenced by cybernetics, quoting extensively the work of Ross Ashby, deeply informed, as cybernetics in general, from a dynamical systems perspective. I'm not claiming here that this mathematical perspective is the only originating matrix of Waddington's images. It is acknowledged that these images fit well with Waddington's concerns and experimental results on induction and competence – of great interest, on this topic, the papers of Scott Gilbert (1991), and of Jean Gayon (1998b). However I think that the convergence of the images defining the epigenetic landscape with a way to graphically express the conceptual results of Waddington's work in experimental embryology underdetermines the landscape images themselves. In sum, beside an inspiration coming from experimental results, the emergence of these images is informed – it is what I claim – from a disposition to mathematical thinking also.

On the other side, looking retrospectively at this notion from a more recent point of view, it is spontaneous to dress a morphological analogy between the epigenetic landscape undulated surface and the maxima and minima characterizing a multi-stationary energy landscape. As a matter of fact, several authors have interpreted Waddington's images from a dynamical systems point of view. Peter Saunders (1993), for example, has analytically developed this interpretation. Jonathan Slack (2002) suggests this interpretation, too[10]. Of great interest for us, the first one to deeply explore this perspective has perhaps been the mathematician René Thom who, in the 1960's, elaborated his catastrophe theory as a mathematical theory of morphogenesis. As he wrote himself, he has been inspired by embryology and in particular by Waddington's images.

Catastrophe theory is a general theory of morphogenesis, intended as the creation or the destruction of forms, without regarding nor the substrate, nor the nature of the forces that determinate it. Waddington and Thom have been involved in a long correspondence, about a possible mathematization of the epigenetic landscape in terms of catastrophes theory. This correspondence shows some misunderstandings both on the theoretical notions associated to the landscape and on the mathematical notions that could describe them. The principle argument of the disagreement is whether homeorhesis, the neologism Waddington introduced to indicate a sort of developmental, dynamic equilibrium that developing embryo presents along each developmental pathway, could be expressed, or not, in terms of the mathematical notion of structural stability (a detailed analysis of this correspondence can be found in Franceschelli, 2011). Despite these misunderstandings, and even more because of the questioning they open, I argue that the images of landscape, if interpreted in a structural, albeit dynamical sense, can be considered as a call for mathematization. They insert themselves in the history of the use of dynamical systems theory to think to processes in the material (not only physical, but also living) world.

But what is properly an epigenetic landscape? Conrad Hal Waddington qualifies it as a mental image:

> "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" (Waddington, 1957, 30).

In Waddington's (1957) version of the epigenetic landscape a ball, lying on the top of an undulated surface, is ready to move along one of the paths opened in front of it. The landscape is completed by a "hidden" part, underlying the undulated surface: a network of pegs fixed in the ground, interconnected by guy-ropes and strings. Some of the links (guy-ropes and strings) are connected to the surface. They can thus, under a proper modification of their tension, determine a modification of the global morphology of the landscape.

Now, what do these images represent? Waddington states it explicitly: 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 far as the underlying part, the epigenetic landscape turns out to be a composite metaphor, offering an explicit and mysterious at a time interpretation of the constitution of the surface itself:

> "*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 modeling of the epigenetic landscape [...] is controlled by the pull of these numerous guy-ropes which are ultimately anchored to the genes" (Waddington, 1957; from the original caption, 36).

This figure points out at least two aspects of Conrad Hal Waddington's vision of embryology: the development of the embryo is canalized along defined pathways (Waddington calls them also, with a neologism, 'chreods'); the undulating surface on which pathways are defined, is molded by the underlying network of genes interactions.

> Waddington's non reductionist position *vis-à-vis* single gene action and its description in terms of molecular mechanisms is explicitly affirmed: "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" (Waddington, 1957, 9)

Moreover, Waddington compares the genetic actions on the whole to the geological structure molding the valleys of the landscape: beyond the field of embryo development, structural and morphological thinking is inscribed in Waddington's images.

It is spontaneous to imagine the form of the undulated surface as an emergent effect of the complex set of relationships underlying it. One can easily imagine that a change in the tension of a link could modify the form of the undulated surface, thus creating a new path. On another side, one can also imagine that some tension modifications could be balanced by other modified tensions, so as to leave unmodified the global tension defining the undulating surface. This would imply that the paths offered by the undulations of the surface to the balls routes would not change, despite some underlying local modifications. This could be seen as the guaranty of a certain form of robustness for the dynamics of the balls (it has to be noticed that Waddington does not use the term "robustness", but he expresses this property through the use of the terms "homeorhesis" or "buffering", or "canalization").

