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The Explanatory Role of *Umwelt* in Evolutionary Theory: Introducing von Baer's Reflections on Teleological Development

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Abstract: This paper argues that a central explanatory role for the concept of *Umwelt* in theoretical biology is to be found in developmental biology, in particular in the effort to understand development as a goal-directed and adaptive process that is controlled by the organism itself. I will reach this conclusion in two (interrelated) ways. The first is purely theoretical and relates to the current scenario in the philosophy of biology. Challenging neo-Darwinism requires a new understanding of the various components involved in natural selection processes. An important prerequisite is to understand developmental change in a teleological way. Here, the concept of *Umwelt* plays a crucial role: if organisms are responsible for generating adaptive variation in specific environments, we need a theory that explains the context-dependent nature of adaptively oriented processes. The *Umwelt* is thus a central element in determining the goal that an adaptive process pursues. The second path in my analysis also has a historical dimension. I will present Karl Ernst von Baer's reflections on teleological development and his influence on Jacob von Uexküll's thinking. I will present various ideas developed by Baer, such as the distinction between *Ziel* and *Zweck* and the use of musical metaphors, which can help to understand development teleologically and give Uexküll's theory a central place in this framework.

Keywords: *Umwelt*; *Ziel-Zweck*; Musical Metaphors; Teleological Development; Karl Ernst von Baer; Jakob von Uexküll

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The highest law of life, which connects all plans in time, has been named 'directedness' by K. E. v. Baer.

Jacob von Uexküll (1936: 144)

Natural forces which are not directed to an end cannot produce order.

Karl Ernst von Baer (1886a: 88)

Introduction

The last decades of theoretical biology have been pervaded by disputes about the status of the Modern Synthesis (henceforth: MS). The goal of reformulating biological theory beyond the gene-centered becomes clear as soon as developmental processes turn out to be highly complex phenomena. A new understanding of development is required to construct an alternative theory of evolution and to explain how its central components –inheritance, variation, and fitness– are produced by developmental processes. As outlined in this paper, philosophers and biologists today are attempting to fulfill this requirement. The view that genes are the controlling and organizing unit of development is being replaced by a picture in which the entire developing system regulates its own developmental course. This introduces a particular kind of vocabulary related to the explanation of inheritance, variation, and fitness, such as the concepts of agency, norms, action, and other concepts belonging to a particular kind of (historically despised) scientific explanation: teleology.

The aim of this paper is twofold. The first is to argue that the concept of *Umwelt* plays a crucial role in understanding teleological development, and hence *Umwelt*'s theory is explanatorily relevant and useful in the context of evolutionary theory. This would also mean connecting *Umwelt*'s theory to other similar concepts in biological theory in use today and considering biosemiotics as an important theory in the construction of an alternative biological theory. There are many reasons why *Umwelt*'s theory deserves careful attention in theoretical biology. The first reason is that *Umwelt*'s theory forms the core of most biosemiotic approaches that call themselves anti-neo-Darwinian and attempt to reconstruct a theory of evolution by providing a semiotic perspective on biological processes. Furthermore, the construction of a scientific theory requires a conceptual apparatus that justifies empirical and theoretical advances. The concept of *Umwelt* may be suitable for this purpose, as it has a rich history of conceptualizations, philosophical considerations, and empirical research. Finally, and related to the previous point, the goal of reconstructing evolutionary theory is linked to an increasing interest in the agential nature of living systems. In this sense, the cognitive sciences, psychology, or the humanities are appropriate places to look for conceptual clarity in order to uncover the agential nature of living systems, the different phenomena associated with agency (e.g. perception, phenomenology, action, intentions), and its role in evolutionary theory. Precisely, the explanatory role of *Umwelt* is tied to the need to understand organisms as agents acting on their environments. The second aim of this essay is more historical. I will present some of Baer's ideas on his teleological view of development. There are several motivations to engage with Baer's inquiry into the nature of teleology. A primary reason is Baer's direct influence on Uexküll. The construction of *Umwelt*'s theory and its role in Uexküll's theoretical biology is strongly motivated by Baer's view. Another reason is that Baer is not seen as a central historical reference in contemporary debates about the foundations of evolutionary theory, although Baer has made several attempts to discuss Darwin's theory and propose his own view. As mentioned above, *Umwelt*'s theory may contribute to new trends in evolutionary theory that aim to reframe evolution beyond the MS enterprise. A common task for philosophers and biologists is to find historically influencing thinkers that went against the mainstream theory of evolution. In this task, we usually found the works of Lamarck, Owen, Goldschmidt, Baldwin, Russell, or Bertalanffy, among many others,

but definitely, Baer is usually not part of this historical reconstruction, nor the Teleomechanistic program Baer belonged to. By recognizing the influence of Baer's thought in biosemiotics, "it can be concluded that the majority of biosemioticians have been quite critical toward the neo-Darwinian school of thought, appreciating considerably higher the views of the followers of Karl Ernst von Baer" (Kull, 2004: 103). A final crucial motivation is that Baer's reflections concern the nature of development and the need for teleological explanations to adequately address it. In this essay, I will argue that an adequate teleological view of development –beyond gene-centered views based on blueprints or genetic codes– is still lacking and, moreover, necessary. Baer's ideas and their influence on *Umwelt*'s theory can thus contribute to the gestation of a teleological theory of development.

1. Teleology and Development

1.1 The Role of Organismic Development in Evolutionary Theory

The role of organismic development in evolutionary theory is a central point of contention in the contemporary philosophy of evolutionary biology (Bateson, 2005; Baedke, 2018; Nicholson, 2014; Huneman, 2010). As might be expected, rivalries and tensions exist between different positions in this area. To understand the theories that advocate that organismal development plays a central explanatory role in evolutionary theory, it is also important to understand the theory that has neglected such an explanatory role, namely the MS or neo-Darwinism.

Based on Darwin's natural selection, Mendelian inheritance, and mathematical models of population change, the MS built its enterprise: The Genetic Theory of Evolution. The central insight was to explain the core components of natural selection in genetic terms without addressing developmental processes. Natural selection requires heritable fitness differences between members of a population (Lewontin, 1974; Godfrey-Smith, 2009). In other words, the individuals in a population must differ, these differences must carry with them different fitness values, and finally, the differences must be heritable. Darwin, of course, did not have a complete theory of natural selection, because he still needed a solid theory of how variation is generated and traits are inherited. Neo-Darwinism provided the needed theory of variation and inheritance, as we will see in a moment. However, it is important to note that the neo-Darwinian proposal is only one way of understanding inheritance and variation within the theory of natural selection. In fact, Darwin himself accepted a form of Lamarckism, while the neo-Darwinian MS opted for "discarding this concept altogether" (Mayr, 1963, 611). As we will see in the next section, the proposal developed here is intended to contribute to a different understanding of the phenotypic variations required for the theory of natural selection.

The genetic theory of inheritance, shaped primarily by the work of Weissmann and Mendel, reduced the processes of inheritance to what was passed down through the germline at conception and rejected the influence of developmental processes in inheritance. In other words, the variations that arise from epigenetic motifs cannot be passed on (there can be no somatic inheritance), nor can they influence what is inherited through the germline (somatic changes do not influence the germline). Although heredity and development were linked in the pre-Weismann era, developmental processes have been displaced from heredity theory (Amundson, 2005). The genetic theory of inheritance is linked to the genetic theory of variation. If variation must be inherited for evolution to occur, the source of variation must be linked to the source of inheritance: evolutionary relevant phenotypic variation must be produced by variation at the genetic level. Since selection is a process that affects phenotypes, the fitness of phenotypes must be closely linked to the fitness of heritable variation. In other words: What is inherited at conception must explain the construction of traits, i.e. it must explain development. If traits are built up by genotypic inheritance, selection can recognize the fitness of the inherited variations (genes) by examining the fitness of the phenotypes. Development is a transparent process (Walsh, 2003): Phenotypes reveal genotypes to natural selection. In this way, inheritance, variation, and fitness can be understood as a property of genes and genetic populations; thus, "changes in the frequencies of alleles by natural selection are evolution"

(Campbell, 1994: 86; emphasis added). Originally, genes were not understood in molecular terms. Mendelian inheritance was cellular inheritance. With the discovery of DNA in 1953, the material nature of genes changed. However, the theoretical role of genes remains intact: Whatever part of matter genes are, they are responsible for explaining the components of natural selection (Ågren, 2021). This way of understanding natural selection leads to the development of organisms being left aside. Development is only the consequence of genetic information and therefore has nothing to do with the theory of evolution: "One consequence of Weismann's separation of the germline and the soma was to make it possible to understand genetics, and hence evolution, without understanding development" (Maynard Smith, 1982: 6).

