



Jacques Monod – A theorist in the era of molecular biology / Un théoricien à l'ère de la biologie moléculaire

## Monod's conception of chance: Its diversity and relevance today



### *La conception du hasard selon Monod : sa diversité et sa pertinence aujourd'hui*

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#### ABSTRACT

In his famous book *Le hasard et la nécessité* (1970), Monod claims that natural evolution is based on the interplay between chance and necessity bringing about adaptive evolutionary change. This article addresses a set of related questions about Monod's conception of chance: what does he mean when he uses the term "chance"? Does he invoke one or many different concepts of chance? What are the implications of his conception about the issue of the deterministic or indeterministic nature of the biological world? Is Monod's view of what chance is relevant in contemporary biology? This paper, structured by these four questions, aims at providing a synthetic study of the way Monod conceptualizes chance, particularly highlighting the metaphysical and epistemological implications of his conception and its value in biology today.

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#### RÉSUMÉ

Dans son fameux livre *Le hasard et la nécessité* (1970), Monod soutient que l'évolution naturelle est basée sur l'interaction du hasard et de la nécessité produisant du changement évolutif adaptatif. Cet article soulève un ensemble relié de questions au sujet de la conception du hasard chez Monod : qu'est-ce qu'il entend par le terme « hasard » ? Invoque-t-il un ou plusieurs concepts différents de hasard ? Quelles sont les implications de sa conception quant à la question de la nature déterministe ou indéterministe du monde biologique ? Sa vision de ce qu'est le hasard est-elle pertinente en biologie contemporaine ? Cet article, structuré par ces quatre questions, vise à fournir une étude synthétique de la manière dont Monod conceptualise le hasard, en soulignant tout particulièrement les implications métaphysiques et épistémologiques de sa conception ainsi que sa valeur en biologie aujourd'hui.

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## 1. Introduction

In his famous book *Le hasard et la nécessité. Essai sur la philosophie naturelle de la biologie moderne* (1970),<sup>1</sup> Jacques Monod claims that the evolution of living systems is based on chance and necessity, which are both required for the interplay of perturbations and invariance to result in evolutionary adaptive change. More precisely, on the one hand, if there was no chance, there would be no new variation because of the intrinsic rigorous invariance of living beings, and so no evolution. On the other hand, with no necessity (i.e., the intrinsic conservative character of living beings), life on Earth would die out driven by the negative effects of chance; anyway, the novelty produced by chance could not be integrated into living systems (the reign of necessity) and would fail to be conserved over evolutionary time.

What does precisely Monod mean when he talks about chance and necessity in the natural world? His conception of chance is the focus of the present article. Before starting to deal with it, and in order to fully understand the origin and role of chance in Monod's view of evolution, three main points about what he means by the term "necessity" should be recalled.

First, according to Monod, the macroscopic level of the organism, where natural selection works, is the reign of necessity, of coherence and rigorous requirements [1]: chance is excluded at this level. In particular, necessity is the characteristic of what he calls the "teleonomic system" or "teleonomic apparatus" (i.e., the organism), whose structures, performances and activities (in particular, the conservative perfection of the DNA replicative apparatus) all contribute to the success of the same essential project: the transmission of the species-specific content of invariance from one generation to the next (i.e., the "teleonomic project" – *ibid.* [1], p. 27).

Second, Monod identifies three main general properties of living systems that, together, allow one to distinguish them from every other kind of objects, especially from artifacts (*ibid.* [1], pp. 22–25):

- *teleonomy*: living systems are objects endowed with a project, which is the transmission of the content of invariance specific to the species. All activities linked to reproduction, as well as to survival and multiplication, can participate in the transfer of the quantity of information that ensures the realization of such teleonomic project;
- *autonomy*: living systems are machines able to perform autonomous morphogenesis, i.e., they can build themselves autonomously via deterministic, internal, morphogenetic interactions and nearly no input from the outside;
- *invariance (or invariant reproduction)*: living systems are able to reproduce and transmit without variation the

information for their complex macroscopic structure, conserving it from one generation to the next.