Within this framework, Waddington apprehended developmental noise as irregularities, lack of complete precision in the operating of the epigenetic mechanisms:

> "It can hardly be expected that any epigenetic mechanism can operate with complete precision. Quite apart from any disturbances due to the external environment of the embryo, there are

[10] See also the contribution of S. Huang, this conference. This interpretation seems however not to be present in other literature on Waddington ideas, see for example Hall and Laubichler (2008).

likely to be slight irregularities in the interactions between the different parts of the germ, which, in a sense, provide an environment for each other. This is particularly noticeable when a developmental process is carried out not by passive tissue but by isolated cells" (Waddington, 1957, 39)

Through the epigenetic landscape Waddington could thus, in a sense, apprehend the effects of developmental noise recently emphasized in research on stochastic gene expression, producing phenotypes varying around some mean value in a constant environment (see for example Elowitz et al., 2002; Paulsson, 2005).

"It is important to distinguish the inherent noisiness of a developmental pathway or chreode from its canalisation. Developmental noise will lead to the formation, in a constant environment, of adults which vary somewhat around some mean value […]. If canalisation is represented as a valley in an epigenetic landscape, the noisiness of the system might perhaps be symbolised by the imperfection of the sphericalness of the ball which runs down the valley". (Waddington, 1957, 40)

6. Discussion

Recent evidences that stochasticity is present in the phenomenon of gene expression seem to challenge today the traditional belief, associated to genetic determinism, that the expression of genes is executed inside the cell as a computer would execute a program – that would guarantee repeatability and stability.

If the expression "genetic program" has entered the world of molecular biology in the 1960's, namely thank to the work of the Nobel prizes Monod and Jacob, the use of metaphors coming from computer science to characterize the nature and the function of the genes was not new at that time. Among the different origins of this view, that has largely dominated and propelled the development of molecular biology, particularly influential has been the argument of the "order by order", that lead the physicist Erwin Schrödinger to imagine, in his masterpiece of 1944 "What is life?", the structure of the chromosome fibers as a code-script.[11] For Schrödinger, due to the low numbers of atoms constituting the genes, the order represented by the durability and permanence of gene activity cannot be explained by statistic laws. Schrödinger argues that order by disorder can in fact emerge, as it is the case in statistical mechanics, in sets composed by a high number of components. But this is not the case for the genes.

"How can we, from the point of view of statistical physics, reconcile the facts that the gene structure seems to involve only a comparatively small number of atoms (of the order of 1000 and possibly much less) and that nevertheless it displays a most regular and lawful activity – with a durability or permanence that borders upon the miraculous?" (Schrödinger, 1944, 46).

For Schrödinger, order in gene activity cannot be explained but by an underlying structural order: order by order, thus. In accompanying this view by the use of the code-script metaphor coming from the rising computer science of his time, Schrödinger introduces in molecular biology the laplacian association between determinism and predictability:

"In calling the structure of the chromosome fibers a code-script we mean that the all-penetrating mind, once conceived by Laplace, to which every causal connection lay immediately open, could tell from their structure whether the egg would develop, under suitable conditions, into a black cock or into a speckled hen, into a fly or a maize plant, a rhododendron, a beetle, a mouse or a woman". (Schrödinger, 1944, 21–22).

At the same time, another accessory effect of this metaphor has been to raise a barrier between biology and physics, concerning the association of determinism and predictability. As we saw, this association, that in the conception known as laplacian determinism seems to be guaranteed, is not any longer defendable at least since the work of Poincaré and Hadamard on sensitivity to initial conditions. Due to this property, the trajectories of certain deterministic systems (deterministic in the sense that they are governed by deterministic equations) exponentially diverge after a certain time, and predictability on trajectories becomes impossible.

Thus how does one know if a system is deterministic? The question "does the state of a system at a given instant *t* determine its state for every following instant *t*'?" is a theoretic question. In practice, if one asks: "can I effectively calculate or predict the future state of the system on the basis of its present state?" the answer is – in most cases – negative. Due to sensitivity to initial conditions, determinism and unpredictability are perfectly compatible: the dynamics of deterministic systems (deterministic in a theoretical, in principle sense, as captured by the deterministic nature of their equations) produces unpredictable behaviors, when they are in their chaotic regime (see for example the dynamics of the dice in the contribution of Michel Le Bellac, this volume). Thus, in general, predictability cannot be taken as a way to discriminate about the determinism or the indeterminism of a system, taken as an ontological property.

In this paper I used the term "deterministic" only to qualify mathematical models, and not the material, experimental systems these models should represent. The problem of predictability, as Poincaré and Duhem understood, lays in the irreducible distance between the mathematical and the physical worlds, this latter being submitted to measure, and thus to finite precision.

I tried and show how, in the field of chaos physics, the nature of this limitation has been a motor of discovery of other forms of predictability. The renouncement to a rigid association between a model and a material system has been a necessary step in this direction, towards an always renewed invention of a meaningful relationship between the mathematical and the material world. Images of epigenetic landscape seem to point towards this direction, too.

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[11] The reader can find a stimulating analysis of the notions of program, life, and causality, following Schrödinger's What is life?, in Longo (2009).

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