The recent attacks against mainstream evolutionary theory are primarily directed against neo-Darwinism, not against Darwin. In other words, the claim that the development of organisms is relevant to evolutionary theory implies that development plays a role in explaining the core components of natural selection. Indeed, various theoretical and experimental advances suggest that it does. Extended inheritance systems and epigenetic modifications of genes have been discovered and used to challenge Weissmann's genetic theory of inheritance. Thus, chromatic marks –causing modifications in histone proteins or methylations affecting DNA bases as well as RNA-mediated inheritance involved in transcription processes have been found in all living systems (see Jablonka and Lamb (2020, 31-37) for an overview and further examples). In addition, several sources of variation are not based on genetic changes, such as phenotypic plasticity, self-organization, or niche construction (see West-Eberhard, 2003; Gilbert and Epel, 2015; Müller and Newman, 2003; Wagner, 2014). *Polygonum*, for example, is a plant in which plasticity has been well studied (Sultan, 2003). It exhibits allometric plasticity –the biomass produced in each tissue and organ is relative to the amount of energy in the environment that each tissue and organ can access– morphological plasticity –the shape and size of roots and leaves varies according to the environmental resources available– and reproductive plasticity –reproductive timing is relative to favorable or stressful environmental conditions. Another crucial experimental advance is that since the post-genomic era (i.e., since the sequencing of the first human genome at the beginning of this century), the role of DNA as the sole source of developmental information has been replaced by a distributed view of development (see Griffiths and Stotz, 2013; Oyama et al, 2001; Keller, 2002; Lewontin, 2000). From this perspective, the synthesis of proteins is therefore not fully specified by the DNA sequence; several resources are involved in the formation of traits, such as genomic (e.g. transcriptional regulation of *cis*- and *trans*- actions in the mRNA that alter the final RNA sequence, or the modification of exons and introns that lead to alternative splicing), intracellular (e.g. cytoplasmic factors involved in self-sustaining feedback loops during transcription processes), extracellular (e.g. hormonal changes that influence the phosphorylation of transcriptional regulators), or exogenous causes (e.g. thermal influences that lead to sex determination in reptiles). The result is that the Genotype-Phenotype Map does not represent a straight and visible path between genes and phenotypes, but that the path to trait formation is complex, and contains multiple pathways, forks, and variables. The connection between genes and phenotypes is not transparent, but opaque. Therefore, the fitness of organisms cannot be directly linked to their genetic basis. To summarise, evolutionary processes cannot be described by looking at genes alone. Developmental processes are part of the theory of evolution.

Certainly, this is a cartoonish depiction of the scenario, but it reflects the core idea of the so-called *developmental* or *epigenetic* turn in theoretical biology. Moreover, it is not the intention of this paper to question the MS but to contribute with some theoretical insights into the emergence of the developmental turn. In this sense, it is important to remember what is at stake in the debates about the role of organismal development in evolution, namely the ability of organismal development to generate heritable variation in fitness.

1.2 The Need for a Goal-Directed View of Change

Most debates in the contemporary philosophy of biology revolve around the developmental turn. Many theories and controversies have arisen to discuss what and how to deviate from the MS. This essay analyzes a specific but

central issue for the foundations of the developmental turn that is a source of intense debate today: *a teleological theory of development.*

The need to construct a goal-directed view of development departs from the purported explanatory role of organismic development. A crucial element that the developmental turn adds to evolution theory is the existence of adaptively directed phenotypic variation. This can be understood in contrast to the genetic theory of variation advocated by the MS. In this framework, the main source of variation arises at the genetic level. As is well known, genetic variation (according to MS) is random. Random merely means that the origin of variation is not causally linked to its adaptive significance. Genetic variation occurs independently of its effects at the phenotypic level. *Random* means that they are not adaptively directed (even if they are ultimately adaptive).

Contrarily, the distributed and context-sensitive view of organismal development advocated by the developmental turn pursues the idea of non-random, adaptively directed (phenotypic) variation: variations that arise to increase the fitness of the organism. This leads to a different understanding of variation and novelty. In the MS, a population faced with a particular environmental problem must wait for a random variation that fits the problem –an adaptive solution. As George Williams (1992: 484) wrote, "adaptation is always asymmetrical; organisms adapt to their environment, never vice versa." Somehow, nature must provide solutions to unknown problems. In this way, the developmental turn calls for the introduction of organismal development as an adaptive force, whereas the MS views natural selection as the sole source of adaptive evolution and views organisms as "*vehicles* in which replicators travel about" (Dawkins, 1982: 82; emphasis in the original), as "merely the *medium* by which the external forces of the environment confront the internal forces that produce variation" (Levins and Lewontin, 1985: 88; emphasis added), as the "*arena* in which this interaction [genome variations and natural selection] is played" (Michel and Moore, 1995: 127; emphasis added), or as "the *superficial face* that genes show to the world" (Sober, 1984: 228; emphasis added). In contrast to the genetic perspective of evolution, the developmental turn adopts an *agential perspective* (Sultan et al., 2022; Walsh and Rupik, 2023). It is based on the recognition of the agency of living organisms: "the capacity of a system as a whole to enlist the causal capacities of its parts and direct them toward the attainment of a robustly stable end-point" (Walsh, 2015, 195). While in the genetic perspective genes explain the properties of organisms, in the agential perspective organisms are considered both *explanans* and *explanandum*: The organism is the actual unit of analysis, and the assumption of this level of explanation is central to an adequate understanding of developmental processes. The agential perspective and the assumption of a holistic, context-sensitive, and non-reductive stance is committed to a certain type of explanation: "Because there are agents, there are goals, means, norms, hypothetical necessity, and a special mode of explanation —teleology" (Walsh, 2018, 172). Certainly, all of these terms are contested in biology. Part of Baer's analysis in Section 3 is devoted to terminological clarification in order to reduce the controversy surrounding these terms. The key message is that the organismic level of analysis is distinct from the sub-organismic and supra-organismic levels of analysis used by molecular genetics and population genetics, respectively. The agential perspective postulates agents pursuing goals as a central *explanans* in evolution.

From this perspective, the developmental turn ties the origin of variation to its adaptive role in an organism embedded in the environment; organisms provide solutions to problems they face during their lifespan.[1] Understanding how organisms can adaptively regulate their conditions of existence is a central scientific goal if we are to replace the gene-centered view of evolution with a sound and coherent theory. Adaptive variation in the agential perspective should be explained by a teleological theory of development. In other words,

[1] This does not mean that all variations must arise for adaptive and functional reasons. Indeed, the idea of non-adaptively directed variation is also central to the developmental turn. Central developmental phenomena such as inherency (Newman, 2019) are based on structural and emergent properties that are independent of functional explanations. Thus, an adaptively directed explanation of developmental change is a prerequisite for understanding the (developmental and evolutionary) origin of *some* traits, but definitely not *all*.

understanding goal-directed developmental processes is not just a topic in itself, but an *essential prerequisite* for the developmental turn, a crucial piece in an incomplete puzzle (Rama, 2023).

There are various proposals for understanding agency and teleology beyond gene-centered and reductive approaches (the most detailed proposal is by Denis Walsh (2015)). In this paper, I will try to contribute to the development of a teleological theory of development. However, I would like to make a preliminary remark on this topic. The point is that *not all* theories of agency and teleology based on organismic biology are suitable for our purpose and our need to explain teleology in development. The main problem is that a teleological view of development should not be confused with a *teleological view of physiology*. There are several reasons why teleological physiology should not be confused with developmental teleology. Crucially, the goal of physiological processes appears to be different from the goal of development. In short, teleological physiology –as espoused, for example, by Autonomous Systems Theory (e.g. Moreno and Mossio, 2015)– is about self-maintenance. Teleological considerations of physiology take an organismic viewpoint to see how the different parts of an agent contribute to maintaining itself under viable conditions (e.g. Barandiaran et al., 2009). Agency in physiological processes is about the regulation of the coupling with the environment and the internal organization to *maintain* the system. However, development is not about maintenance but about change, an opposite phenomenon. Certainly, the organism is maintained while it changes. But development is not about the maintenance of an internal structure, a set of elements in specific functional relationships (as in teleological physiology), but about the construction of elements and relationships. Organisms go through different internal configurations and different couplings with their environment. This cannot be explained from a physiological perspective alone, which only considers how an organism maintains its life. The difference between developmental goals and physiological goals is crucial and reveals the inadequacy of some teleological perspectives on our aims of explaining developmental change. A similar point was recently noted by Nuño de la Rosa (2023), who argues that the processes of reproduction require specific goals that cannot be adequately explained from a physiological perspective (i.e., the goals of reproduction are not about maintenance).

Until we are able to separate the different goals that an organism pursues (Rama, 2022), our *explanandum* remains without sufficient *explanans*. That is, we need to understand how ontogenetic changes are adaptively directed and how organisms construct themselves in an adaptively directed manner. The reference to the fact that an organism is capable of orienting its processes towards conservation is correct, but it does not explain how this system was constructed. Teleological physiology is not suitable for explaining development, because the system that is maintained by physiological processes was constructed by developmental processes. In this sense, teleological physiology says nothing about how organisms produce themselves. It is about how organisms maintain themselves. If we keep in mind the place that teleological development occupies within the evolutionary approach to the developmental turn, we cannot be satisfied with these accounts of teleology and agency. This does not mean, of course, that these theories of teleological physiology are wrong. It only means that they are not suitable for our explanatory goals. Nor am I suggesting that teleological development has not been explored in the current literature. I am trying to clarify the scope of our analysis in order to understand what we need: a theory of how an agent deploys its developmental resources at a particular stage of ontogeny to bring about appropriate change.

I am not proposing a theory of teleological development here. I will merely point out some of the problems associated with teleological development and suggest some ways of dealing with them. The concept of *Umwelt* developed by Jakob von Uexküll is the linchpin of my analysis. Here I offer both a historical and a theoretical examination. In Section 2, I will first emphasize the central explanatory role of the *Umwelt* in the contemporary context of the developmental turn. This means that the concept of *Umwelt* should be used in goal-directed explanations of development (Section 2.1) and that the theory of *Umwelt* should be linked to different areas of contemporary theoretical biology (Brentari, 2018). In Section 3 I move on to the historical side of my analysis. I will present Baer's view of teleological development and its influence on Uexkull's work. First, I will outline some of Baer's reflections on the nature of teleology in natural science, then I will present his distinction

between *Ziel* and *Zweck* as an appropriate strategy for naturalizing teleology, and finally, I will argue that his use of *musical metaphors* represents a heuristic device that has been replaced in contemporary biology by different domains within the developmental turn. In the conclusion, I will bring together the ideas from Section 2 and Section 3 by highlighting how Baer's ideas specify the explanatory role of *Umwelt* within the developmental turn.