Third, as said above, Monod claims that the macroscopic structure of living systems is the result of complex processes that have nearly nothing to do with the action of external forces. The entire structure, from its general form to the details, is rather the result of internal morphogenetic interactions. He qualifies them as "autonomous, precise, rigorous determinism implying a nearly total freedom with respect to external agents or external conditions" (*ibid.* [1], pp. 23–24). Thus, according to him, the structure of living systems attests to their internal determinism, which turns out to be a defining property of their own organization. Monod also implicitly seems to conceive forces external to organisms as indeterministic, or chancy, which sends me back to the main question of this article about his conception of chance.<sup>2</sup>

The analysis I provide here is mainly based on Monod's book *Le hasard et la nécessité* (1970). Similar analyses can be developed with reference to the paper he wrote in 1973 in order to react to the criticisms provoked by the publication of his book, as well as to the conference he gave at the Rockefeller Foundation, in Italy, in 1972 (then published in 1974). I like to point out that I do not intend to deal with Monod's view about the role of chance in the origin of human species and, more generally, in the origin of life. So, for instance, I will not discuss Monod's claim that life and the evolution of human species are very improbable and even unique events.

The present study is driven by the following interconnected questions: what does Monod mean when he uses the term "chance"? Does he invoke one or many different concepts of chance? Then, if he mobilizes several concepts, what are the similarities and differences among them, in particular as concepts of subjective or objective chance and on their implications about the issue of the deterministic or indeterministic nature of the biological world? Finally, is Monod's view of what chance is still relevant today in biology, in particular with respect to the research advances of the last 20 years?

The article is structured in four sections. The first introduces the usual answer to the question of what chance is according to Monod. In the second section, I identify three concepts of chance in his writings (mainly, in *Le hasard et la nécessité*) and analyze their main features, their differences and analogies, as well as the connections among them. The third section is focused on some specific features of Monod's concepts of chance that are particularly controversial or puzzling, and so could be put into question. Finally, in the fourth section, I evaluate the current empirical relevance of Monod's concepts of chance in the light of the research advances, in biology, of the last 20 years. My objective is to provide a synthetic study of the way Monod conceptualizes chance, which highlights its metaphysical and epistemological implications and helps to perceive its actual value in contemporary biology.

<sup>1</sup> All the passages quoted in this article come from the original edition of Monod's book, published in French in 1970. Unless otherwise indicated, translations are mine.

<sup>2</sup> I will come back later on to the question of whether Monod actually attributes indeterminism to forces external to living systems.

## 2. What is chance according to Monod? The usual answer

“The initial elementary events opening the path of evolution to those intensively conservative systems that are living beings are microscopic, fortuitous and without any relation to the effect they can produce in the teleonomic functioning.

But once recorded in the DNA structure, the singular accident, and as such essentially unpredictable, is mechanically and faithfully replicated and translated, namely both multiplied and transposed in millions or billions of exemplars. Taken out from the reign of pure chance, it enters into the reign of necessity, of the most remorseless certainty. For it is at the macroscopic level, the organism level, that selection works.

... Selection works on the products of chance and cannot fuel elsewhere; but it works in a domain of rigorous requirements from which chance is banished” [1].

This passage contains all the elements we need to answer the question addressed by the title of this section: it is a sort of implicit summary of Monod’s (multiple, as we will see) conception of chance and of the way he interprets the opposition between chance and necessity in the natural world as well as their interaction.

First of all, Monod clearly distinguishes the levels at which chance and necessity respectively intervene: chance pertains to the microscopic level, where genetic mutations (“the initial elementary events”) occur, producing new hereditary variation; necessity pertains to the macroscopic level of individual organisms where natural selection takes place. Second, according to Monod, microscopic events are “fortuitous and without any relation to the effects they can produce in the teleonomic functioning”. Moreover, they are “essentially unpredictable” events “taken out from the reign of pure chance”. On the contrary, macroscopic events belong to the reign of “necessity, of the most remorseless certainty”. At this level, natural selection operates on chance products and integrates some of them – those which “do not reduce the coherence of the teleonomic apparatus” – into “the domain of rigorous requirements where chance is banished” (ibid. [1], p. 136).

