

Autonomy and Development:

Distinguishing teleological development from teleological physiology

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Abstract: An agential and organismic view of development has brought back certain concepts in biology, such as teleology and normativity. What are the goals and norms that a developmental system pursues? Where do phenotypes in ontogenesis come from? The common answer is that genes contain the recipe to build organisms. However, the agential and organismic view of development seeks to offer a different answer beyond any reductionist explanations. For this reason, teleological development has become a central *explanans* in developmental and evolutionary biology. However, the motivation for this article is that teleological development as an *explanandum* has not been treated with the same intensity and rigor despite its ubiquity as an *explanans*. In particular, a common and now widely adopted strategy for explaining teleological development is to appeal to a closely related, yet fundamentally distinct, conception of teleology: the theory of autonomous systems, a theory designed to deal with physiological-level processes, not developmental ones. This article explores the (generally unanalyzed) differences between teleological development and teleological physiology by arguing that autonomous systems theory falls short of explaining the specificity of teleological development. The main conclusion is that the agential and organismic views in biology ought to be broadened to include different goals beyond self-maintenance; that to be alive is not only about the maintenance of an organization. The distinctiveness of teleological development entails specific philosophical puzzles—what I call Bernard and Baer’s *desiderata*—that are neither present in nor solved by autonomous systems theory.

Keywords: Biological Agency; Teleological Explanations; Developmental Biology; Biological Change; Regulation.

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

Karl Ernst von Baer, 1886, 88

1. Introduction: on temporal scales

The revival of teleology in the philosophy of biology is not surprising when part of biology is moving towards an organismic perspective of life. The timeliness and relevance of teleological explanations make the need for an adequate explanation of natural teleology even more urgent. Much of the literature to be reviewed here is based on very recent edited volumes (Corning et al., 2023; Fábregas-Tejeda et al., 2024; Švorcová, 2024a; Mossio, 2023) and special issues (Moczeck and Sultan, 2023; Moss, 2024a; Vane-Wright and Corning, 2023) that represent a major effort in this philosophical and scientific enterprise towards an “organism-centered perspective” (Laland et al., 2015). Why has teleology come to the fore in recent decades? Some kind of scientific explanation might be necessary insofar as a certain aspect of a particular phenomenon—some real pattern (Dennett, 1991)—remains unexplained if we do not include this explanation in our toolkit. Psychological explanations, for instance, are justified insofar as purely behaviorist or neurophysiological accounts of behavior and cognition leave many phenomena unexplained (Walsh, 2017). A similar rationale has been invoked to justify the need for teleological explanations (Rama, 2024a): certain aspects of living systems remain inadequately accounted for if teleology continues to be regarded as a tainted concept within scientific inquiry and if mechanistic explanations are treated as the only game in town. Teleological explanations are therefore indispensable for accounting for particular patterns of responsiveness in nature—regularities that resist explanation within purely mechanistic, reductionist, or eliminativist approaches. However, teleological explanations have traditionally been considered at odds with the foundations of modern science, and vitalistic approaches have accordingly been dismissed as unscientific. Driesch’s embryological analysis of the equifinality of sea urchin development famously led him to posit vital forces to account for phenomena that eluded a mechanistic worldview. Today, however, developmental biology is equipped with richer theoretical, experimental, and technological tools to overcome the obstacles of teleological explanations without stepping outside the bounds of science. But which obstacles?

Teleological explanations postulate *end*-states, *future*-oriented goals to be achieved, or *final* causes that guide the global action of the system. At its core, teleology is intertwined with

time and causation, as recently explored by Gontier (2023) in a deep historical and theoretical inquiry. When the temporal structure of causal relationships in teleological explanations is analyzed, backward causation appears as a classic headache associated with teleology. Teleological explanations seem to reverse the order between causes and effects considered in science. In teleological jargon, how is it possible for ends to explain the means if the means precede the ends? How do “ends modify means” (Moczek, 2023, 1)? Teleological explanations give the impression that they violate the principle of causal asymmetry (Potochnik, 2017), which states that the cause-effect relationship is always asymmetrical and cannot be reversed.