2. The *Umwelt* in Evolutionary Theory

2.1 Healing the Blindness

According to MS, the adaptability of living systems is generated by the evolution of genetic information. The teleonomic view of development presented by Mayr (1961, 1974) explains how the adaptability of an organism arises on the basis of its genetic blueprint. This view results in the blindness of organisms: the genetic program represents –in terms of information– the traits to be constructed, and no representative abilities are attributed to the developing organisms. The organism does not seem to be able to construct traits according to what it "sees" of its environmental conditions. As Dawkins (1989, ix) famosuly sentenced, "we are survival machines –robot vehicles blindly programmed to preserve the selfish molecules known as genes." However, as soon as genes lose control over development, control over development is taken over by the developing system itself. This is the main tenet of the post-genomic era: genetic blueprints thus cannot tell the whole story about the construction of adaptability during development. Different sources of developmental specificity go beyond DNA sequences. So if the whole developing system is responsible for order[2] in living systems, we must replace the genetic view of evolution. In other words, if we view development as a goal-directed, context-sensitive process driven by the whole developmental system, we should explain how an organism "sees"[3] its context to guide its development into an adaptive harbor; we must cure the blindness of organisms.

Umwelt's theory might be a suitable candidate for such a cure.[4] Following Uexküll's definition, the *Umwelt* is defined in terms of an organism-environment relationship: a relationship or organism that perceives and acts upon a world: "[A]ll that a subject perceives becomes his perceptual world and all that he does, his effector world. Perceptual and effector worlds together form a closed unit, the *Umwelt*" (Uexküll, 1992, 320; see Tønnessen et al. (2016) for a detailed introduction to the contemporary and diverse use of the concept of *Umwelt*). The ability of developing systems to perceive and respond to their developmental context must be recognized if development is to be viewed as a goal-directed process. Most of the developmental phenomena at the heart of the developmental turn – e.g. plasticity, self-organization, niche construction, epigenetic regulation– give organisms the ability to "see" their external (and internal) context in order to regulate the course of development. Perceptual abilities affect several well-studied developmental phenomena, whether in animals (such as vocal learning in songbirds or visual perception of the amount of water in an amphibian's niche during metamorphic changes), in bacteria (E. Coli bacteria distinguishing toxins from food) or in plants (light recognition during growth or the perception of solid and rocky soil during root development).

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[2] The order of living organisms concerns their unique, far-from-equilibrium and functional organization. These organizational properties, which are paradigmatic of living systems, are the main target of goal-directednees explanations in biology, just as in Baer's account (see Section 3).

[3] The expression "see" could be problematic insofar as it could suggest that real seeing is attributed to organisms, which is not the case. Here it is used in a metaphorical sense, in contrast to the metaphor of blindness. So "seeing development" has the same metaphorical character as being "blind to development". This means that the organism is able to regulate its developmental trajectories depending on the context. Later in this article, we will see how this metaphorical expression can be replaced by an explanation of the directionality of development.

[4] It is important to note that Uexküll expressed a critique of evolutionism. Therefore, it is necessary to reconcile his critical view of evolution with our aim of using his theory of *Umwelt* in an evolutionary context. While this is a detailed and complex task that is beyond the scope of this article, it is important to note two points. First, Uexküll rejected the neo-Darwinian view of his time, but not the idea of evolution itself; rather, he provided his own ecological view. Secondly, his critical reflections on evolutionary theory do not prevent us from using his thoery of *Umwelt* for current purposes of evolutionary theory.

More precisely, the *Umwelt* becomes crucial for the control of development. It is an answer to the question: directed towards what? In teleological explanations, directionality is oriented towards goal states. In the teleonomic view of MS, the target states are represented in the genetic program. But in an organismic view of development, the target states must be represented differently. This is where the concept of *Umwelt* comes into play. The thesis here is that the target states of development are defined in relation to the *Umwelt* (and the *Innenwelt*) of the developing systems.[5] The *Umwelt* comes to replace the metaphor of the genetic blueprint in our understanding of teleological development.

The active role of organisms in development is linked to the process of interpretation –the process of constructing an *Umwelt*. Gene-based accounts of development employ the word "read" to explain how developmental information is expressed during ontogeny. Developmental systems read genetic information in a way that leaves no room for the active and agentive participation of organisms: Inherited information is an instruction (Shea 2013). In contrast to this view, the notion of *interpretation* suggests a transfer of organizational unity in development from the inherited information to the organism that interprets that information. The construction of the *Umwelt* as a central element in goal-directed activities is a process that is controlled and produced by the agent itself –not the passivity of reading an inherited text, but the active manipulation and utilization of inherited information. Interpretation in biosemiotics thus refers to the organic process of attributing a certain semiotic value to a perceived signal, which contributes to a functional and adaptive response to such a signal. Interpretation is a central process in the agential regulation of development.

Moreover, the phenomenological and subjective nature of *Umwelt* emphasizes the fact that it is the organism itself that constructs its own “views" of ” the world. Understanding development as an agent-directed process introduces a set of vocabularies that refer to the phenomenological –e.g., sensibility, perception– and cognitive –e.g., memory, learning– capacities of developmental systems. While there is an ongoing debate about which phenomenological, cognitive or mental terms should be extended to the realm of the living (Rama, forthcoming; see Section 3), the notion of *Umwelt* –and its renewed interest in various corners of theoretical biology– is a theoretically rich term for dealing with the vicissitudes and complexities of development.

2.2 *Umwelt*’s Theory in the Developmental Turn

The relevance of the concept of the *Umwelt* in evolutionary theory becomes clear when one realizes that various approaches in connection with the developmental turn have resorted to concepts similar to that of the *Umwelt*. A first approximation shows relevant similarities between the constructivist ideas of Richard Lewontin (2000) and the concept of *Umwelt*. It would not be inconceivable to attribute Lewontin Uexküll’s words (1923: 266): “Nobody is a product of their environment –everybody is the master of one’s *Umwelt*”. Lewontin’s critique of the externalism of neo-Darwinism is deeply motivated by the active role of organisms in creating their environmental conditions and, like Uexküll, emphasizes the subjective character of organism-environment relationships.

In this context, the concept of *affordance* (Heras-Escribano, 2019) is used in evolutionary biology, for example. The concept of affordance refers to the possibilities for action that an organism has in a given environment –or as Uexküll (1992: 323) said, following a similar idea, “[e]xternal stimuli [...] approach the animal in the form of

[5]This does not mean that my thesis entails an externalist position on goals (e.g. Babcock and Shea (2021)). The claim that goals can be directed toward external elements is consistent with an internalist position (e.g., intentional human behaviour (e.g., cooking) is usually directed toward the environmental context, even if it is intrinsically determined (e.g., hunger)). The distinction between intrinsic and extrinsic teleology concerns the entity/process that (causally) determines the goals of a system *A*, rather than what *A* is directed towards (see Rama (forthcoming) for a discussion). Extrinsic teleology argues that external processes are the causal factors in the specification of goals. My thesis is an intenralist position: the organism defines its own goals, which are directed toward adaptive coupling with both the external world (*Umwelt*) and the internal world (*Innwenwelt*).

questions." Both terms are understood primarily in relation to the relationship between organisms and the environment. In both cases, they confer context sensitivity on organisms. Moreover, both affordances and *Umwelt* are not created externally, but are the result of the organisms' internal, active participation –i.e., interpretation; the organism is an agent capable of constructing its connection with the environment. Certainly, the relationship between *Umwelt* and affordances deserves a proper and detailed study.[6] Apart from the similarities between the two terms outlined earlier, they play a similar role in explaining the direction of development. Affordances have often been used in an organismic view of evolution. The clearest example, which also draws on Lewontin's insights, is Denis Walsh's notion of *Affordance Landscape*, as part of his *Situated Darwinism* (Walsh, 2012, 2013, 2015). The claimed explanatory role coincides with the explanatory role of *Umwelt* outlined above: the attribution of a goal-directed and context-sensitive capacity to organismic activity.