On the basis of all these elements, the usual answer, in the literature, to the question of what is Monod’s conception of chance (namely, the chance of genetic mutations at the origin of new hereditary variation) gives a special attention to the first paragraph in the quotation above, claiming that genetic mutations are not produced with a view to the adaptation of the organisms concerned and their species (see, e.g., [2,3]). This is nothing but the Darwinian concept of chance variation [4], which is reminiscent of Aristotle’s idea of *tuché* [5], the term “chance” referring to the fact that variation is “non intentional” or “not by design”.<sup>3</sup>

Such a common answer is certainly not wrong, but should need additional clarifications. In fact, the idea of “chance variation”, which is one of the central tenets of the theory of evolution since Darwin, have been put into question on the basis of recent empirical results about mechanisms of genetic mutation (see, e.g., [7]). Thus, it should be defined more precisely in order to deal with attacks against its current validity. But this is the topic of another paper [8]. The important point to stress here is the univocal character of such usual answer about Monod’s conception of chance: it is limited to one specific concept of chance and does not exhaust the several meanings Monod attributes to it, which is particularly apparent in *Le hasard et la nécessité*.

## 3. Three meanings of Monod’s concept of chance

The first meaning I have just mentioned is what Monod calls “absolute coincidence” (ibid. [1], p. 128). This concept is contained in the Aristotelian idea of chance as “absence of design” that later, in the 19th century, Cournot defined in meaningful terms: he claimed that a chance event arises from the intersection of two (or more) totally independent causal chains [9]. Monod does not explicitly make reference to either author. However, he illustrates this concept of chance by an example similar to those used by Aristotle and Cournot (that which probably attests that he might know their views): the story of Doctor Dupont and the plumber Dubois. Dr. Dupont is urgently called to visit somebody who is ill. In the meantime, Dubois, the plumber, works in the building just next to the house of the ill person, Dupont’s patient. At some point, Dubois drops his hammer by mistake, which falls from the window and hits Dupont, who is walking in the street just under the window. The hammer smashes Dupont’s head and he dies.

In Cournot’s terms, the accident (Dupont’s death) is provoked by the intersection of two deterministic causal chains that are totally independent from each other. Actually, in the first chain bringing Dr. Dupont to walk under that window at that moment, there is no reason for the fact that Dubois, the plumber, drops his hammer by error just from that window at that same moment, and vice versa. In the same way, a genetic mutation (e.g., a replication error which has been integrated into the genome) emerges from the intersection of the two following, totally independent, causal chains: the series of events provoking the change in the DNA sequence during replication on the one hand, and the causal chain determining the functional consequences of the genetic change, which depend on many other factors and variables such as the structure of the protein produced from the modified DNA sequence, the role of the modified protein, its interactions and the reactions it catalyzes, and more generally the internal and external environment, on the other hand. From a Darwinian perspective Monod sticks to, the first causal chain is totally independent of the second one, which determines the adaptive value of the replication error (the mutation), involving a causal role for the environment.

<sup>3</sup> For a synthetic analysis of Darwin’s concept of chance variation and its relationship with the Aristotelian account of chance, see [6] and ibid. [1], p. 128.

The concept of chance as “absolute coincidence” is, according to Monod, a concept of essential chance (“objective” chance, as Cournot would say): genetic mutations are not just “operationally” unpredictable, but because of their very nature, “essentially”, and so we can make no prediction about them (ibid. [1], pp. 128–129). More precisely, what Monod sometimes also qualifies as “uncertainty” about genetic mutations is not due to our ignorance of their proximate and ultimate causes or, as in the case of the wheel of fortune or of the game of dice, to our practical inability to know and precisely govern all the variables involved in the mutational process. In other words, chance as “absolute coincidence” is not a way to account for our lack of knowledge or, more appropriately, a way to call it and fulfil the epistemic gap it leaves. On the contrary, Monod strongly argues that this concept refers to an objective feature of the natural world.

It is also interesting to note that the idea of “absolute coincidence” is non-committal with respect to the metaphysical issue of determinism or indeterminism, which means, in the case of genetic mutation, that it does not imply to conceive genetic mutations as the result of a deterministic or indeterministic molecular process. At some point, Monod conveys this idea by claiming that the causes of mutation can be deterministic or not (ibid. [1], p. 129). Then, he adds (and Cournot would agree with him) that chance as “absolute coincidence” is not compatible with Laplacian determinism, i.e., a metaphysical conception of determinism as global: in a Laplacian universe, the entire universe and each particle composing it were, are and will always be governed by the same deterministic and necessary laws; as a consequence, every event is in principle predictable with absolute certainty. Actually, there is no possibility for independent deterministic causal chains *à la* Cournot, and so no place for essential or objective chance (but only for chance as ignorance, i.e., “operational chance” – ibid. [1], pp. 128–129).

