Is a Cognitive Revolution in Theoretical Biology Underway?

Preprint · January 2024

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Abstract: The foundations of biology have been a topic of debate for the past few decades. The traditional perspective of the Modern Synthesis, which portrays organisms as passive entities with a limited explanatory role in evolutionary theory, is giving way to a new paradigm where organisms are recognized as active agents, actively shaping their own phenotypic traits for adaptive goals. Within this context, this article raises the question of whether contemporary biological theory is undergoing a cognitive revolution. This inquiry can be approached in two ways: from a theoretical standpoint, exploring the centrality of the cognitive sciences in current theoretical biology; and from a historical perspective, examining the resemblance between the current state of theoretical biology and the Cognitive Revolution of the mid-20th century. Both inquiries yield affirmative answers, though important nuances will be emphasized. The cognitive sciences' explanatory framework is employed to elucidate the agentic characteristics of organisms, establishing a clear parallelism between the Cognitive Revolution and the present state of theoretical biology.

Keywords: Cognitive Revolution; Theoretical Biology; Conceptual Change; History and Philosophy of Biology; Cognitive Science; Behaviorism.

Competing Interests: Not Applicable

Funding: National Agency of Investigation and Innovation (Uruguay) through grant PD_NAC_2023_1_176930 and the Sectoral Comision of Scientific Investigation (Uruguay) through grant 22520220100257UD

Introduction

Is a cognitive revolution taking place in theoretical biology? Undoubtedly, the question itself needs to be clarified before an answer can be proposed. To this end, I will propose two possible interpretations.

The first interpretation I will call the *theoretical interpretatio*n. From this perspective, we want to know whether part of the explanatory apparatus of the cognitive sciences is beginning to play a central role in current theoretical biology. This means that a theory (from one discipline) influences or interferes with another theory (from another discipline). This entails an epistemic extension of the concepts and explanations we find in the cognitive sciences to biology. So the theoretical interpretation is tied to other questions: are concepts such as representation, perception, or memory central to biology? Is it necessary to introduce *cognitive explanations* in biology?

On the other hand, there is a *historical interpretation*. According to this interpretation, we ask ourselves whether the events in the history of science from which cognitive science emerged are similar to the current situation in theoretical biology and the various controversies that have been on the table for several decades (which we will discuss in the next section). In this sense, the expression *Cognitive Revolution* (with capital letters) refers to a historical event in science that took place in the 1950s and that led to the emergence of the cognitive sciences and the abandonment of the behavioral model that had prevailed until then. It is therefore a question that is posed from the history and philosophy of science through a metatheoretical analysis of each discipline. The historical interpretation thus asks the following question: Is something similar to what caused the move away from behaviorism and the emergence of the cognitive sciences happening now in theoretical biology?

We will analyze each interpretation separately in Sections 2 and 3, even though their connection will be clear. Before we embark on this task, however, we need to ask ourselves a question: What is all this about? On what grounds do we ask ourselves whether or not there is a cognitive revolution in theoretical biology? In this way, it is necessary to introduce the current panorama of theoretical biology.

1. What Is Going on in Contemporary Theoretical Biology?

It is generally known that the foundations of biology were systematized in a sub-discipline of biology itself: evolutionary biology. The other areas of knowledge in biology converge in a unified way in this field to give rise to an organized vision of the world of living beings. In this sense, the first solid and complete theory of evolution is known as the Neo-Darwinian Modern Synthesis (henceforth: MS), it was developed in the first half of the last century, and represents the foundations of mainstream biology. The conceptual apparatus of the MS is rich and sophisticated; at the same time it has several aspects that will not be explored in detail in this paper. Instead, I will focus on one particular phenomenon: the null explanatory function of organisms and their development in evolutionary theory, and consequently, in theoretical biology. As Goodwin (1994, 1) points out:

> Something very curious and interesting has happened to biology in recent years. Organisms have disappeared as the fundamental units of life. In their place we now have genes, which have taken over all the basic properties that used to characterize living organisms [...] Better organisms made by better genes are the survivors in the lottery of life.

How was it that the MS was able to dispense with organisms themselves when explaining organisms and refer to genes instead? When interpreted as a material entity, the concept of the gene has certainly changed throughout history (Griffiths and Stotz (2013). It was initially understood as something found in inherited cells. Then, at the beginning of the 20th century, the gene was placed in the chromosomes. Later, in 1953, Crick and Watson defined the gene at the molecular level. However, the material nature of the gene is not decisive for its explanatory role. As we can see, beyond their physical nature, genes have always been central to the MS. As Ågren (2021, 52) points out, "[t]he key take-home message is that the gene's-eye view wants to talk about genes in an abstract way and happily accepts a bit of fuzziness regarding their physical basis." So what is this abstract use of the word gene that can replace the explanatory role of organisms? The answer lies in the ability to reduce the three central elements of evolution by natural selection to the genetic level (Lewontin, 1974; Godfrey-Smith, 2009): heredity, variation, and fitness. This was the reduction made in the emergence of the MS. Lamarckism was rejected and inheritance was taken to be purely genetic, and to the extent that heritable variations are caused and reduced to the genetic level, the fitness of organisms in a population can ultimately be defined at the genetic level. Over these pillars, Dobzhansky (1951, 16) concluded that "[e]volution is a change in the genetic composition of populations. The study of mechanisms of evolution falls within the province of population genetics."

This view of natural selection encloses a central commitment:[1] Genes must be able to explain the ontogenetic history of organisms. That is, to the extent that traits (and not genes) are the ones that confront the environment that determines the fitness of a species, there must be a link between what is inherited (genes) and what is selected (phenotypes). This link is called the Genotype-Phenotype map (GxP map), i.e. the development of organisms. This was exactly what Crick (1958) postulated in his Central Dogma of Molecular Biology.

[1] It is good to remember that Darwin did not postulate this genocentric view of natural selection, first because the notion of "genes" was introduced in 1909 by Wilhelm Johannsen, and second because Darwin himself accepted Lamarckian inheritance of some kinds, particularly in his 6th edition of *Origin of Species*. In this way, the theory of natural selection was developed into the Genetic Theory of Evolution by Neo-Darwinism, but the genocentric view is not a demand of natural selection theory: natural selection can be embedded in a non-gene-centered position about inheritance, variation, and fitness.

According to Crick's version, the information is transferred from DNA to RNA to the production of proteins in the cells, and never the other way around. There is therefore a causal correspondence between the genetic information and the constructed phenotypic trait, which is essential for the genetic theory of evolution. Given this panorama, it is predictable that, when explaining evolution, organisms are considered as "*vehicles* in which replicators [genes] travel about" (Dawkins, 1982, 82; emphasis in the original). As Hamburger (1980) stated, organisms and their development were put into a *black box* that did not need to be looked into to understand evolutionary processes.