Another case, also related to Lewontin's work, can be found in the theory of niche construction, particularly in the notion of *experiential niche construction* introduced by Sonia Sultan (2015). In the recent literature, there are various classifications of niche construction processes (see Chiu (2019), Baedke et al. (2021), Aaby and Ramsey (2022), Uller and Helanterä (2019); Trappes et al. (2022), and Rama (forthcoming) for general taxonomies of niche construction concepts). A first distinction to be drawn for our purpose of locating the concept of *Umwelt* in niche construction theory, following Trappes et al. (2022), concerns individual niche construction (involved in proximate processes, especially *developmental niche construction* (Stotz, 2017)) and population niche construction (involved in evolutionary processes and *selective niche construction* (Stotz, 2007)). The concept used by Odling-Smee et al. (2003) in their well-known book refers to the ability of a population to change its fitness by altering the external environment; ostensibly, population niche construction is an important variable within population biology. Individual niche construction, on the other hand, is part of developmental biology (Stotz, 2017; Flynn et al., 2013). It is about the processes by which an organism constructs its niche during its development. As Chiu (2019, 301) points out, echoing Lewontin's original insight, there are two types of processes within individual niche construction: the processes that physically construct the environment in which an organism lives, and the processes that experientially construct the environment. In the first case, construction involves changing the material nature of the environment (e.g. nest building). In the second case, on the other hand, there are no external changes, but the construction has an epistemic connotation. Accordingly, the organisms construct the way in which they experience their niche: An organism's perceptual ability is relative to the signaling mechanisms that connect different parts of the environment to the organisms. *Construction* here refers to the signaling processes that an organism must produce in order to achieve a perception of the world to which it must respond. In this sense, the sensitivity of an organism is not predetermined from the outside, but is actively constructed by the organism itself: it depends on the existence of specific signaling systems and the need to process the signals received from the environment. We note once again that the notion of experiential niche construction plays a similar explanatory role as the notion of *Umwelt* (see Baedke et al. (2021) for a further conceptualization and refinements of the notion of experiential niche construction and its relation to the concept of *Umwelt*). The experiential niche becomes a central element in explaining agency and adaptability. As already emphasized various developmental studies (in the context of niche construction theory, eco-devo, or epigenetics) require the concept of *experience* to understand how developmental responses can be context-sensitive and targeted to the external conditions of organisms.

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[6] The similarities between affordances and the concept of *Umwelt* are controversial (see Fultot and Turvey, 2019; Feiten, 2020; Heras-Escribano and DeJesus, 2018). While the concept of affordances emphasizes the unmediated nature of the relationship between organism and environment (affordances are not internal, representational constructs), the concept of *Umwelt* states that "the relationship that binds an organism to its environment is never immediate or automatic: between the reception of stimuli and the response of the organism, there is room for an activity of interpretation or elaboration of the stimuli themselves" (Brentari, 2018: 157). In this sense, the anti-representationalist spirit of affordances is not (necessarily) present in the concept of *Umwelt*. Be that as it may, this debate does not invalidate my point: that beyond the differences there are relevant commonalities that have been explored in the philosophy of biology.

In this section, I have emphasized the importance of *Umwelt* in evolutionary theory by linking it to other interrelated approaches. These conceptual and interdisciplinary relationships illustrate the importance of biosemiotics within the developmental turn (Rama, 2021). An important step in biosemiotics is to understand that the *Umwelt* exists because of the multiple semiotic processes that every living system undergoes. The picture that emerges depicts the organism as a complex system interconnected by many semiotic processes that create a context-dependent ability and opportunity to act adaptively in an environment. Crucially, a similar picture is drawn of the different areas of developmental turn. Ecological developmental biology (eco-devo) is primarily dedicated to understanding how developing systems use different signaling systems to adapt their developmental trajectories to their ecological contexts. Or Sultan (2015: 20) states, "ecological development, or 'eco-devo,' seeks to explicitly include the organism's particular environment in studying both the signaling pathways and the ecological and fitness consequences of phenotypic expression." Organic processes –whether in development, physiology or reproduction– are always mediated by signaling pathways that enable reciprocal regulation between the parts of the organism and the environmental context (see Sultan (2015) and Gilbert and Epel (2015) for many examples of signal-mediated developmental processes). As a semiotically grounded account of the *Umwelt*, the signaling-based account of development becomes a key to understanding the adaptively directed nature of living activities in terms of "semiotic agency" (Sharov and Tønnessen, 2021). A biosemiotic view of development also has important similarities with the post-genomic stance of Developmental Systems Theory (Oyama et al., 2001). The distributed view of biological information in development points in the same direction as semiotic and signaling accounts of development (Griffiths and Stotz, 2013). The link between biosemiotic and biological information may provide an important unifying framework for introducing biosemiotic within the developmental turn (Deacon, 2015, 2021), and thus "connecting the concepts of theoretical biology with the concepts of semiotics is a programmatic task for furthering both fields" (Kull, 2021: 129).

So far, in Section 2.1, I have emphasized the explanatory role of *Umwelt* in the developmental turn. In addition, in Section 2.2 I have shown some links between *Umwelt*'s theory and specific proposals within the developmental turn. On the one hand, the concept of *Umwelt* is related to other scientific concepts used by the developmental turn that have a similar explanatory function, such as the concept of affordances or experiential niche construction. On the other hand, the biosemiotic theory of the *Umwelt* also deserves to be considered as a discipline within the developmental turn, and its similarities with other theories such as eco-devo and DST need to be exploited. If the developmental turn is the foundational niche for contemporary approaches to *Umwelt* theory, the connections highlighted here may enable future investigations and further theorizing.

3. Karl Ernst von Baer on Teleological Development

In this section, I will present some core ideas about Karl Ernst von Baer's view of teleological development. As mentioned in the introduction, there are several reasons for introducing this historical contribution. One of them is that Baer has a direct influence on the work of Uexküll (Tamm and Kull, 2016), as we will see in a moment. Another reason is that Baer and the teleomechanistic framework to which he belongs are not seen as a reference and inspiration in recent debates –unlike Lamarck, Baldwin, Goldsmith, Owen, and others. With his theoretical and experimental reflections on teleological development, Baer can be seen as an important contribution to the development of the teleological view of development in contemporary debates. In an effort to link development and evolution, Baer "should become the focus of renewed research" (Abzhanov, 2013, 712). A further motivation is that Baer's ideas on teleology were developed in contradiction –though not outright opposition– to Darwin's view of evolution (or as Lenoir (1987, 248) said, in 1866 "he [Baer] chose to write not *gegen* [against] *Darwin* but *Ober* [about] *Darwins Lehre*") and were central to his own construction of evolution (Brauckmann, 2012). In discussing neo-Darwinism, Baer's reflection on Darwin's theory can thus also be applied to a "neo-teleomechanicism": a teleological view of development for a new evolutionary biology. I will present several of Baer's ideas, which were later also taken up by Uexküll. In addition, Baer's reflections will shed light on important questions of teleological development. Consequently, the conclusion of this paper is devoted to

understanding how Baer´s ideas on teleology contribute to specifying the role that the concept of *Umwelt* plays in explaining development.

3.1 Teleology in Nature: Kant's Puzzle

To provide historical insight, Kant's conception of teleology is an appropriate starting point. Furthermore, analyzing Kant's view will help to understand the mechanistic foundations that neo-Darwinism has adopted to render organisms explanationless in evolutionary theory. Kant's view was heavily influenced by the scientific revolution and the adoption of a single acceptable method of explanation: the mechanistic explanation (a position referred to as the *Newtonian paradigm* (Smolin, 2013)). The so-called Kant's Puzzle arises from the assumption of a different principle: that teleological explanations are unavoidable in order to understand nature. Kant's puzzling conception of teleology is presented in his work *The Antinomy of the Teleological Power of Judgment* (Kant, 2007, 214-215). Kant's Puzzle is based on two contradictory *maxims*: the *thesis* that only mechanistic causal explanations are adequate scientific explanations, and the *antithesis* that to understand living systems we need a non-mechanistic explanation that involves final causation. The human mind cannot detach itself from the purposes of nature (*Naturzweck*) to explain the various intrinsic and characteristic properties of living beings, but final causation does not fit in with the mechanistic view of the scientific revolution it proclaims. It is an epistemic tension between what is explanatorily useful (teleological explanations) and what is explanatorily valid (mechanistic explanations), between the Newtonian paradigm and the teleological paradigm (Rama, 2023). The causal structure of the teleological explanation, in which future events (end states) appear to have some kind of causal influence on present activities (means), does not fit the temporal structure of the mechanistic explanation, in which causes always precede their effects. Under this scenario, Kant argued, there can be no science that includes teleological explanations in its toolkit. Kant rejected a *constitutive* view of *Naturzweck*: natural purposes are not a real part of nature, but humans inevitably and irreducibly describe purposes to living systems. Instead, he advocated a *regulative* view of teleology: teleological explanations are not genuine scientific explanations, but they can lead scientific inquiry to a genuine mechanistic explanation (see Quarfood (2006) for a contemporary analysis of the regulative/constitutive distinction). In sum, Kant was an "ontological reductionist and an epistemological anti-reductionist" (Weber and Varela, 2002, 108).

Following Rama (2022, 163), we can define three central questions about teleology in nature. First, the ontological question: are purposes a real part of nature? Secondly, the epistemological question: Can teleological explanations be reduced to non-teleological explanations? And finally, the scientific question: Can teleological explanations be scientifically comprehensible? From Table 1 we can see that the main positions on teleology arise from different answers to these questions. Eliminativism is the position that teleology is not a real part of nature. Therefore, they are epistemologically anti-reductionist, insofar as a teleological explanation must have a genuine mechanistic explanation. Consequently, they argue that teleological explanations are scientifically comprehensible: They can be reduced to non-teleological scientific explanations. In this sense, teleological explanations can be heuristically valuable and help in scientific research. However, teleological explanations are only "as if" talk: we talk about living systems "as if" they were teleological systems, but we always intend to provide a mechanistic explanation. Eliminativism thus takes a shortcut position: teleological explanations are a shortcut to scientifically valid mechanistic explanations. Naturalism claims that teleology is a real part of nature (ontological question), arguing that it cannot be reduced to non-teleological explanations (epistemological question), and seeks scientific explanations for teleological systems (scientific question). The non-naturalist position shares the ontological and epistemological view with naturalism but considers that teleological explanations extend beyond the scope of scientific explanations.