As such, this classical puzzle is fundamentally a question of time. Different time scales may entail different means-end relationships and, consequently, specific problems regarding the causal structure of teleological explanations. It would, therefore, be useful to distinguish between different temporal dimensions in biology. We can rely here on the classification proposed by Waddington (1957, 6, 7), not necessarily as an uncontroversial taxonomy, but as an analytical guiding tool for our investigation (see DiFrisco (2017) and Gontier (2023) for further analysis). First, the *evolutionary scale* encompasses the phylogeny of populations and includes processes such as cladogenesis, anagenesis, or extinction, among others. Secondly, the *developmental scale* concerns the life cycle of a single individual and includes processes such as gastrulation, organogenesis, metamorphosis, and others. Finally, the *physiological scale* regards the functioning of organisms at different levels of organization (e.g., cell physiology, tissue-specific physiology, systems physiology) that contribute to their maintenance, taking into account processes such as metabolism or behavior. Each scale could provide its own teleological explanations (whether these explanations are justified or not is another question) and, therefore, raise the problem of backward causation in the context of the temporal relations pursued in time-specific teleological explanations. At the evolutionary time scale, for example, one might assume that natural selection acting on populations is a kind of goal-directed process of adaptation. At the developmental scale, embryonic development can be said to be directed towards the construction of adaptive phenotypic outcomes. Metabolic activity at the physiological scale can be explained teleologically if we show that it contributes to the goal of maintenance.

This analysis leads to the central concern of this article: to investigate whether the theoretical framework used to naturalize teleological explanations at one scale also applies to another temporal scale. In particular, I argue that the developmental time scale has distinctive features with respect to teleological explanation, making it inaccurate to reduce development to either physiological or evolutionary scales. Developmentalist tendencies

within organism-centered views (discussed below) emphasize that developmental processes cannot be explained merely by tracing them back to naturally selected genes—that the goal-directedness of development cannot be reduced to an evolutionary time scale. However, in attempts to naturalize teleology within an organismic philosophy of biology, disproportionate attention has been given to teleological explanation at the physiological scale. This has resulted in a well-developed account of teleological physiology, in which teleology is treated both as *explanans* and *explanandum*. At the developmental scale, by contrast, teleology as *explanans* has outpaced attention to teleology as *explanandum*: agential and teleological accounts of development “do not aim to naturalize teleology, but they employ the notion to explain and naturalize other phenomena,” as Bich (2024a, 4) aptly notes. This imbalance is significant because teleological development plays a crucial explanatory role in central biological questions, such as the nature of variation, the genotype–phenotype map, and the stability of different modes of inheritance. I do *not* question here the necessity or ubiquity of teleological explanations in development. I take it as given that many authors (discussed below) endorse a teleological—agential, organismic—view of development. My claim is rather that, despite its relevance as *explanans*, developmental teleology as *explanandum* has not consistently been the object of systematic analysis; it has either been neglected or conflated with a related but distinct approach, namely teleological physiology. This article aims to clarify this situation by calling for a well-developed account of teleological development as *explanandum*: teleological explanations of development cannot be reduced to teleological analyses at either the physiological or evolutionary scales. For this purpose, it is therefore essential to distinguish teleological physiology from teleological development.

The core of my view can be stated quite straightforwardly: teleological physiology must be distinguished from teleological development because the former concerns maintenance, whereas the latter concerns change. Development cannot be adequately explained as the mere regulation of organic processes aimed at preserving an existing organization. Rather, development should be understood as a process of regulated change oriented toward the attainment of a particular organization. This, I suggest, provides a central motivation for pursuing a distinct theory of developmental teleology that extends beyond the goal of self-maintenance. More broadly, this article aims to contribute to the recognition of the diversity of organismal goals in nature and to emphasize that not all such goals are concerned with maintenance—much as Nuño de la Rosa (2023, 7) has recently argued for the need to address goals in reproduction that are “irreducible to the goals of self-generation and self-maintenance.”

I proceed as follows. Section 2 introduces teleological development as an *explanans* in developmental and evolutionary biology. Section 3 presents autonomous systems theory. Section 4.1 outlines reasons why physiological and developmental teleology have been conflated, while Section 4.2 articulates the main motivation for postulating developmental goals. Section 5, the most extensive section, examines the crucial differences between the two scales. Finally, Section 6 highlights specific puzzles that arise when developmental teleology is treated as the *explanandum*.

2. Teleological development as an *explanans*

From an organicist standpoint, teleological development is asserted as a replacement for the gene-centered preformationist view inherited from the Modern Synthesis (MS). From the MS perspective, the adaptive force in evolution is attributed solely to natural selection, as expressed by Huxley: “*Natural selection*, acting on the heritable variation provided by the mutations and recombination of a Mendelian genetic constitution, is the *main agency* of biological evolution” (quoted in Huneman, 2017, 71; emphasis in the original). This commitment led to the displacement of development from evolutionary theory, on the assumption that its theoretical role could be fully reduced to genes (Noble and Noble, 2023a)—that development itself is *not* an adaptive force. Accordingly, the task of explaining how adaptive organisms are reconstructed across generations—thereby generating inherited variation in fitness (Godfrey-Smith, 2009; Sober, 1984; Lewontin, 1970)—was assigned to genes, conceived as immortal entities (Dawkins, 1976), chemical givens (Walsh, 2023), or unmoved movers (Monod, 1971). In this gene’s-eye view (Ågren, 2021), genes usurped the explanatory role of development as the primary source of inherited variation in fitness (Amundson, 2005; Walsh, 2010; Jaeger, 2023; Rama, 2024b).