There is another way Monod conceives the chance of genetic mutations, which seems to take a much more prominent place in his writings, especially in his 1970 book: “pure chance” or chance governing the microscopic quantum (atomic and subatomic) level. Monod’s idea is that, as genetic mutations are microscopic events, they cannot escape quantum perturbations: they are quantum events to which the uncertainty principle<sup>4</sup> applies; thus, they are “essentially unpredictable because of their very nature” (ibid. [1], p. 129).

The concept of “pure chance” also designates something essential or objective: chance is a property of the

physical matter at the microscopic level. However, the uncertainty and unpredictability it refers to is more radically essential than the unpredictability due to “absolute coincidence”. The main difference between the two is that “pure chance” implies a commitment to indeterminism, in particular to the indeterministic character of genetic mutations from the metaphysical point of view.

It is worth underlying that Monod presupposes an indeterministic interpretation of quantum mechanism (see footnote 4). He knows that there is no consensus about how to interpret the uncertainty principle, and admits this point (ibid. [1], p. 129). This is the reason why he suggests to go back to chance as “absolute coincidence” and to stick to it, which is a concept of objective chance as well. He is, in fact, particularly attached to the idea of chance as something objective, even though he insists on the essential, unavoidable, character of chance at the microscopic level (i.e., “pure chance”). Unfortunately, he does not seem to see, or to explicitly acknowledge, the important difference between “absolute chance” and “pure chance”, namely, their different commitment with respect to the metaphysical question of determinism and indeterminism.

In *Le hasard et la nécessité*, Monod invokes another concept of chance, this time for characterizing the result of gene expression, i.e., the chain of polypeptides (amino acids) composing a protein. He argues, as follows, that protein sequences are governed by the laws of chance:

“... these structures are ‘by chance’ to the extent that, by exactly knowing the order of 199 residuals in a protein of 200, it is impossible to formulate a rule, theoretical or empirical, allowing one to predict the nature of the only residual that has not yet been identified by the analysis” (ibid. [1], p. 110).

It is easy to see the strong resemblance to the way chance, or randomness, is defined in the context of the algorithmic theory of information (see, e.g., [12,13]). More explicitly, Monod claims that no rule can allow us to infer which amino acid will follow another one along the polypeptide sequence of a protein, because no structure, no regularity, characterizes this sequence: no other law than the laws of chance (i.e., probability laws) applies to it. Winking to Kolmogorov’s particular definition of randomness in terms of complexity [14], I suggest calling this third meaning of chance “incompressibility”. In fact, even though Monod makes no explicit reference to the algorithmic theory of information and complexity, the concept he applies to polypeptide sequences sends us back to it, in particular to the concept of a random sequence or string (a binary sequence of 0 and 1), which is defined as follows: a string is random if and only if the minimal (binary) program able to produce it is at least as long as the string (in other words, the program consists in the complete transcription of each element of the string). Thus, the string is incompressible: it cannot be reduced to a more compact and economic form because of its lack of regularity, structure, pattern; in other words, because it is not constructed on the base of any rule or law.

<sup>4</sup> According to the uncertainty principle, formulated by Heisenberg in 1927, the properties of a quantum system, for instance, the position and the momentum of an electron, are not independent, but complementary variables. As a consequence, there is a fundamental limit to the precision with which certain pairs of properties, such as position and momentum, can be known simultaneously. This principle can have different interpretations. According to the dominant, indeterministic one, the exact values of the properties of a microscopic system cannot be known in principle because they are fundamentally indeterminate [10]. This is not the case for the deterministic interpretation, which introduces the idea of hidden non-local variables in order to account for the uncertainty of measure [11].

Monod applies this same idea to the polypeptide sequence of a protein. Analogously to a random string, the only thing one can say about it is in terms of probability. In a random binary string, the frequency of 0 and 1 tends, in the limit, to be equal (50% of 0, 50% of 1), and this is in part because of the independence between the two digits (0 and 1). In an analogous way, the average frequency with which some amino acid  $a$  follows another one  $b$  along a polypeptide sequence is equal to the product of the average frequencies of the two amino acids in the protein sequence, i.e.,  $P(a \text{ and } b) = P(a) \cdot P(b)$ , the occurrences of  $a$  and of  $b$  being independent.