	Ontological Question	Epistemological Question	Scientific Question
Eliminativism	No (K)	Yes	Yes

Naturalism	Yes	No (K)	Yes
Non-Naturalism	Yes	No	No (K)

Table 1: Different positions concerning natural teleology; the letter *K* singles out those answers supported by Kant. Reprinted with permission from Rama (2022, 165).

Note that Kant's view is a mixture of all these positions. He endorsed and rejected some of the answers to these three positions.[7] Regarding the ontological question, his regulative view entailed an eliminativist position. However, as far as naturalism is concerned, we have seen that Kant was also an epistemological anti-reductionist, insofar as teleological explanations cannot be reduced to purely mechanistic explanations. After all, as a non-naturalist, he did not believe that teleological explanations are scientifically comprehensible within the framework of the (mechanistic) foundations of science. This fact can explain why Kant influenced every position in the history of biology. Concerning eliminativism, Kant became the main reference point for the epistemological foundations of the scientific revolution through his support of the Newtonian style of science and consequently influenced the post-Kantian mechanistic view by promoting a "reductionist-leaning reading that has been most influential in the Anglo-Saxon world" (Weber and Varela, 2002, 103). The non-naturalist position of early vitalists such as Driesch or Bergson and the German post-Kantian romantic *Naturphilosophie* (Richards, 2002) was also directly influenced by Kant's reflections on teleology. Finally, as far as naturalism is concerned, Kant's emphasis on the irreducible and inevitable nature of teleological explanations (expressed in the second maxim of *The Antinomy*) has fostered several naturalistic positions and, more importantly, several scientific advances.

With respect to naturalism, a specific point should be emphasised. Kant believed that there could be no "Newton of the Grassblade"; i.e. that teleological explanations could never be introduced into science, as Newton did with the physical world. This non-naturalistic spirit, as mentioned, fostered several scientific advances. What is most interesting for our analysis, however, is the fact that these attempts to understand teleology from a Kantian point of view led to the contemporary view of *teleological physiology* described in Section 1. This means that the main scientific advances influenced by the Kantian paradigm have revealed how teleological physiology can fall within the realm of scientific explanation. Kant's contemporary footprints lie primarily in a scientific account of teleological physiology (Weber and Varela, 2002; Gambarotto and Nahas, 2022). However, this is not our explanatory aim here. I intend to see Kant's footprints in teleological development. This means to analyze Kant's influence on the scientific understanding of teleological development. This leads us to the teleomechanistic program and more specifically to Karl Ernst von Baer.

3.2 Absolute Necessity is not Enough: Reviewing Darwin

Kant's ideas influenced much of German biology in the 18th and 19th centuries. An entire enterprise –known as Teleomechanicism (Lenoir, 1989)– was constructed to analyze and ultimately solve Kant's Puzzle, to achieve a "teleology without regrets" (Lenoir, 1981). Within Teleomechanicism, according to Lenoir (1989: 16), Baer can be seen as the last and most important figure whose attempts to approach teleology converged towards a naturalistic position.[8] I will rely here on a series of posthumously published works, principally on two lectures

[7] Zammito (2006) rightly argues that these positions were only defined after Kant, so the question of whether Kant was a naturalist or not is not entirely meaningful. However, this does not prevent us from analyzing his view from today's perspective and seeing whether neo-Kantians are naturalists or not.

[8] There is an ongoing debate about the adequacy of Lenoir's historical analysis. It seems that there are various differences between Kant's teleological view and the view of other teleomechanicists. For example, Blumenbach –as well as von Baer– held a constitutive view of teleology instead of Kant's regulative view (Zammito, 2012; Richards, 2000). So it is not clear why we should group them all under a similar theoretical and historical trend. While this historical analysis is important, it has no bearing on the analysis of this paper. Therefore, I will not go into detail about whether adopting a regulative view is a prerequisite for belonging to teleomechanicism.

he gave in Berlin in 1866 (Baer, 1886a, 1886b). While he devoted a long monograph to review Darwin's theory principally from an empirical standpoint (Baer, 1886c), in the lectures of 1866 he dealt with central foundational assumptions of Darwin's theory –all these works and others were published in Baer (1886d). These lectures are extremely useful as they summarise most of Baer's ideas on teleological development. Furthermore, he also provides a rich historical analysis, from Ancient Greeks to Darwinism, of how "teleophobia" (Baer, 1886a: 72) arose in natural science (he also deals with other interesting topics such as free will, the philosophy of mind, and cosmology).

Baer's historical analysis shows how teleological explanations came into conflict with the foundations of science. The only supposedly justifiable explanation of nature is based on "absolute necessities": the application of physico-chemical, mechanical laws. All natural beings are a necessary result of the action of these laws. The same explanatory model that Newton applied to the movement of inert objects was introduced into the realm of living beings (he discusses in particular Haeckel's interpretation of Darwin's theory, i.e. the first step of neo-Darwinism). According to this view, living beings are created exclusively through mechanical effects on the material substrate of living beings. No goals –no teleological explanation– are needed to explain how living beings are constructed. It is sufficient to establish laws that necessarily produce adult organisms. However, he did not accept this position because "if you deny all goals or purposes in nature in this triumphant feeling [explaining nature only through absolute necessity], in my opinion, you go too far, far too far" (Baer, 1886a: 65). If teleological explanations are set aside in favor of a purely mechanistic framework, many biological problems remain unsolved for him, especially in developmental processes.

According to Baer, the rejection of goals in development is "a scientific superstition" (Baer, 1886a: 73) rather than a justified rationale. For him, there should be no tension between mechanistic and teleological explanations: "Do purpose and "absolute necessities" always exclude each other? […] Doesn't purpose have to look for means?" (Baer, 1886a: 68). So his criticism of Darwin's view is precisely that it does not recognize that the necessities in living organisms are the *means* that organisms use to achieve goals. Goals are responsible for the construction of the order we find in nature; absolute necessities are interviewed and oriented by organisms's goals to produce orderer matter; or as Baer (1886a: 88) said "natural forces which are not directed to an end cannot produce order." It is the goals of development that *orchestrate* the means of constructing traits. While Darwinists see development as a blind process guided by absolute necessities, Baer sees these absolute necessities as the result of organisms pursuing goals, an idea also held by current views of goal-directedness (see the definition of goal-directedness in Section 2). The ideas noted in Section 2 about the explanatory role of *Umwelt* was well recognized by Baer: The blindness of developmental processes was constructed in direct opposition to teleological explanations; teleological explanations need to be constructed in direct coherence with mechanistic explanations: "The origins of life are not to be dissociated from the organization of matter obeying physicochemical laws; but the principles of organization cannot be themselves reduced to physicochemical laws" (Lenoir 1987, 263). Absolute necessities of mechanical processes must be seen as means towards goals.

To argue in favor of a teleological ingredient in developmental explanations, he gives many examples of developmental processes to demonstrate the future-oriented character of development. The organs of the body that are formed in the egg are constructed so that they can be used in later stages; body parts are constructed long before they are used: "The caterpillar bites or cuts its food into pieces; –for this purpose, the tools are formed before they are needed, on the embryo within the egg (Baer, 1886a: 4) […] It is absolutely impossible to ignore that all these changing states are set up in such a way as to achieve the ultimate goal, the development of the butterfly" (Baer, 1886a: 55). In this sense, the neglect of teleological explanations ignores not only organismal capacity of regulating development but also the future-oriented nature of development –the fact that the function and structure of phenotypes at a given life stage depends on the construction of these traits at earlier ontogenetic stages. Baer's ideas about time and development suggest a view of development as a sequential stage of changes, where in each stage an organism's goals drive mechanical processes to produce a suitable outcome in future stages. Development is a stage-by-stage process in which "the present state is only possible

through the preceding ones" (Baer, 1886a: 52). Baer advocates a processual view of development (Nicholson and Dupre, 2018). According to this view, “the essence of life can only be the process of life itself or the course of life, that is, the series of states following each other.” Development is thus a continuous accumulation of changes in form and function, changes in the physicochemical composition of living beings. These changes and their future (structural and functional) implications during ontogeny cannot be accounted for without a teleological view of development: order cannot arise without goals and goals are present at each ontogenetic stage in the regulatory mechanism of development –i.e. in the way an organism directs its means. As Baer (1886b: 180) stated, in a quite fashioned way from a contemporary standpoint, “every organism in the process of coming into being has a goal. Without goals how could anything subject to regulation come about?”

3.3 *Ziel* and *Zweck:* shortcut without eliminativism

Certainly, Baer did not propose a robust teleological theory of development, mainly because many developmental phenomena were unknown. Nevertheless, he provides some interesting insights that help us to construct a teleological theory of development. I will present two important ideas that were mainly taken up by Uexküll. First, the distinction between *Ziel* and *Zweck*, and second, the use of the musical metaphor as a heuristic device to deal with the regulatory capacities of developmental systems.

For Baer, most criticisms of teleological explanations arise from "a confusion of terms” (Baer, 1886a: 72) and that natural languages are “extremely poor for everything spiritual [meaning the intentional concepts associated with teleological languages, such as purposiveness, consciousness, deliberation, or rationality]” (Baer, 1886a: 74). Part of the reason for teleophobia lies in the subtle semantic nuance between the German words *Zweck* (roughly translatable as “purpose”) and *Ziel* (typically rendered in English as “goal”), a distinction that is not clearly grasped in “Western languages” (Lenoir, 1989: 272). Once this distinction is noted, he calls for a defense of goals and a rejection of purposes, mainly because “we should not picture the primordial source of existence too human-like, and must consider distance and diversity unattainable […] A large part of the attacks [to teleology] on the essence of the matter seems to me to lie in the inadequacy of this word and concept [*Zweck*]” (Baer, 1886a: 79-80).