The reason that raises the question of the cognitive revolution, however, is that "the black box [of development] is now being opened to provide a more complete picture of what really happens" (Bateson and Gluckman, 2011, 17). Much of the philosophy of biology today revolves around the role of organisms and their development in evolution and the extent to which the inherited genocentric view is appropriate. A fundamental turning point that has led to the (re)emergence of the organism as a central explanatory element in evolution in recent years is precisely the fundamental empirical advances in developmental biology. In particular, the idea that the development of an organism can be explained solely by looking at its genetic basis was discarded when the Human Genome Project was completed and the true complexity of developmental systems began to be recognized -in the context of so-called *post-genomics* (see Griffiths and Stotz, 2013; Keller, 2002; Moss, 2003; Rheinberger and Müller-Wille, 2020). The idea that genes encode phenotypic traits is being replaced by a holistic view of development in which various genetic, epigenetic, and exogenous resources play a central role in the construction of phenotypes (Oyama et al., 2001), reintroducing the importance of behavior and inner (mental) states in the explanation of gene expression (Rossi, 2002; Michel and Moore, 1995). Likewise, the true role of epigenetic processes in the origin of phenotypic variation has begun to be recognized (Sultan, 2015; West-Eberhard, 2003) and epigenetic inheritance systems have been found in all living things (Jablonka and Lamb, 2020).

The aim of this article is not to revive this debate. Rather, I would like to give a metatheoretical analysis of this debate that helps to shed light on the current scenario in the philosophy of biology and to indicate a possible path that this debate could take in the future. The moral for this section is that the contemporary philosophy of biology is experiencing a moment of intense controversy in which various empirical advances invite us to rethink the foundations of biology, especially because in the reductionist model of the MS "an immense amount of biology was missing" (Lewontin, 2010). Today, organisms are once again at the center of theoretical biology (Baedke, 2018; Bateson, 2005; Nicholson, 2014; Gilbert and Sarkar, 2000).

In this article, I will use the term *developmental turn* (Rama, 2022) to refer to the proposals that have generated new areas of knowledge in biology, which in turn aim to reconsider and reformulate some of the ideas inherited from the MS, such as Eco-Devo, Evo-Devo, Developmental Systems Theory, Niche Construction Theory, Autonomous Systems Theory, Extended Inheritance Systems Theory, Extended Evolutionary Synthesis, and Systems Biology, among others.

2. Interpretation 1: The Use of the Conceptual Apparatus of Cognitive Science

Organisms are once again the protagonists of their own history. They are once again the key to explaining their own existence and the producers of those central characteristics in evolution. The question we now face is whether or not the cognitivist apparatus in biology is necessary to explain the causal role of organisms in evolution. Once organisms are no longer passive systems controlled by genetic engineering that evolved over millennia, their role as active agents capable of adaptive action becomes more important. How do we explain this agency and the diverse processes it entails?

As a first approach to this question, we can note the recent growth and importance of *cognitive biology* (Auletta, 2011; Baluška and Levin, 2016). Cognitive biology combines different approaches in biology that take into account the cognitive abilities of organisms. Cognitive biology analyzes a wide variety of living systems and the various natural abilities that are characteristic of cognitive systems. A central question within cognitive biology concerns the existence of cognition in unicellular organisms, both eukaryotes and prokaryotes (e.g. Lyon, 2015; Shapiro 2007; Kováč, 2006; Reber et al., 2024; Ford, 2017). The main task behind this question is to investigate the presence of various cognitive phenomena in cells, from memory, learning, movement, or perception, and how cells can manipulate and process different types of information, both endogenous and exogenous, to produce behavior that corresponds to their living conditions (see special issue on basal cognition in Levin et al.

(2021) and Lyon et al. (2021)). This ability appears to be a minimum requirement for cognition which many discuss under the term *minimal cognition*. Research into signaling systems, signal processing, and signal transmission in various information networks thus brings together research into cellular cognition.

Another area with a strong cognitive approach in biology is plant cognition. Here we find a variety of approaches to the cognitive abilities of plants, from their neurobiological basis (Brenner et al., 2006), their ability to feel (Calvo et al., 2017), to experience a specific ecological niche (Sultan, 2015), to behave adaptively (Calvo and Kijzer, 2011) or intelligently (Trewavas, 2014), or even to have consciousness (Segundo-Ortín and Calvo, 2021) or thoughts (Marder, 2013). Again, this involves information processing and signaling systems associated with the intrinsic ability of plants to regulate their interaction with the environment through various responses, be it through morphology, movement, behavior, and other physiological changes.

As we can see, there are various proposals in the field that defend and use the cognitivist apparatus, even to explain unicellular organisms. It is important to point out that the question of cognition in biology is an independent topic –or not necessarily related– to questions about the foundations of evolutionary biology (Section 1). Some of the proposals mentioned here simply ask about cognition in cells or plants, without assessing what consequences this has for evolutionary theory; they are worried about cognitive biology, not its evolutionary implications. In Section 2.3, I will outline some of these implications. First, however, it is important to make some categorizations about the different ways in which cognitive science and biology are connected. Although there are different fields of knowledge devoted to the study of biological cognition in various kinds of organisms, there are also several nuances in the use of the explanatory apparatus of cognitivism in biology. Not all proposals agree on what we should transfer from cognitive science to biology. We will therefore present various proposals, their commonalities, and their inconsistencies below.

2.1 Which Theories Need to be Extended to Biology?

The panorama of cognitive sciences is diverse and there are different approaches to cognition with many ramifications. Consequently, different positions in biology arise depending on the model and framework adopted from cognitive science. Cognitive approaches to biology inherit the inherent pluralism of cognitive science.

In a strict terminological sense, *cognitivism* refers to the classical approach in cognitive science, which we will refer to here as *classical cognitivism*. A central pillar of classical cognitivism is the Representational Theory of Mind (RTM): the idea that cognition consists of the processing of information with semantic content, referred to as *mental representation*s (see Schulte (2023) for a recent introduction to the topic). Processing mental representations about external features allows us to describe intentional states and to explain behavior as something caused by intentional states. Another pillar is the so-called Computational Theory of Mind (CTM): the idea that the processing of mental representations in cognitive processes can be described in terms of computational operations. If we rely on this classical view, cognitive biology can appeal to the explanatory role of representational and computational explanations to deal with organisms' activities (Bray, 2009; Prusinkiewicz and Runions, 2012; Lahoz-Beltr et al., 2014; Arnos, 2004; Dodig-Crnkovic, 2014)