It is worth asking whether chance as “incompressibility” is a concept of objective chance. Again, Monod presents it as an essential unpredictability, in part because of his categorical refusal of subjective chance as ignorance. However, incompressibility does not seem to involve any commitment to the deterministic or indeterministic character of the process producing the random sequence (which is, originally, the process of genetic mutation in the case of the polypeptide sequence, as we will see below). It could be a deterministic one, like in the case of the function “random”, deterministically producing random numbers or strings of numbers. But it can also be an indeterministic process, such as a quantum generator. Actually, we cannot know whether the generating process is deterministic or not on the basis of the random character of its result, i.e., the sequence of binary bits or, in the case of proteins, the sequence of amino acids.

To sum up, Monod does not invoke one but three different concepts of chance: “absolute coincidence”, “pure chance”, and “incompressibility”. They are all intended to be concepts of essential unpredictability or, in different terms, of objective chance. Only “pure chance” implies a strong commitment to indeterminism at the microscopic level, even though this depends on another, questionable, commitment to an indeterministic interpretation of the quantum theory. On the contrary, chance as “absolute coincidence” and as “incompressibility” is less demanding than “pure chance” from the metaphysical point of view.

Is there a connection among these three concepts according to Monod? When he talks about the random character of the primary structure of a protein (i.e., its polypeptide sequence), he suggests that the incompressibility (as I call it) of its sequence is “the pure product of a choice made by chance” (ibid. [1], p. 111). Does he refer to “absolute coincidence” or to “pure chance”? Apart from that, Monod certainly refers to the process of genetic mutation, which reiterates at each generation and thus creates the DNA sequence involved in the synthesis of the polypeptide chains of proteins.

#### 4. Monod about chance: a radical view?

Monod’s three different ways to conceive chance are, from some respects, too radical. For instance, let us consider chance as “absolute coincidence”. By claiming that the two (or more) causal chains whose intersection generates a chancy event are “absolutely” independent, he seems to maintain that such chains cannot have a common

cause. In the case of genetic mutation, it means that the causal chain leading to a replication error (the mutation) and the one determining the functional adaptive role of it cannot have a common cause, if their intersection is conceived as an “absolute coincidence”. Unfortunately, Monod does not seem to admit that, on the contrary, moving back along these chains, it could be possible, and even probable, to find a cause common to them all. Let us consider again the case of a genetic mutation that turns out to be functional for the organism concerned. Imagine a situation (largely acknowledged in biology at the time of the publication of *Le hasard et la nécessité*) where an environmental change (e.g., a thermal stress) induces an increase of mutation rate, which turns out to be useful for the organisms concerned in that environment. In this kind of situation, there is no absolute causal independence between the two following chains: the one producing the increase of mutation rate and, more specifically, some modification of the DNA sequence; the other one producing the environmental change and so, in part, at the origin of the adaptive value of the increase of mutation rate and of the specific genetic mutation that occurred. The lesson we should take from this example is that, literally speaking, Monod’s idea of total independence, conveyed by chance as “absolute coincidence”, is too radical: not only is it empirically inadequate, but it also does not correspond to the consensus view, in molecular and in evolutionary biology, at that time (on this point, see [3]).

Monod would have gained a deeper understanding of “absolute coincidence” by a close look into Cournot’s work, who clearly explained the nature of the independence characterizing the relationship between causal chains giving rise to a chance, or fortuitous, event [9]. In fact, Cournot does not eliminate the possibility that two or more causal independent chains could have a common cause. How is that possible in his account of what chance is? He distinguishes between causes and reasons, and argues that independent causal chains can have a common cause, if we go back up along them, but are not governed by the same law, i.e., by the same reason. In other terms, they are not causally but nomologically independent, that allows the rise of chance events at their intersection.<sup>5</sup>

On this basis, two interpretations of Monod’s conception of chance as “absolute coincidence” are possible:

- he uses the words “totally” and “absolute” in an inappropriate manner and really conceives chance according to Cournot’s meaning;
- he literally means what he says, but does not realize that his conception of chance is empirically inadequate because too radical.