In this sense, as Baer argued, the word “purposes” has an anthropomorphic character that may not be sufficient to explain living systems. Moreover, the notion of purposes seems to be linked to the inference or explicit intention to do something, such as intelligent design. It is therefore a good strategy, Baer advised, to be careful with the chosen world. As noted in one of the epigraphs of this paper, Uexküll adopted Baer’s recommendation (Kull, 2001: 6) and rejected the notion of purpose for practically similar reasons: “Instead of seeing in it [teleology] merely a rule stretching across time and space, men have spoken of ‘purpose’ and ‘purposefulness’ in Nature as a sort of human being […] it is advisable therefore to dismiss from biology, for all time, expressions such as ‘purpose’ and ‘purposefulness’” (Uexküll, 1926: 270).

Moreover, this semantic analysis proposed by Baer was given while he was analyzing the construction of teleophobia. In this context, Baer stressed that the notion of purpose (*zweck*) was an obstacle towards a naturalistic program. Precisely, Kant’s term for the teleological character of living systems was *natural purpose* (*Naturzweck*). While this semantic conundrum is not the only problem, Baer’s distancing from Kant’s teleological ideas is linked to Baer’s rejection of the notion of natural purpose used by Kant. Also, various counter-positions, such as vitalism or eliminativism, may arise from linking teleological explanations to Kant’s natural purposes. In other words, when the question is asked about the possibility of explaining *purposes (zwecke)* in scientific terms, the expected polarized answers may arise. If you deny purposes, you are an eliminativist and intend to explain development in terms of absolute necessities, and according to Baer, you are likely to fail in this task. But if you accept purposes, you will end up as an anti-naturalist. The connection between this semantic conundrum and Baer’s criticism of “absolute necessities” becomes clear in the following quotation:

> A century ago, Kant taught that all parts of an organism are both purpose [*Zweck*] and means. We would prefer to say: goals [*Ziele*] and means. Now it is announced emphatically and confidently: purposes [*Zwecke*] do not exist in nature, there are only necessities in it; and does not want to recognize that these very necessities are means to ends. Becoming without goals is not at all conceivable (Baer, 1886b, 231).

As already mentioned, Baer did not subscribe to any of the polarized positions (eliminativism and anti-naturalism): He rejected natural purposes without rejecting teleology. In other words, he took *a shortcut without eliminativism* (Rama, 2022). We have seen that eliminativism argues that teleological explanations are a shortcut to genuine mechanistic explanations. We take organisms "as-if" they have purposes, but ultimately we are only trying to explain necessities (i.e. mechanisms). From Baer's point of view, explanations based on purposes are a shortcut, not for mechanistic explanations, but for genuine teleological explanations: These explanations are based on developmental goals and the regulation of means. In short, *purposes are an explanatory shortcut to goals*: developmental goals are *constitutive* of nature, whereas puposes are a vestige of anthropomorphic views. Goals seem to be more appropriate and explanatorily sufficient for the treatment of developmental phenomena. Goals, stripped of any anthropomorphic or non-naturalistic connotation, refer to the targetability (*Zielstrebigkeit*) of a particular action; the direction that an organic process takes in order to reach a certain stable end state. In the course of its development, as it passes through ontogenetic stages, the organism constructs itself in order to acquire new properties. The directionality of this process and the way it influences the means of constructing traits is what Baer understands as goals.

3.3 Musical Metaphors

The regulation of the various developmental pathways towards the target state at each ontogenetic stage is thus the starting point for teleological explanations of development. As already mentioned, this gives developing organisms a relevant degree of explanatory power (beyond their genetic basis; cf. Section 1). How did Baer explain these regulatory abilities? The main explanatory device provided by Baer is that of a metaphor: the musical metaphor (see Wellman (2014) for a recent analysis of the rhythm metaphors used by Baer). This is another element that Uexküll adopted from Baer. The work of both thinkers is full of metaphors that refer to musical phenomena.

There are various metaphors based on musical phenomena –such as *rhythm*, *tones,* or *melodies*. The most interesting, however, is that of *harmony*. As Baer pointed out, "the reciprocal interconnections of organisms with one another and their relationship to the universal materials that offer them the means for sustaining life, is what has been called the *harmony* of nature, that is a relationship of mutual *regulation*" (Baer, 1886b, 228–229; emphasis added). The harmony of living beings results from the mutual regulation of the different parts of the system and its environment. The other musical metaphors are therefore subordinate to the metaphors of musical harmony. Just as musical harmony consists of the relationship between the elements (notes, chords) of a harmonic arrangement, harmony in living beings is based on the connection between the various elements of a living system and its environment.

It is important to understand the explanatory role of a metaphor. Metaphors are heuristic devices that guide our knowledge and investigation. They help us to think about things and to search for a scientific explanation. In the context of our analysis, Baer's use of metaphors is closely related to the restriction imposed by Kant that there can be no science that explains teleological phenomena. If we think of teleological physiology (see section 1), the scientific disciplines that deal with it were built in the twentieth century (dynamic systems theory, cybernetics, artificial intelligence, complex systems theory, etc.). Certainly, these fields did not exist when Kant thought about teleology but were inspired by Kant's ideas, as noted before. Naturalization is an epistemic task, so it is always relative to how we know the world; the possibility of understanding a certain phenomenon in

scientific terms relies on scientific knowledge at disposition. If we look at teleological development, it seems that Baer was in a similar situation. He did not have the explanatory weapons to deal with teleological development. That's one of the reasons why he uses a metaphor. So the question is whether or not nowadays there are scientific disciplines that deal with teleological development.

This question has already been answered in Section 1. The developmental turn aims to construct development as a goal-oriented theory. In this sense, several scientific disciplines attempt to explain development teleologically –e.g. post-genomics, eco-devo, niche construction theory, or development systems theory. Of course, this does not mean that we already have a complete and solid theory of teleological development, but new areas of research and theoretical approaches have been developed in recent decades that were certainly not available in Baer's era. This does not mean that musical metaphors must remain explanatorily unuseful as the sciences evolve. Metaphors still retain many heuristic values that are independent of the development of science (Haraway, 1976); indeed, musical metaphors are often used today in the context of the developmental turn (e.g. Noble, 2006; Oyama, 2001; Robert, 2004). Rather, it means that developmental biology now studies Baer's *harmonic regulations* in developmental processes. The above areas of research are dedicated to understanding the regulatory capacity of developmental systems, that is, what musical metaphors attempt to illuminate. In analyzing phenomena such as phenotypic plasticity or niche construction, the focus is precisely on how developmental systems are able to regulate their relationship with their environment during ontogeny. At the cellular level, molecular epigenetics, anchored in a post-genomic view of genetics, seeks to discover the different ways in which cells integrate the various information resources to regulate cellular development.

4. Conclusions: Bridging Baer and Uexküll with the developmental turn

The theoretical reflections on Baer's view of teleological development are of interest for the current philosophy of biology. We have seen in Section 2 that the concept of *Umwelt* is a central explanatory component for our goal of developing an alternative, non-Neo-Darwinian theory of evolution. Given the alleged explanatory role of *Umwelt*, what do Baer's ideas contribute to the construction of a teleological theory of development? First of all, it should be noted that the call for a developmental turn is partly similar to Baer's critique of the Darwinian view of his time. The developmental turn emphasizes that developmental processes and the intrinsic properties of organisms are core elements of evolutionary theory and that sub-organismal, molecular, and mechanistic biology cannot explain the unfolding of development. Baer's criticism was precisely along these lines: development is not the expression of "absolute necessities". As Baer stated and the developmental turn demands, something else is required. Where Darwinism saw necessities, Baer described them as means towards goals; whereas the Modern Synthesis saw genetic programs, the agential perspective postulates organismic regulation of genetic expressions as the means towards goals. To call for a developmental turn is to understand that development is not just about the operation of "blind" mechanisms, but that developmental mechanisms are means towards goals, the way a developing system deploys its means according to what it "sees"; this is what it means to be a developmental agent: Aligning mechanisms with goals.

On the way to a teleological view of development, Baer's ideas can be combined with the explanatory power of the concept of *Umwelt*. First, Baer envisioned development as a stepwise process in which the ontogenetic stage in *t2* depends on the developmental processes in *t1*. This suggests that the developing system has a constructed *Umwelt* (and *Innenwelt*) at each ontogenetic stage to define the directionality of development at each stage. A sequence of ontogenetic stages is accompanied by a sequence of *Umwelt* relative to the intrinsic and extrinsic conditions of development. At each stage, the *Umwelt* is central to defining the directionality of the developmental processes that produce the relevant changes that locate the developing system in the next ontogenetic stage. The construction of the *Umwelt* is a central prerequisite for the regulatory processes at each ontogenetic stage, at each ontogenetic change. Second, the way in which development produces adaptive responses at each ontogenetic stage has been explained by a metaphor: the harmonious regulation between the parts of an organism and its external world. As explained in Section 2, adaptive regulation in developmental

processes requires context sensitivity. If we want to think of development as an adaptive process of mutual regulation between its elements, we need to postulate developmental systems that "see" their developmental context; i.e., we must place the concept of *Umwelt* at the centre of developmental theory. This also explains why Uexküll also used musical metaphors: both aimed at explaining adaptive regulation; now the developmental turn has developed several ways of understanding adaptive regulation in development beyond metaphors.