However, beyond the boundaries of classical cognitivism, other positions in cognitive science have had a major influence on biology. For example, *enactivism* is presented as a radical theory in cognitive science (Hutto and Myin, 2013; Thompson, 2010). According to this view, the classical representationalist model has serious foundational problems. Cognition is not the processing of representations in the brain, but an action that takes place in a particular environment and is distributed across the organism's body. In contrast to classical representationalism, enactive approaches generally assume an "intentional directedness that is not contentful" (Hutto and Myin, 2013, 82), i.e. intentional processes are based on the directedness of organic action. Without entering into the debates of the philosophy of cognitive science, the relevant point is that the conceptual apparatus of enactivism has been applied to biology (e.g. Di Paolo et al., 2017; de Jesus, 2016; Froese and Di Paolo, 2011). As expected, the non-contentful account of intentionality is easier to digest by biologists: It is not necessary to assume internal cognitive constructs with semantic properties to explain cognitive biology, but merely a kind of directedness in action. In particular, enactive explanations of cognition are associated with non-linguistic cognitive abilities. In this way, enactive approaches to cognition are more seductive for biological explanations: There is no need to assume complex mental phenomena inherent in higher cognitive functions such as language.

Moreover, other positions in biology adopt, for example, the apparatus of Ecological Psychology, a radical position in cognitive science developed by James Gibson in 1979. The central idea in this case is that the information available to cognitive systems should not be understood as something internal to the system and detached from the environment. Instead of appealing to the internal manipulation of mental representations, they use the term *affordance* (Heras-Escribano, 2019). An affordance is defined as a relationship between the environment and the organism: affordances are opportunities to act in a particular environment. A clear example of the use of this cognitivist apparatus in biology can be found in the work of Walsh (2013; 2015; see also Withagen and Wermeskerken (2010)), who claimed that "[a]daptive evolution is not most perspicuously described as the process of form solving adaptive problems set by the organism's physical environment, but as form creating and then responding to an ever-changing system of affordances" (Walsh, 2015, 178). Walsh's proposal probably represents the most integrated vision between evolutionary theory and the use of the apparatus of cognitive science in biology, which he calls *Situated Darwinism*. Moreover, Richard Lewontin (2000), a forerunner of the developmental turn embraces a similar position to organismic activities as the one developed by Gibson. Lewontin's famous quote "[t]here is no organism without an environment, but there is no environment without an organism" could be attributed to Gibson (Lewontin and Levins, 1997, 76). In this sense, ecological psychology is offered to the new trends in theoretical biology as a well-developed and philosophically founded approach to organism-environmental relationships, and central phenomena in the attempt to construct a context-sensitive view of organismic development (Sultan, 2015).

Besides the different approaches in cognitive biology, in all these cases –classical cognitivism, enactivism, and ecological psychology– cognitive science overlaps with biology. This is partly because in some cases it has been biology itself that has inspired various theories in cognitive science. Uexkull's work in ethology and his concept of *Umwelt* influenced post-cognitivist approaches in ecological psychology (Heras-Escribano and DeJesus, 2018; Feiten, 2020) and today von Uexküll is called to play a central role in theoretical biology (Rama, 2021, forthcoming). Similarly, the work of Maturana and Varela in cybernetics were cornerstones of enactivism, and today enactivism is useful in theoretical biology. In this sense, an exchange between cognitive science and biology has been taking place for decades, sharing philosophical foundations and ways of understanding the living sciences.

The aim here is not to defend a particular cognitivist theory. However, it is relevant to note that the discussion about which theories need to be extended to biology runs parallel to the "explanatory turn" in cognitive science (Schulte 2020, chapter 7). The explanatory turn consists of evaluating different theoretical approaches in terms of the explanatory power gained. Importantly, the role of cognitivist theories in theoretical biology is relative to their explanatory value. As expected, the requirements of each discipline are different: the adequacy of a cognitive theory is evaluated on different grounds in biology than in cognitive science.

A clear difference is that certain explanations seem to be at odds with biological explanations. This is true of the notion of representation, a highly controversial issue in cognitive science and the reason why many scientists have chosen to move beyond classical cognitivism. While it is not radical to assume explanations for complex human behavior through mental representations, the assumption of mental representations in all biological taxa does seem radical. Unsurprisingly, post-cognitivist theories in biology are more "biology-friendly", as they can achieve similar explanatory gains without involving single-celled organisms in "mental puzzles". In other words: If we pay a high price (e.g., accepting counterintuitive representationalist claims), we expect a valuable explanatory *quid pro quo*. However, classical cognitivism has its own advantages and a well-developed philosophical framework. Firstly, there are different interpretations of the CTM as well as different representational theories of mental content. Thus, it is not necessary to be committed to *mental representation*, but only to certain representational capacities. Furthermore, classical cognitivism presents representations in a symbol-like manner, but other types of representational theories are not based on symbolic-like structures. These positions reject classical views without adopting radical positions: they are non-classical and non-radical theories. In these cases, representational explanations require a central element, which can be understood differently depending on the representationalist theory: *normative information*. Information processing plays a crucial role in mechanisms that produce an organism's activity and can be judged on normative grounds (e.g., misrepresentations). As we will see in Section 3, information and normativity are central and ubiquitous concepts in the developmental turn. If we take this informational account, representational theories can still be relevant to cognitive biology (Rama, 2022; Shea, 2007; Miller et al., 2023).

There is also a converse situation in which a weakness of radical cognitivism does not affect its usefulness for biology. For example, enactivism is strongly motivated by explanations based on dynamic systems theory; it explains behavior in terms of dynamic changes that occur over time as a result of the interaction of different components. Classical cognitivism argues that this is not a mechanical explanation of behavior; we are not pointing to causal processes that lead to a behavioral outcome (e.g., Bechtel (1998)). Thus, if we extend the dynamic explanation to developmental biology, we would not show how organisms causally affect evolutionary trends. Without entering into a discussion about the validity of this argument, dynamic explanations are useful in developmental biology. For example, various dynamic approaches have been used by the developmental turn to define goal-directedness in various biological phenomena, such as plasticity or niche construction, using the concept of an attractor to define a stable endpoint in biological processes, as proposed long ago, by Waddingoton in his Epigenetic Landscape (Tronick and Hunter, 2016).

This debate is open for further research and the land is fertile for future interdisciplinary investigations. There are several possible bridges between cognitive science and biology. Each of them has its advantages and disadvantages, both in cognitive science itself and in biology. The discussion of the explanatory utility of each theory in biology thus may help to shape future research in cognitive biology.

2.2 Which Concepts Need to be Extended to Biology?

Aside from the various theories that exist about cognition and its nature, a variety of approaches to biology arise when we ask which phenomena associated with cognition are present in all living systems. Do all organisms have a mind? Is an organism with memory functions a cognitive system? Does context sensitivity include perception? Is all learning a cognitive process?