Another point on which Monod is open to criticism is his use of epistemic terms such as “uncertainty” and “unpredictability” in the context of an essential, or objective, conception of chance. He should have rather talked of “indeterminacy”, for instance. In fact, his

<sup>5</sup> For a clear analysis of Cournot’s distinction between causes and reasons, see [15].

vocabulary is confusing because it mixes up epistemological and metaphysical concepts: the concepts of uncertainty and unpredictability referring to our epistemic relationship with the world on the one hand, the metaphysical concept of essential chance on the other hand. But, of course, being charitable, we can make sense of Monod's use of these epistemological terms (uncertainty, unpredictability): he aims at stressing that, because of objective reasons, no prediction can be made about intrinsically chancy events such as genetic mutations. It is not a matter of epistemic boundaries.

There is also a nearly paradoxical aspect of Monod's view of chance and evolution it is worth stressing. He claims that chance is an external perturbation and the only source of variation: without chance, there would be no evolution (ibid. [1], p. 130). In this context, does he mean that chance is not biological, in the sense that it is simply a matter of the physical properties at the microscopic level, and therefore that evolution is not an intrinsic feature of living beings? In the following passage, Monod seems to positively answer to my suggestion:

“... modern biology acknowledges... that all the properties of living beings lie on a fundamental mechanism of molecular conservation. According to modern theory, *evolution is by no means a property of living beings* because it takes root in the *very imperfections* of the conservative mechanism that is their unique privilege” (ibid. [1], p. 130).

This passage tends to favor the thesis, I maintain, that Monod conceives the chance of genetic mutation, first of all, as “pure chance”: chance is not a biological but a merely physical feature of the microscopic level. This goes hand in hand with the interpretation of Monod's reflection in *Le hasard et la nécessité* as committed to a deterministic view of the internal functional organization of living systems: he adheres to the deterministic paradigm characterizing molecular biology at his time and, more precisely, to the idea of a genetic deterministic program for development and evolution (in particular, ch. 4–5).

Last but not least comes Monod's surprising idea, mentioned above, of chance as no more than a mere, inescapable, matter of fact: it is not specifically biological and characterizes perturbations affecting non-living systems as well. However, as he says, chance intervenes in his view of natural evolution as an explanation of the origin of new variation (i.e., novelty) and accounts for the “complete creative freedom” of evolution (ibid. [1], p. 131). Therefore, chance plays a much more relevant role in Monod's view than a mere matter of fact: chance is external, non-biological but, with natural selection, it is plainly part of the explanation of how natural systems evolve.

## 5. Monod's concepts of chance and biology today

A closer look at Monod's conception of chance reveals some of its questionable or puzzling aspects I have mentioned above. Moreover, it opens a discussion on its current relevance with respect to research advances in biology, since the last twenty years, about genetic

mutation and the evolutionary process. Let us highlight three critical aspects of his view in this respect.

First, because of the total, or absolute, independence Monod sees between the occurrence of a genetic modification and its functional adaptive value, his concept of chance as “absolute coincidence” fails to be empirically adequate. Let us just think of what biologists call “mutator mechanisms”, discovered in the 1970s and studied all over the last thirty years: they are molecular mechanisms producing an increase of mutation rate in response to stressful environmental conditions (i.e., when more variation could be useful for the organisms concerned in their environment) (see, e.g., [16,17]). In this kind of situation, mutations are causally induced by a change in the environment, and the probability of an adaptive mutation to take place is higher than in a similar situation with a lower mutation rate. Therefore, there is a link, and even a common cause, between the chain leading to the change in the DNA sequence (the mutation) and the chain making this change adaptive: the common cause is the environment.

Second, Monod's idea that chance is just an external perturbation finds a strong challenge in recent researches on mutation rate and on molecular noise (see, e.g., [18,19]). In fact, the trend in current biology is to consider that both of them can be fine-tuned via natural selection depending on the environmental conditions experienced by living systems. More explicitly, these two molecular processes are largely interpreted as traits of living systems, which can be selected and adaptively evolve. This thesis goes in the opposite direction to Monod's conception of chance as something that has nothing to do with the properties of life.