A final point that emerges from our analysis concerns the link between Baer's distinction between *Ziel* and *Zweck* and the concept of *Umwelt* itself. As mentioned above, the adherence to the word *Ziel* is to avoid any non-natural connotation to teleology. The concept of *Umwelt* might suffer from a similar scenario, insofar as the *Umwelt* can be understood as a human-like conception of the world. If we are to ascribe an explanatory role to *Umwelt* in development –e.g. in cell development or morphogenesis– a different, less anthropomorphic interpretation is required, just as one should avoid the notion of *Zweck* in biology. The *Umwelt*, therefore does not have to be understood in this way in order to be useful in evolutionary theory. If we understand it in terms of signals in which different information is exchanged in different physico-chemical processes –as suggested in Section 2.2– then the *Umwelt* is the construction of a context-dependent ability to act on the environment and regulate the organism's own structure and functionality; i.e. as a construction of the phenomenology of the organism that allows organic systems to be treated as agents in their own right. In sum, the concept of *Umwelt* is relevant to explain the targetability (*Zielstrebigkeit*) of development, the *Umwelt* is not part of natural purposes but of the goal of nature.

The view of development as a sequential process of changes mediated by goal-directed and context-sensitive responses is not new, but this paper intends to bridge historical forerunners and important theoretical ideas to the contemporary arena. This article is about the foundations of teleological explanations. By looking at this issue from a historical perspective, I argue that developmental biology is now building its own theoretical and experimental foundations for dealing with teleological development. Whereas Kant neglected this possibility and Baer relied on metaphors, the biological sciences now provide the correct answer to the old puzzle. This article contributes to constructing a teleological view of development that is necessary for a new evolutionary paradigm. On the way to realizing the developmental turn, it is necessary to understand various interdisciplinary, historical, and theoretical contexts. In the quest to understand the adaptive nature of life or, as Darwin said, the endless forms most beautiful, it is not possible to avoid the beauty of the complexity of developmental processes, insofar as "it is precisely the recognition of the mutual interrelation of all the processes in nature and the harmony in their institutions that gives them the greatest pleasure" (Baer, 1886a: 51).

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References

Aaby, B. H. and Ramsey, G. (2022). Three kinds of niche construction. *The British Journal for the Philosophy of Science,* 73, 2. https://doi.org/10.1093/bjps/axz054

Å̊gren, J. A. (2021). *The Gene's-Eye View of Evolution.* Oxford: Oxford University Press.

Amundson, R. (2005). *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo.* Cambridge: Cambridge University Press.

Abzhanov, A. (2013). von Baer's law for the ages: lost and found principles of developmental evolution. *Trends in Genetics*, 29(12), 712-722.

Babcock, G. and McShea, D. W. (2021). An externalist teleology. *Synthese*, 199(3), 8755–8780.

Baedke, J. (2018). O organism, where art thou? Old and new challenges for organism-centered biology. *Journal of the History of Biology,* 52(2), 293–324. doi: 10.1007/s10739-018-9549-4

Baedke, J., Fábregas-Tejeda, A. and Prieto, G.I. (2021) Unknotting reciprocal causation between organism and environment. *Biol Philos,* 36, 48.

Baer, K. E. v. (1886a). Uber den Zweck in den Vorgängen der Natur — Erste Hälfte. Uber Zweckmäßigkeit oder Zielstrebigkeit uberhaupt. In *Studien aus dem Gebiete der Naturwissenschaften. Reden gehalten in wissenschaftlichen Versammlungen und kleinere Aufsätze vermischten Inhalts.* Zweiter Theil (Studien aus dem Gebiete der Naturwissenschaften) (pp. 49–106). Braunschweig: Friedrich Vieweg und Sohn.

Baer, K. E. v. (1886b). Uber Zielstrebigkeit in den organischen Körpern insbesondere. *In Studien aus dem Gebiete der Naturwissenschaften. Reden gehalten in wissenschaftlichen Versammlungen und kleinere Aufsätze vermischten Inhalts.* Zweiter Theil (Studien aus dem Gebiete der Naturwissenschaften) (pp. 170–234). Braunschweig: Friedrich Vieweg und Sohn.

Baer, K. E. v. (1886b). Über Darwins Lehre. *In Studien aus dem Gebiete der Naturwissenschaften. Reden gehalten in wissenschaftlichen Versammlungen und kleinere Aufsätze vermischten Inhalts.* Zweiter Theil (Studien aus dem Gebiete der Naturwissenschaften) (pp. 235-480), Braunschweig: Friedrich Vieweg und Sohn.

Baer, K. E. v. (1886d) *Studien aus dem Gebiete der Naturwissenschaften. Reden gehalten in wissenschaftlichen Versammlungen und kleinere Aufsätze vermischten Inhalts. Zweiter Theil (Studien aus dem Gebiete der Naturwissenschaften).* Braunschweig: Friedrich Vieweg und Sohn.

Balari, S., & Lorenzo, G. (2014b). The end of development. *Biological Theory*, 10(1), 60–72. doi: 10.1007/s13752-014-0180-0

Barandiaran, X., Di Paolo, E., & Rohde, M. (2009). Defining agency: Individuality, normativity, asymmetry, and spatio-temporality in action. *Adaptive Behavior,* 17(5), 367–386. doi: 10.1177/105971230934381

Bateson, P. (2005). The return of the whole organism. *Journal of Biosciences,* 30(1), 31–39. doi: 10.1007/bf02705148

Brauckmann, S. (2012). Karl Ernst von Baer (1792-1876) and evolution. *International Journal of Developmental Biology,* 56(9), 653-660.

Brentari, C. (2018). *Jakob von Uexküll: the discovery of the umwelt between biosemiotics and theoretical biology*. Dordrecht. Springer

Campbell, J. H. (1994). Organisms create evolution. In J. H. Campbell & J. W. Schopf (Eds.), *Creative Evolution?!* (pp. 85–102). Boston, MA: Jones & Bartlett.

Chiu, L. (2019) Decoupling, commingling, and the evolutionary significance of experiential niche construction. In T. Uller and K. N. Laland (Eds.) *Evolutionary causation: biological and philosophical reflections* (pp 299-322) MIT Press, Cambridge, MA.

Dawkins, R. (1982*). The Extended Phenotype*. Oxford: Oxford University Press.

Dawkins, R. (1989). *The Selfish Gene (2nd ed.)*. Oxford, UK: Oxford University Press.

Deacon, T. W. (2015). Steps to a science of biosemiotics. *Green Letters*, *19*(3), 293-311.

Deacon, T. W. (2021). How molecules became signs. *Biosemiotics*, *14*(3), 537-559.

Feiten, T. E. (2020). Mind after Uexküll: A foray into the worlds of ecological psychologists and enactivists. *Frontiers in Psychology*, *11*, 480.

Flynn, E. G., Laland, K. N., Kendal, R. L., & Kendal, J. R. (2013). Target article with commentaries: Developmental niche construction. *Developmental science,* 16(2), 296-313.

Fultot, M., & Turvey, M. T. (2019). Von Uexküll's theory of meaning and Gibson's organism–environment reciprocity. *Ecological Psychology*, *31*(4), 289-315.

Gambarotto, A., & Nahas, A. (2022). Teleology and the organism: Kant's contro- versial legacy for contemporary biology. *Studies in History and Philosophy of Science*, 93, 47–56. doi: 10.1016/j.shpsa.2022.02.005

Gilbert, S. F., & Epel, D. (2015). *Ecological Developmental Biology: The Environmental Regulation of Development, Health, and Evolution.* Sunderland, MA: Sinauer.

Godfrey-Smith, P. (2009). *Darwinian Populations and Natural Selection*. Oxford: Oxford University Press.

Griffiths, P. E., & Stotz, K. (2013). *Genetics and Philosophy. An Introduction.* Cambridge: Cambridge University Press.

Heras-Escribano, M. (2019). *The Philosophy of Affordances.* Cham: Palgrave Macmillan.

Heras-Escribano, M., & De Jesus, P. (2018). Biosemiotics, the extended synthesis, and ecological information: Making sense of the organism-environment relation at the cognitive level. *Biosemiotics*, 11(2), 245–262. doi: 10.1007/ s12304-018-9322-2

Haraway, D. J. (1976). *Crystals, fabrics, and fields: Metaphors that shape embryos*. Yale University Press.

Huneman, P. (2010). Assessing the prospects for a return of organisms in evolutionary biology. *History and Philosophy of the Life Sciences,* 32(2-3), 341–371. doi: 10.2307/23335078

Jablonka, E., & Lamb, M. J. (2020). *Inheritance Systems and the Extended Evolutionary Synthesis.* Cambridge: Cambridge University Press.

Kant, I. (2007). *Critique of Judgement*. Oxford: Oxford University Press.

Keller, E. F. (2002). *The Century of the Gene.* Cambridge, MA: Harvard University Press.

Kull, K. (2001). Jakob von Uexkull: An introduction. *Semiotica*, 2001(134), 1–59. doi: 10.1515/semi.2001.013

Kull, K. (2004). Uexküll and the post-modern evolutionism. *Σημειωτκή-Sign Systems Studies*, *32*(1-2), 99-114.

Kull, K. (2021). The aim of extended synthesis is to include semiosis. *Theoretical Biological Forum,* 119-132.