When we ask ourselves what it is that is transferred from the cognitive sciences to biology, it is useful to make some distinctions. The question that heads this Section 2.2 is linked to various theses about the *continuity* between organisms and cognitive systems. The best-known and at the same time most radical thesis is the *life-mind continuity thesis* (e.g. Dennett, 2017; Godfrey-Smith, 2016; Thompson, 2010; Wheeler, 2011; Wiese and Friston, 2021). According to this thesis, the mental and the living are coextensive; every living system has a mind, and every system with a mind has life. However, there are other theses about the continuity of properties in the organic world, for example, the *cognition-life continuity thesis* (e.g. Bechtel and Bich, 2021; Shapiro, 2021; Kováč, 2006; Lyon, 2015; Maturana and Varela, 1991). This thesis does not assume that mental states must be attributed to every living system. Rather it assumes that “life requires cognition at all levels” (Shapiro, 2011, 7), and that every living system has cognitive abilities (which can be diverse, of greater or lesser complexity, such as memory, learning, communication, or perception) and vice versa; i.e. that the living and the cognitive are co-extensional. An even weaker thesis could be categorized as a continuity thesis between sensorimotor (SM) systems and the living systems, the *SM-life continuity thesis,* i.e. a coextension between living systems and those systems that adapt their actions to what is perceived in the environment, without this in itself implying the attribution of any mental, phenomenological, or cognitive capacity to living systems (e.g. Van Diujn et al., 2006; Damasio, 2019; Baluška et al., 2022, Barandiaran, 2008).

Furthermore, we need to distinguish between different cognitive phenomena. Perhaps the use of the cognitivist apparatus in biology does not mean that every organism has thoughts or engages in reasoning, but rather that every living system performs tasks that require, for example, memory, learning, or complex communicative systems with their environment. In this sense, only some properties of the cognitive sciences can be extended to biology, without implying continuity between the paradigmatic organisms of the cognitive sciences (animals) and the rest of the living realm. For example, as already mentioned (see references above), the field of plant cognition is very diverse. While some limit themselves to postulating the sensorimotor abilities of plants, others emphasize that plants can think and have consciousness. While some are dedicated to understanding the physiological basis of perception in plants, others summarise this study under the term *plant neurobiology.* When it comes to extending cognitive abilities beyond organisms with a nervous system, the situation is undoubtedly no different from other non-cognitive traits; not all traits that we find in human cognition need to be extended, and those that are extended need not have the same complexity as in the case of human cognition.

The endorsement of some of these theses and the rejection of others is largely related to a semantic question inherent in epistemological debates, namely what we mean by cognition, perception, or mind. The various answers to the question of a cognitive revolution are intersected by a particular position on the semantic value of the categories used in cognitive science. This does not mean that it is a purely terminological question, but theoretical biology inherits from cognitive science various conceptualizations that are in themselves complex and controversial. Again, the explanatory turn is a metatheoretical frame of reference: Whether or not the existence of a cognitive concept in biology is accepted depends on the explanatory power gained. Even if it may seem dubious to attribute consciousness to bacteria, we can achieve an explanatory benefit that justifies our controversial commitment.

However, we could present some positive and negative aspects of each position. For example, the life-mind continuity thesis proposes an evolutionary continuum of mental life. Mind need not be hardwired into neuronal systems, but can be present in various material substrates; mental properties evolved across species and are also relevant to the evolution of species. However, this position is counterintuitive in several respects (e.g., do bacteria have consciousness?), and unless it provides a way to draw boundaries, it is difficult to grasp the differences and distinctiveness of animal and non-animal minds. Similarly, the life-cognition continuity thesis is committed to the idea that at least some cognitive abilities are present in all living systems. This allows for rich explanatory power, as cognitive processes such as learning and memory may be central to explaining cellular and unicellular life. However, it is also difficult to draw boundaries: On the one hand, mental properties must be distinguished from cognitive properties, and on the other hand, it must be explained whether there is a qualitative difference between animal and non-animal cognition. To gain explanatory power, the terms must refer to identifiable natural species with specific natural properties: If we define cognitive categories too broadly, their meaning is lost, and with it the meaning of the continuity theses. Finally, the SM-life continuity seems to be less radical and therefore more suitable for biological explanations, as well as for explaining the active and context-dependent character of life. However, when it comes to overcoming the view of organisms as machines controlled by molecules (genes), we may need something cognitively stronger than sensorimotor abilities.

2.3 The Point of Convergence: Agency

The aim of this article is not to argue for or against any of the various positions described in this section. I have merely limited myself to pointing out various positive answers to the question of the cognitive revolution in theoretical biology (under its theoretical interpretation). All of the proposals mentioned in this section accept that at least some elements of cognitive science have important epistemic value for understanding organisms.

Despite the variety of connections that may exist between theoretical biology and the cognitive sciences, it is possible to find a point of convergence within this pluralism. In all cases, the goal is to justify the role of organisms as *agents*. As Dennett and Levin (2020) point out: "Biology's next great horizon is to understand cells, tissues, and organisms as agents with agendas". Generalizing, we can claim that all applications of the cognitive science apparatus aim to capture or are related to the agentive dimension of organisms. In other words, the thesis that unites the various applications of cognitivism can be called the *agency-life continuity thesis:* Every living system is an agent, and every agent has life (no doubt the notion of agent is also complex, and although there is an entire discipline devoted to artificial agents, there have been various efforts to clarify what characterizes the agency of living systems (e.g., Barandiaran et al, 2009; Kauffman and Clayton, 2006; Okasha, 2023)).

It is therefore not surprising that the concept of *agency* plays a central role in the developmental turn, and that agency is the converging concept of many conceptualizations of the nature of developmental processes and organismal activities. This very idea contrasts with the MS vision in which organisms are not active agents but passive objects when it comes to explaining evolution, as argued most notably by Lewontin (1983; see also Godfrey-Smith (2017)). The clearest approach to evolutionary theory based on the concept of agency in organisms has been recently developed under the term *agential perspective* by Sultan et al. (2022; see Moczek and Sultan (2023) for a special issue on Agency in Living Systems).

Sultan et al. (2022, 1) define agency as "the capacity of living systems at various levels to participate in their own development, maintenance, and function by regulating their structures and activities in response to conditions they encounter". This is the idea that "the agent negotiates its situation" (Walsh, 2015, 210): developmental systems are capable of directing their developmental resources to produce an adaptive and functional phenotypic outcome. Other approaches in biological theory also define agency on these grounds. For instance, autonomous systems theory states that "an autonomous agent is a physical system that can act on its own behalf in an environment" (Kauffman, 2000, 8).