Third, all along his 1970 book, Monod repeatedly stresses the dichotomy between mutation and selection, respectively the source of error and that of conservation, which is based on the chance-necessity dichotomy. However – and this is the case since the first evolutionary models of population genetics in the 1920s –, selection is not conceived as a deterministic process, i.e., a process in which, starting from a given set of initial conditions (gene frequencies in a population and fitness values at time  $t$ ), there is just one possible, unique, result (gene frequencies at time  $t + 1$ ). Selection is rather conceived as a probabilistic sampling process allowing for different final results (in terms of gene frequencies) according to a certain probability law (see, e.g., [20]). Thus, the opposition between mutation and selection cannot literally correspond to the extreme alternative between “pure chance” on the one hand and “strict necessity” on the other one: biological processes should rather be viewed as in between the two.

To conclude, the fact that recent research advances put into question these three aspects of Monod's view of chance does not imply that the three concepts he argues for are no more relevant. Some of them are in need for clarification (in particular, “absolute coincidence” and “pure chance”, as shown above). Moreover, some features characterizing the chance-selection dichotomy, on which he bases his vision of the living world, should be reevaluated and nuanced. However, Monod's account still

represents a very rich analysis of chance in biology and provides a clear starting point for further reflection on the meaning and role of this concept.

## References

- [1] J. Monod, *Le hasard et la nécessité. Essai sur la philosophie naturelle de la biologie moderne*, Seuil, Paris, 1970, p. 135.
- [2] B. Fantini, M.D. Grmek, Le rôle du hasard dans la naissance du modèle de l'opéron, *Rev. Hist. Sci.* 35 (3) (1982) 193–215.
- [3] F. Merlin, *Mutations et aléas : le hasard dans la théorie de l'évolution*, Hermann, Paris, 2013.
- [4] C. Darwin, *The variation of animals and plants under domestication*, 2 vols, John Murray, London, 1886, p. 249.
- [5] Aristote, *La physique*, II, 4, 36 and II, 5, Vrin, Paris, 1999, pp. 32–36.
- [6] F. Merlin, Le « hasard évolutionnaire » de toute mutation génétique, ou la vision consensuelle de la synthèse moderne, *Bull. Hist. Épist. Sci. Vie* 18 (1) (2011) 79–108.
- [7] E. Jablonka, M. Lamb, *Evolution in four dimensions: genetic, epigenetic, behavioral, and symbolic variation in the history of life*, The MIT Press, Cambridge, MA, USA, 2005.
- [8] F. Merlin, Evolutionary chance mutation: a defense of the Modern Synthesis' consensus view, *Philos. Theory Biol.* 2 (2010) e103.
- [9] A.A. Cournot, *Exposition de la théorie des chances et des probabilités*, Vrin, Paris, 1843/1984, p. 55.
- [10] W. Heisenberg, *Physique et philosophie*, Albin Michel, Paris, 1958/1971.
- [11] D. Bohm, A suggested interpretation of the quantum theory in terms of "hidden" variables, I and II, *Phys. Rev.* 85 (1952) 166–193.
- [12] R.J. Solomonov, A formal theory of inductive inference, part I, *Inf. Control* 7 (1964) 1–22.
- [13] G.J. Chaitin, On the length of programs for computing finite binary sequences, statistical considerations, *J. ACM* 16 (1966) 145–159.
- [14] A.N. Kolmogorov, Three approaches for defining the concept of information quantity, *Probl. Inf. Transm.* 1 (1965) 3–11.
- [15] T. Martin, *Probabilités et critique philosophique selon Cournot*, Vrin, Paris, 1996.
- [16] A. Giraud, M. Radman, I. Matic, F. Taddei, The rise and the fall of mutator bacteria, *Curr. Opin. Microbiol.* 4 (2001) 582–585.
- [17] O. Tenaillon, E. Denamur, I. Matic, Evolutionary significance of stress induced mutagenesis in bacteria, *Trends Microbiol.* 12 (2004) 264–270.
- [18] M. Radman, F. Taddei, I. Matic, Evolution-driving genes, *Res. Microbiol.* 151 (2000) 91–95.
- [19] R.J. Johnston Jr., C. Desplan, Stochastic mechanisms of cell fate specification that yield random or robust outcomes, *Annu. Rev. Cell Dev. Biol.* 26 (2010) 16.1–16.31.
- [20] D.L. Hartl, A.G. Clark, *Principles of population genetics*, Sinauer Associates, Sunderland, MA, USA, 1989.