Lenoir, T. (1981). Teleology without regrets. The transformation of physiology in Germany: 1790–1847. *Studies in History and Philosophy of Science Part A, 1*2(4), 293–354. doi: 10.1016/0039-3681(81)90019-4

Lenoir, T. (1989). *The Strategy of Life: Teleology and Mechanics in Nineteenth-Century German Biology*. Chicago: The University of Chicago Press.

Levins, R., & Lewontin, R. C. (1985). *The Dialectical Biologist.* Cambridge, MA: Harvard University Press.

Lewontin, R. C. (1974). *The Genetic Basis of Evolutionary Change.* New York: Columbia University Press.

Lewontin, R. C. (2000). *The Triple Helix: Gene, Organism, and Environment.* Cambridge, MA: Harvard University Press.

Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge, UK: Cambridge University Press

Mayr, E. (1961). Cause and effect in biology: Kinds of causes, predictability, and teleology are viewed by a practicing biologist. *Science*, 134(3489), 1501–1506. doi: 10.1126/science.134.3489.1501.

Mayr, E. (1963). *Animal Species and Evolution.* Harvard University Press.

Mayr, E. (1974). Teleological and teleonomic, a new analysis. In R. S. Cohen & M. W. Wartofsky (Eds.), *Methodological and Historical Essays in the Natural and Social Sciences* (pp. 91–117). Dordrecht: Reidel.

Michel, G. F., & Moore, C. L. (1995). Developmental Psychobiology: An Interdisciplinary Science. Cambridge, MA: MIT Press.

Minelli, A. (2011). Animal Development, an Open-Ended Segment of Life. *Biological Theory,* 6(1), 4–15. doi: 10.1007/s13752-011-0002-6

Moreno, A., & Mossio, M. (2015). Biological Autonomy. A Philosophical and Theoretical Inquiry. Dordrecht: Springer.

Müller, G. B., & Newman, S. A. (Eds.). (2003). *Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology.* Cambridge, MA: The MIT Press.

Newman, S. A. (2019). Inherency of form and function in animal development and evolution. Frontiers in Physiology, 10, 443732.

Nicholson, D. J. (2014). The return of the organism as a fundamental explanatory concept in biology. *Philosophy Compass,* 9(5), 347–359. doi: 10.1111/phc3 .12128

Nicholson, D. J., & Gawne, R. (2015). Neither logical empiricism nor vitalism, but organicism: What the philosophy of biology was. *History and Philosophy of the Life Sciences*, 37(4), 345–381. doi: 10.1007/s40656-015-0085-7

Nicholson, D. J., & Dupré, J. (Eds.) (2018). *Everything flows: towards a processual philosophy of biology*. Oxford University Press.

Noble, D. (2006). *The Music of Life: Biology Beyond Genes.* Oxford: Oxford University Press.

Nuño de la Rosa, L. (2023). Agency in Reproduction. *Evolution & Development*. (25) 418-429.

Odling-Smee, J., Laland, K. N., & Feldman, M. W. (2003). *Niche Construction: The Neglected Process in Evolution.* Princeton, NJ: Princeton University Press.

Oyama, S. (2001). Terms in tension: What do you do when all the good words are taken? In S. Oyama, R. Gray, & P. E. Griffiths (Eds.), *Cycles of Contingency: Developmental Systems and Evolution* (pp. 177–193). Cambridge, MA: The MIT Press.

Oyama, S., Gray, R., & Griffiths, P. E. (Eds.). (2001). *Cycles of Contingency: Developmental Systems and Evolution.* Cambridge, MA: The MIT Press.

Quarfood, M. (2006). Kant on biological teleology: Towards a two-level interpretation. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 37(4), 735–747.

Rama, T. (2021). Biosemiotics at the bridge between Eco-Devo and representational theories of mind. *Rivista Italiana di Filosofia del Linguaggio*, 15(2), 59–92. doi: 10.4396/2021203

Rama, T. (2022). Agential Teleosemantics. PhD Thesis. Autonomous University of Barcelona.

Rama, T. (2023). Evolutionary causation and teleosemantics. In *Life and Mind: New Directions in the Philosophy of Biology and Cognitive Sciences* (pp. 301-329). Cham: Springer International Publishing. doi: 10.1007/978-3-031-30304-3_14

Rama. T. (Forthcoming). Is a Cognitive Revolution in Theoretical Biology Underway? *Foundations of Science.*

Rama, T. (Forthcoming). Individual and Populational Niche Construction: Agency, Reciprocal Causation and Explanation.

Rama, T. (Forthcoming). The Historical Transformation of Individual Concepts into Populational Ones: An Explanatory Shift in the Gestation of the Modern Synthesis.

Rama, T. (Forthcoming). Explanatory Internalism: Challenging Selected-Effect Functions.

Richards, R. J. (2000). Kant and Blumenbach on the Bildungstrieb: a historical misunderstanding. *Studies in History and Philoso*phy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences, 31(1), 11-32.

Richards, R. J. (2002). *The Romantic Conception of Life: Science and Philosophy in the Age of Goethe.* Chicago, IL: The University of Chicago Press.

Robert, J. S. (2004). *Embryology, Epigenesis and Evolution: Taking Development Seriously.* Cambridge: Cambridge University Press.

Sharov, A., & Tønnessen, M. (2021). *Semiotic agency*. Springer International Publishing.

Shea, N. (2013). Inherited representations are read in development. *The British Journal for the Philosophy of Science*, 64(1), 1–31. doi: https://doi.org/10.1093/bjps/axr050

Smolin, L. (2013). *Time reborn: From the crisis in physics to the future of the universe*. HMH.

Sober, E. (1984). *The Nature of Selection. Evolutionary Theory in Philosophical Focus.* Chicago, IL: The University of Chicago Press.

Stotz, K. (2017). Why developmental niche construction is not selective niche construction: And why it matters. *Interface Focus,* 7(5), 20160157. doi: 10.1098/rsfs.2016.0157

Sultan, S. E. (2003). Phenotypic plasticity in plants: a case study in ecological development. *Evolution & Development*, 5(1), 25-33.

Sultan, S. E. (2015). *Organism & Environment: Ecological Development, Niche Construction, and Adaption.* Oxford: Oxford University Press.

Sultan, S. E., Moczek, A. P. and Walsh, D. (2022). Bridging the explanatory gaps: what can we learn from a biological agency perspective?. *BioEssays*, 44(1), 2100185.

Tamm, M., and Kull, K. (2016). Toward a reterritorialization of cultural theory: Estonian theory from Baer via Uexküll to Lotman. *History of the Human Sciences*, 29(1), 75-98.

Tønnessen, M., Magnus, R., & Brentari, C. (2016). The biosemiotic glossary project: Umwelt. *Biosemiotics*, *9*, 129-149.

Trappes, R., Nematipour, B., Kaiser, M. I., Krohs, U., Van Benthem, K. J., Ernst, U. R., Gadau, J., Korsten, P., Kurtz, J., Schielzeth, H., Schmoll, T., & Takola, E. (2022). How individualized niches arise: defining mechanisms of niche construction, niche choice, and niche conformance. *BioScience*, 72(6), 538-54

Uexküll, J. v. (1923). *Weltanschauung und Gewissen. Deutsche Rundschau*, 197, 253–266.

Uexküll, J. v.(1926). *Theoretical Biology.* London: Kegan Paul, Trench, Trubner & Co.

Uexküll, J. v. (1936). *Niegeschaute Welten. Die Umwelte meiner Freunde*. Berlin: S. Fischer Verlag.

Uexküll, J. v. (1992). A stroll through the worlds of animals and men: A picture book of invisible worlds. *Semiotica*, 89(4), 319-391.

Uller, T., & Helanterä, H. (2019). Niche construction and conceptual change in evolutionary biology. *The British Journal for the Philosophy of Science,* 70(2), (351-375).

Wagner, G. P. (2014). *Homology, Genes, and Evolutionary Innovation.* Princeton, NJ: Princeton University Press.

Walsh, D. M. (2003). Fit and diversity: Explaining adaptive evolution. *Philosophy of Science,* 70(2), 280–301. doi: 10.1086/375468

Walsh, D. M. (2012b). Situated adaptationism. In W. P. Kabasenche, M. O'Rourke, & M. H. Slater (Eds.), *The Environment: Philosophy, Science, and Ethics* (pp. 89–116). Cambridge, MA: The MIT Press.

Walsh, D. M. (2013). The affordance landscape: The spatial metaphors of evolution. In G. Barker, E. Desjardins, & T. Pearce (Eds.), *Entangled Life. Organism and Environment in the Biological and Social Sciences* (pp. 213– 236). Dordrecht: Springer.

Walsh, D. M. (2015). *Organisms, Agency, and Evolution.* Cambridge: Cambridge University Press.

Weber, A., & Varela, F. J. (2002). Life after Kant: Natural purposes and the autopoietic foundations of biological individuality. *Phenomenology and the Cognitive Sciences,* 1(2), 97–125.

Wellmann, J. (2015). Folding into being: early embryology and the epistemology of rhythm. *History and Philosophy of the Life Sciences,* 37, 17-33.

West-Eberhard, M. J. (2003). *Developmental Plasticity and Evolution.* Oxford: Oxford University Press.

Williams, G. C. (1992). *Natural selection: Domains, levels, and challenges*. Oxford University Press.

Zammito, J. H. (2006). Teleology then and now: The question of Kant's relevance for contemporary controversies over function in biology. S*tudies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 37(4), 748–770.

Zammito, J. H. (2012). The Lenoir thesis revisited: Blumenbach and Kant. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 43(1), 120–132.