As already mentioned, the central idea behind biological agency is that an organism actively participates in shaping its own conditions of existence, both internally (e.g. through phenotypic plasticity) and externally (e.g.

through niche construction). First, it should be noted that the concept of biological agency is also influenced and motivated by cognitive science and its philosophical foundations. As mentioned earlier, the agentive perspective is motivated by Walsh's view of affordances in biological systems. Similarly, autonomous agents have been influenced by enactivist and phenomenological views of cognition. Other views of agency are linked to the ability of living systems to regulate information processes (e.g. Rama, 2022; Miller, 2017), as we will see in detail in the next section. In this sense, we can conclude that agency is a point of convergence that brings together several proposals from cognitive science. However, biological agency is also a field that has different nuances in relation to the topics discussed in this section: Agency can be associated with different theories of cognitive science (Section 2.1) and with different concepts of cognitive science (Section 2.2). In addition to this pluralism of viewpoints, biological agency is clearly interrogated by agentive views in cognitive science.

A final element to discuss, which may help to understand the current epistemological blending between theoretical biology and cognitive science, is the role of biological agency in evolutionary theory: biological agency is crucial for defining the central components of natural selection. Indeed, this is the central tenet of the agential perspective, to "discuss how incorporating agency helps to bridge explanatory gaps left by [..] prevailing gene-focused approaches in our understanding of phenotype determination, inheritance, and the origin of novel traits" (Sultan, 2022, 1). Such *explanatory gaps* concern different biological phenomena that cannot be properly accounted for just by looking at genes (see Section 1). In particular, Sonia et al. (2022) pointed out three important gaps in evolutionary theory that may be accounted for by introducing biological agents and that are relevant to evolutionary theory.

First, development itself is a process mediated by agents. Developmental processes remain misunderstood if we only look at DNA sequences. We need a theory of development that recognizes the complexity, multicausality, and multilevel dynamics of developmental processes coupled with a rich environment. On the way to understanding how multiple causal resources interact to produce a suitable trait as a function of living conditions, the notion of agency becomes central: "This feedback [between developing organisms and their living conditions] in turn results in agency-influenced effects on selective trajectories that can suggest new evolutionary implications" (Sultan, et al., 2022, 5). There are several well-studied examples where the agentive properties of developing systems (and some of the concepts discussed in previous sections) are relevant to genetic expression and the construction of phenotypes. For example, perceptual inputs could be central triggering causes of development. These include the perception of natural light and dark cycles that activate genes related to the circadian rhythm in Drosophila and mice, several functionally relevant features of gene expression in yeast and bacteria, or the visual perception of the amount of water in an amphibian's niche during metamorphic changes. Plants show a high degree of phenotypic variability depending on different exogenous causes that are utilized in different ways, such as the perception of firm and stony soil during root development or the shape and pattern of leaves as a consequence of the temperature and humidity of the environment. The key idea behind these cases is that understanding development as an agent-driven process allows us to close an explanatory gap: to explain how developmental systems adaptively regulate and process multiple causal resources. Second, inheritance as a mechanism of cross-generational resemblance is also better explained by introducing an agent-driven perspective. In this case, the explanatory gap is that the resemblance of several traits cannot be explained from a purely genetic perspective. Agency is central here to explain how developing systems regulate epigenetic sources of inheritance to ensure intergenerational stability. A clear case of an agent-mediated inheritance process is ecological inheritance, which occurs through the cases of parental effects, the inheritance of diseases, or climate changes. Finally, the emergence of evolutionary innovations is another process whose explanation can be enriched by introducing the agential perspective. As explained earlier, a key missing element in Darwin's view is the origin of variation. The MS framework provided a theory of variation based on chance. However, the alleged cognitive revolution in theoretical biology aims to explain how developing systems can produce adaptively directed variation thanks to the internal processing of developmental information. This allows for a different theory of the origin of novelty. Instead of waiting for a random solution to an environmental problem, agentive developmental processes can provide a suitable biological novelty for that problem. To summarize,

> Agency offers biology a distinctive explanatory strategy, the agency perspective, in which the dynamics of the system, and the activities of its components, are explained by appeal to the agent's adaptive responsiveness. This perspective can complement and enrich gene-based approaches by revealing how the flexible response processes that characterize organisms contribute to their adaptive, resilient, and innovative features (Sultan, et al., 2022, 14).

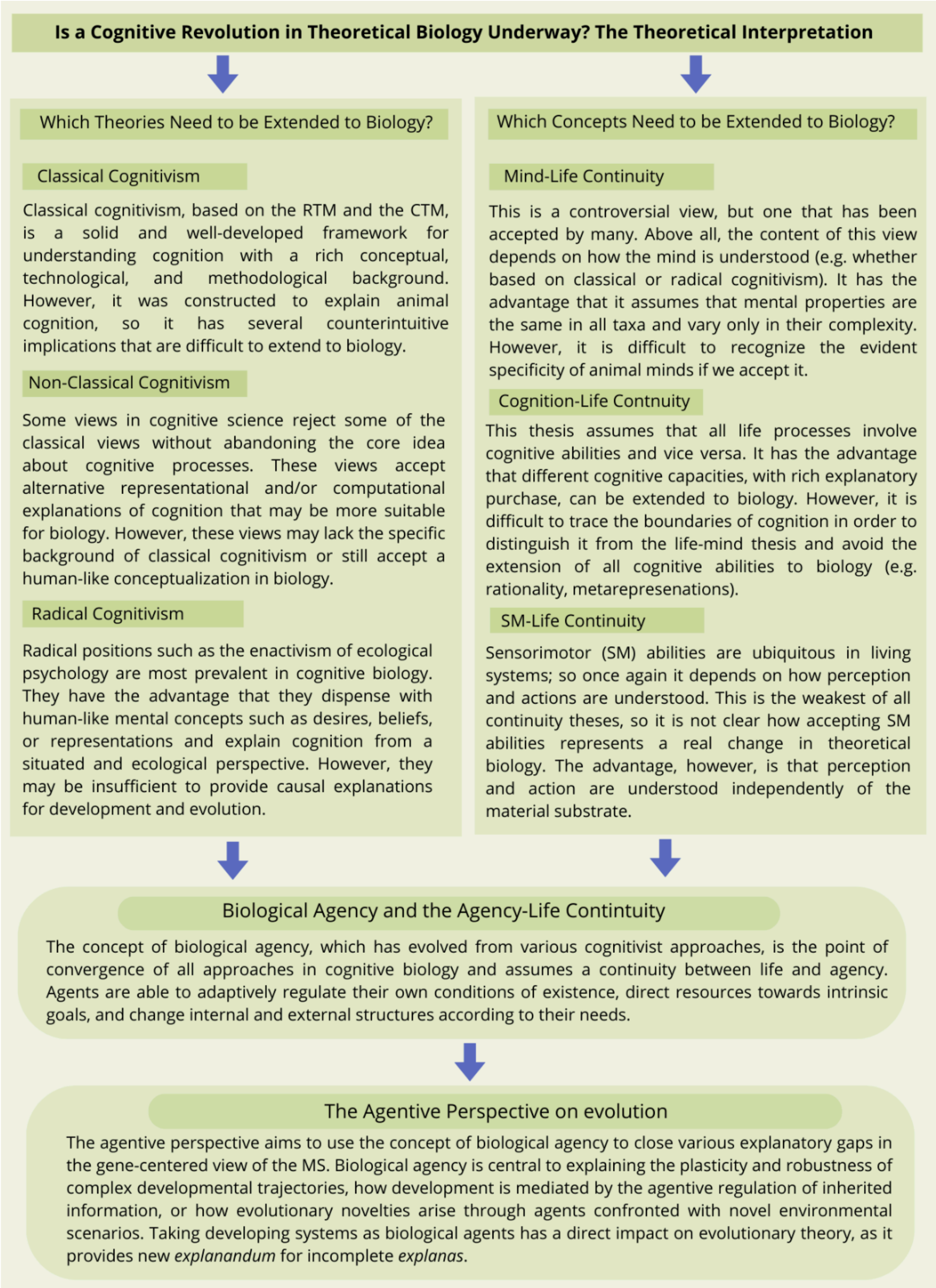


Figure 1: Is a Cognitive Revolution in Theoretical Biology Underway? The theoretical interpretation.

2.4. Interim Summary: Many Bridges, Many Options

We can draw a first conclusion concerning the theoretical question: Theoretical biology is undergoing a cognitive revolution in which the explanatory apparatus and conceptual models of cognitive science are beginning to play a central epistemic role in theoretical biology, especially in developmental biology. However, as noted above, many options are available, so this conclusion requires several considerations.

Figure 1 systematizes the situation. Using the cognitivist apparatus in biology is not a task that is approached with great systematicity or with a consensus on how to do it. Various possibilities emerge from the analysis carried out in Sections 2.1 and 2.2. Some of the advantages and disadvantages of each position have been suggested and are illustrated in Figure 1. Beyond this pluralism, we have also identified a point of convergence. The use of the cognitivist apparatus is in part because the cognitive sciences explain what the developmental turn begins to deal with: *agents*. Biological agency, which feeds into the agentive perspective of evolution described in Section 2.3, is the most robust attempt to reconcile evolutionary theory with cognition-based approaches to development and evolution.

3. Interpretation 2: The Parallelism With the Cognitive Revolution

The analysis in the previous section has given us an overview of the current landscape concerning the theoretical interpretation. Now it is time to look at the historical interpretation. In this case, we are not concerned with potential conceptual shifts, the expansion of epistemic domains, or the adoption of theories from one discipline to another. Nevertheless, these issues have an impact on the assessment of the historical question. If the explanatory framework of cognitive science is applied to biology –whatever this framework and application may entail– then the historical question becomes more important; a certain similarity between the approaches to cognition and the approaches to living systems becomes clear. Our task now is to situate these approaches within the historical context of their respective disciplines: the role of the cognitive sciences in the history of behavioral sciences and the position of the developmental turn within the history of biology itself. We will first present the case of the cognitive sciences and then assess the parallels with theoretical biology. The result of the analysis is that the current landscape of theoretical biology can indeed be compared to the Cognitive Revolution.

3.1 Within the Mind: Cognitive Science Opening the Black Box

The expression *Cognitive Revolution* usually refers to the emergence of the cognitive sciences and the move away from prevailing behaviorist theories. This event took place in the middle of the 20th century as a result of various experimental and theoretical advances (the beginning is usually dated to 1956 when various innovative papers were disseminated (Miller, 2003)). The interdisciplinary character of the cognitive sciences is already evident in their beginnings. Cognitive psychology, neuroscience, linguistics, artificial intelligence, and philosophy, among other disciplines, played a crucial role in the critique of behaviorism and later became key figures in the development and advancement of the cognitive sciences. Chomsky's work in linguistics, the neural network models of McCulloch and Pitts, the rats experiments of Tolman and Honzik, the insights into the limits of information processing by Miller, and the advances in computing made by Turing (extended by influential figures in artificial intelligence such as Minsky, McCarthy, Newell, and Simon) are generally recognized as catalysts for the field of cognitive science (see Bermudez (2014) for a classical textbook in cognitive science).

These advances paved the way for a new way of understanding the mind and behavior. The element that brings these advances together is precisely the idea that runs counter to the behaviorist model: that the processes *internal* to the system that generate behavior can be studied scientifically. In other words, there can be a science of mental processes and mental states, that not only behavior is observable, but also mental states are. All that is needed is an appropriate theory to make them visible. The acceptance of this idea is referred to as "opening the black box" in which behaviorism had put the mind.

Behaviorism has put the mind and the internal processes of the organism into a black box for historical, philosophical, and experimental reasons. First, behaviorism was defended in a context in which the technological infrastructure for studying cognition was not well-developed. Second, the mind was considered a purely subjective and speculative field, far removed from any possibility of understanding the underlying causes of mental processes. The Cartesian legacy proclaimed a vision in which the mind could not enter the reach of science. And finally, the experimental model of behaviorism itself did not depend at all on how the mind worked. The behaviorist model was simply based on the relationships between stimuli, responses, and reinforcement, while "the mind, contained in the organism, is not depicted. It is treated as a 'black box,'

meaning that it is unfathomable and unexplainable. The mind becomes simply an entity that serves to convert stimuli to responses” (Friedenberg and Silverman, 2006, 86).
`

The question of the cognitive sciences consists of “how to analyze the behavior of a complex network, instead of treating it as an unintelligible black box” (Boden, 2008, 957). The conceptual and experimental apparatus of the cognitive sciences emerged from this question. As we have already seen, various more or less orthodox positions in the cognitive sciences accept the ideas of classical cognitivism in whole, in part, or not at all. Despite this plurality of views exposed in Section 2, it is possible to emphasize the central proposal developed during the Cognitive Revolution: Mental processes can be understood as internal information processes that represent external states of the world. Such states and processes are the causal bases that produce the behavior that links the stimulus to a response.

This core tenet built during the Cognitive Revolution deals with three central concepts: information, intentional-internal states, and causation. First, mental processes perceive *information* from the environment, manipulate it, and produce it to perform adaptive behavior (Fresco, 2022). Second, we can conceptualize the system's internal states as states of an agent with intentions. We can explain why a system performs a behavior by invoking a mentalistic language without implying dualism or anti-scientificity (Braddon-Mitchell and Jackson, 2007). *Perceptions, intentions, desires, thoughts, or goals* are different mental categories that can be understood as informational states of a system. Finally, the psychological explanation derived from this points to the *causes* of behavior: mental states causally produce a behavior; intentional explanations are adequate because they describe the causal structure of the mind.

Undoubtedly, the sketch presented in the previous paragraph is extremely schematic and reflects the classical vision developed at the beginning of cognitive science –and not the variety and depths that nowadays we find in the discipline. The aim, however, is to show how the box of the mind was opened. In this way, if we stress that the main idea of all cognitivist theories is the agentive explanation of behavior (Section 2.3), the main moral of the Cognitive Revolution (CR) is as follows:

> *(CR) The adaptability of the system must be explained in terms of what happens within the system. To abandon the internal processes of a system is to abandon the causes that give rise to interaction with its environment.*

3.2 Within Organisms: Developmental Biology Opening the Black Box

What parallels are there between the Cognitive Revolution and the current disputes about the foundations of biology? This also means that we need to ask ourselves about the parallels between behaviorism and the MS, and the parallels between the cognitive sciences and the developmental turn.

Apart from the fact that both theories were forged in the first half of the 20th century and developed mainly in the Euro-American world, the most remarkable parallelism between behaviorism and the MS occurs when we consider their explanatory models. Here we find the fact that in both cases a black box is postulated into which we do not need to look in order to achieve our scientific goals. The behavioral model is based on three variables: a perceptual input, a behavioral output, and a reinforcement –positive or negative– of the link between input and output. We also find these three elements in the evolutionary model of the MS: a genetic input (inheritance), a phenotypic output (variation), and selection –positive or negative– of traits (fitness). This is how Amundson (1990, 578) summarizes the similarity between the two models (see also Skinner (1984) and Campbell (1974) for a similar analysis and conclusion):

> Natural selection explains phylogenetic adaptation by positing a nondirected ("random") source of heritable variation within the lineage, together with selection by the environment of those variants which happen by chance to be better suited to survival and reproduction. The Law of Effect [of behaviorism] … explains the ontogenetic adaptation of individual behavior by positing nondirected ("spontaneous”) variations in behavior, together with some form of selection by the environment which allows successful behavior to persist and the unsuccessful to die out …[Both models are] virtually identical in its structure to that used to explain the phylogenetic adaptation of the evolving species.

As we see, the mind and the development of organisms are conspicuous by their absence. We can explain behavior and evolution without paying attention to the processes that take place inside the mind and organisms. It is not a matter of explaining the causal process that leads from an input to an output. That is, it is not necessary to explain the developmental process that links the inherited genetic material of an organism to the constructed phenotype (the GxP map), nor is it necessary to understand the mental processes that produce behavior in the face of particular perceptual inputs. The development of organisms and mental processes are transparent (Rama, 2022): The MS can see phenotypes through the genetic material, just as behaviorism is able to see behavior through the input the system receives. Given the similarities between these models, we can argue with Fodor and Piattelli-Palmarini (2010, xvi), that "Skinner's [behaviorist] account of learning and Darwin's account of evolution are identical in all but name."

The central historical observation is that both black boxes had to be opened as a consequence of important explanatory gaps in each model. In this sense, the parallelism between behaviorism and the MS is not only found in their models, but they are also similar in their rejections. That is, the MS is criticized for the same reasons that behaviorism was criticized in the last century. The black box of development leaves many explanatory gaps unresolved, such as the explanation of the GxP map, epigenetic inheritance, or the evolutionary origin of phenotypic innovations. Many cognitive phenomena could also not be explained with the behaviorist model. In order to understand how language is processed, decisions are made, memories are stored or perceptions are formed, we need to open the black box of the mind and close the explanatory gap of behaviorism.

The fact that both theories leave explanatory gaps unsolved evidences the parallelism between the theories that oppose the MS and behaviorism, i.e. between the developmental turn and the cognitive sciences. These disciplines have used the same strategy to open the black boxes of mind and development, respectively, and close the explanatory gap between behaviorism and the MS. As mentioned in Section 1, the developmental turn categorically rejects the idea that an organism's phenotypes are fully encoded in its genome. On the contrary, organisms are active agents that can adaptively regulate their own development and living conditions. In this context, various phenomena play a central role, such as phenotypic plasticity, niche construction, or self-organization processes, to name but a few. So when it comes to understanding development as something that is controlled and produced by the organism itself, we find the same central components that triggered the Cognitive Revolution (see Section 3.1): *internal states* constituted by *information processes* are the c*ausal* basis of developmental change.

In this way, we can first find the idea that developmental processes can be understood as *informational processes*. This idea emerged at the same time as the molecular genocentric view described by Crick in Central Dogma in Molecular Biology. Instead, the current proposal is situated in post-genomics: the idea is that different elements in development, genetic, epigenetic, and exogenous, provide crucial information throughout ontogeny (Rama, 2023). As we saw in Section 2, much of cognitive biology is based on the ability of organisms to process information. When it comes to explaining how organisms adapt to their environment as they develop, the focus is on the study of signaling systems that inform the system about its internal and external conditions so that it achieves an appropriate coupling to its environment. Nor can the organism be regarded as an inert object at the mercy of the chance of mutation and the vicissitudes of the environment. The internal states of an agent can be viewed as informational states. Agents process information from different channels and produce an adaptive response that is consistent with that information. As in the cognitive sciences, it is internal processes that promote an adaptive relationship between organisms and the environment. And just as the cognitive sciences have allowed us to understand how behavior is caused by states internal to the system, current theoretical biology emphasizes that a true explanation of development requires explaining the different stages of a developmental system, rather than summarizing it to a genetic code. In other words, the causes of development do not precede development; they are distributed throughout ontogeny. A true explanation of development is to understand the interaction between the different causes and how organisms regulate their own development; or as Robert (2004, 22) says: "To take development seriously is to take development as our primary explanandum, to resist the substitution of genetic metaphors for developmental mechanisms."

Is a Scientific Revolution in Theoretical Biology Underway? The Historical Interpetation

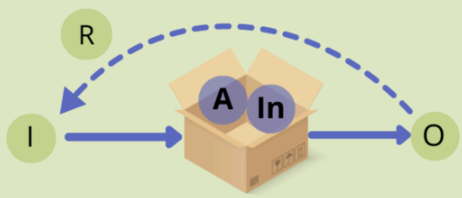
Figure 2.1 The Black Box Model of Behaviorism and the Modern Synthesis

The black box model is the central explanatory method of behaviorism and the Modern Synthesis.
The explanation of behavior in this model is based on a perceptual input (I) that elicits a behavioral outcome (O) that is reinforced (R) to influence future outcomes prior to new inputs. Recursive and biased I-O interactions lead to intelligent behavior, regardless of the processes linking I to O.
The explanation for adaptability and diversity in nature is based on inherited inputs (I) producing phenotypic outcomes (O) that are selected by inherited information and reproduced in further generations (R). The variability of biased and recursive I-O interactions leads to adaptations, regardless of the processes linking I to O.

Figure 2.2 The Black Box and the Explanatory Gap

The black box model leaves an explanatory gap for many biological and cognitive phenomena without an adequate explanation.
The criticism of behaviorism was related to the fact that several cognitive processes remained unexplained in this model. Discoveries in linguistics, cognitive psychology, neuroscience, and computational models of the mind, among others, led to an explanatory gap in behaviorism.
The criticism of the Modern Synthesis is related to the fact that several biological processes remained unexplained for this model. Discoveries in developmental biology, heredity, physiology, and ecology, among others, have led to an explanatory gap in behaviorism.

Figure 2.3 Opening the Black Box: Agency and Information:



Cognitive science and the developmental turn use similar strategies to open the black box of the mind and development and close the explanatory gaps of behaviorism and the Modern Synthesis.
Cognitive science is based on the idea that the intentional agent (A) uses the internal processing of semantic information (in) to produce an adaptively directed behavior.
The developmental turn aims to construct a view of development based on the idea that the developing agent uses the internal processing of biological information to produce adaptively directed phenotypes. The relationship between the inheritance (I) and the phenotypic outcomes (O) to be selected and reproduced (R) is mediated by an agent (A) regulation of developmental information (In).

Figure 2: Is a Cognitive Revolution in Theoretical Biology Underway? The Historical interpretation.

The parallelism between CR and the developmental turn (DT) is easy to recognize since theoretical biology advocates the same tenet of the cognitive sciences:

(DT) The adaptability of the system must be explained in terms of the processes within the system. To abandon the internal processes of a system is to abandon the causes that give rise to interaction with its environment.

Figure 2 summarizes the analysis of this section. We can conclude that, effectively, the current panorama of theoretical biology can be seen as parallel to the Cognitive Revolution of the last century. Such a conclusion arises from the analysis of three points:

1. The similarity between the behaviorist model and the evolutionary model of the MS (Figure 2.1).
2. The transition from behaviorism to the cognitive sciences and the transition from the MS to the developmental turn is due to the same reasons: mental processes and developmental processes have been put in a black box and this produced several explanatory gaps (Figure 2.2).
3. The similarity between the explanatory model of cognitive science and the explanatory model of the developmental turn: the agentive regulation of internal processing was the key used for opening both black boxes; i.e., CR = DT (Figure 2.3).

However, like the answer to the theoretical question, the answer to the historical question also requires a certain amount of nuance. In particular, it is noteworthy that we are not claiming that the developmental turn has done a scientific revolution. The term *scientific revolution* has a strong connotation and usually implies the abandonment of old theories and their incompatibility with new theories. The debate on how to view the relationship between the MS and the developmental turn is open and on the table (Gefaell and Saborido, 2023). Again, there is a gradient of more or less radical possibilities, from those who believe that nothing new poses a problem for the old, to those who think that new proposals require an extension of the MS Synthesis, to those who point to certain points of the MS that need to be abandoned and completely reconstructed. In any case, there are no signs in the current panorama of theoretical biology that a revolution –in the narrower Kunian sense as a paradigm shift– has taken place. The biological practice remains quite independent of these theoretical discussions and many biologists think that mainstream biological theory should not be changed at all. In this episode of the history of biology, we find ourselves *in media res.* Many biologists claim that the MS needs to be rethought, but there is not yet a consolidated and accepted vision to replace it. The claim of a scientific revolution taking place in biology does not seem to be justified given the fact that, as Laland et al. (2013, 807) say, "it is probably fair to say that these various lobbies currently more resemble a disorganized protest movement than a viable alternative government." In this sense, the parallelism between cognitive science and the developmental turn is incomplete: While cognitive science has displaced behaviorism, the developmental turn has not removed the MS from the center of theoretical biology, at least not yet. This does not detract from the aims of this article: the historical and theoretical ideas presented here help to understand the current scenario of theoretical biology and to find future directions based on the epistemological crossover between cognitive science and theoretical biology, especially in developmental processes.

4. Conclusions

This paper aims to systematize the connection between the cognitive sciences and contemporary theoretical biology. Undoubtedly, various interesting elements have not been taken into account, and the analysis carried out does not intend to emphasize any particular proposal. Moreover, we dealt with *cognitive biology,* not *biological cognition* (Huebner and Schulkin 2022). Certainly, the two fields may be related or overlap, but they differ in which discipline feeds the other. If biology is the input for cognitive studies, we are pursuing biological cognition. Our aims fall within cognitive biology: to provide, in a schematic way, a synthesis of the role played by the conceptual apparatus of cognitive science (together with its own history) in theoretical biology. The emphasis on the connection between disciplines was analyzed in a unidirectional way, i.e. without taking into account the role that theoretical biology plays in cognitive science.

The analysis began in the second section with the theoretical question. This section concludes that the cognitive sciences do indeed provide central conceptualizations and experimental frameworks for understanding the cognitive capacities of organisms. However, this conclusion requires different nuances due to the different positions that can be taken. First, we can ask which theories in cognitive science should be applied to biology. There are several possibilities related to the different propositions in cognitive science –from classical cognitivism to radical post-cognitivism. At the same time, there are also discrepancies regarding the concepts that should be applied to cognitive science. While some defend that all living organisms have mental properties, other, less radical positions claim that some paradigmatic properties of cognitive systems, such as memory, perception, or learning can be found in unicellular organisms. The current panorama is therefore diverse. As already mentioned, there is a core idea in all positions: that organisms are active agents in their own existence and not passive systems controlled by their genetic engineering. In this way, we can understand the multiple uses of the apparatus of cognitive science in biology as an attempt to explain the agency of organisms and their evolutionary consequences in different biological processes. As we have argued, the historical question can also be answered affirmatively. The situation in the mid-20th century in mental and behavioral science resembles the current panorama in theoretical biology. We have highlighted three relevant parallels: (i) between the black box model of behaviorism and the MS, (ii) between the explanatory gaps of behaviorism and the MS, and (iii) between the explanatory model of the cognitive sciences and developmental turn based on agency and information processes.

Acknowledgments: I am grateful to Sergio Balari for the discussion of the ideas presented here. The research done here received the support of the National Agency of Investigation and Innovation (Uruguay) through grant PD_NAC_2023_1_176930 and the Sectoral Comision of Scientific Investigation (Uruguay) through grant 22520220100257UD.

Declarations

Ethical Approval: Not Applicable.

Funding: National Agency of Investigation and Innovation (Uruguay) through grant PD_NAC_2023_1_176930 and the Sectoral Comision of Scientific Investigation (Uruguay) through grant 22520220100257UD

Availability of data and materials: Not Applicable.

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