One of the main motivations for agential and teleological views of development is the recognition that the explanatory reduction of development to genetics was empirically unwarranted and thus theoretically flawed—so much so that “an immense amount of biology was missing” (Lewontin, 2010). In response to this deficit, several research programs over recent decades have sought to place developing organisms back at the center of biological theory (Nicholson, 2014; Baedke, 2019; Baedke and Fábregas-Tejeda, 2023; Rama, 2025a). Crucially, across most of these approaches, agency and teleology play a central explanatory role (Okasha, 2024; Uller, 2023; Walsh, 2015; Ball, 2023; Rama, 2024a; see DiFrisco and Gawne, 2025; Moss, 2024b; Aaby et al., 2024 for critical discussion). *Niche construction theory* emphasizes the adaptive, goal-directed modification of environments by organisms and their evolutionary consequences (e.g., Laland et al., 2019; Stotz, 2017).

Molecular epigenetics addresses the problem of development by treating the cell as a minimal agent capable of regulating gene expression in adaptive ways, including through the harnessing of stochasticity (Griffiths and Stotz, 2013; Keller, 2014; Noble and Noble, 2018). *Eco-devo* invokes goal-directed regulation of environmental information to explain phenotypic plasticity (Sultan, 2015; Gilbert and Epel, 2015), while *extended inheritance frameworks* highlight organismal agency in the transmission of ecological and epigenetic resources across generations (Jablonka and Lamb, 2014). *Symbiotic interactions*, too, are understood as sources of evolutionary change that require interacting systems to be treated as agents (Gilbert et al., 2015; Corning, 2023). Even *evo-devo*, traditionally closer to structuralist perspectives, now acknowledges the importance—if not the sufficiency—of agential explanations of development (Newman, 2023; Walsh, 2021).

Overcoming the gene-centered view is a central debate in the philosophy of biology, with a clear theoretical aim: to restore development to its displaced explanatory role. If variation cannot be fully explained by genes, if heredity is more than genetic transmission, and if phenotypic space is underdetermined by genotypic space, then taking “development seriously” (Robert, 2004) becomes a key motivation for contemporary biology to address the explanatory gaps left by the MS (Sultan et al., 2022; Aaby et al., 2024). In alternative accounts of adaptive evolution, goal-directed development emerges as a central factor, along with related notions such as agency, normativity, and repertoire. Development is not the execution of a preformed program: “the development of phenotypes is under the active control of the developing organism” (Sultan et al., 2021, 9), and morphogenesis is “something the embryo ‘does,’ as opposed to something that merely ‘happens’ to it” (Potter and Mitchel, 2024, 132). The issue, then, is not merely to acknowledge complexity in development, but to recognize that this complexity calls for a distinct explanatory framework and scientific *perspective* (Walsh and Rupick, 2023; Sultan et al., 2022; Jaeger, 2023). This is not a peripheral addendum to empirical research, but a debate at the conceptual core of biology.

This shift has motivated the rejection of an object-view of the organism (Walsh, 2018), in which natural selection is portrayed as the “composer,” “poet,” or “sculptor” of nature (Gould, 1992, 44), while organisms are reduced to passive “vehicles” (Dawkins, 1982, 82), “mediums” (Levins & Lewontin, 1985, 88), “interfaces” (Walsh, 2006, 775), or “superficial faces” (Sober, 1984, 228) linking inherited genes and selective environments. By contrast, recent work advances an agent-view (Sultan et al., 2022; Walsh and Rupik, 2023; Nadolski and Moczek, 2023), according to which “rather than explaining the dynamics of evolution by appeal to the capacities of genes, we should think of evolution as a consequence of how organisms work

and what they do” (Walsh and Sultan, 2024, 114). Within this emerging—extended, revised or whatever—evolutionary synthesis, goal-directed development is invoked to explain how adaptive variation and stable cross-generational resemblances arise from organisms pursuing goals throughout ontogeny, such that “organismal goals themselves can be explanatory for evolutionary change” (Uller, 2023, 325).

Where do phenotypes come from? “From nowhere,” an organismic theorist might reply, echoing Oyama (1985). Phenotypes arise in ontogeny through the organism’s active regulation of, and participation in, its own development. Yet this immediately raises a further question: regulation toward what goal? Which goal does the developing organism pursue, and on what basis does development generate *adaptive change*?

3. Teleological physiology: the autonomous system view

Influenced by the scientific revolution he helped to shape, Kant held that means–end relations in living systems resist full naturalization. Mayr (1998, 131) famously claimed that “Darwin had solved Kant’s great riddle,” but an alternative reading suggests that this problem was instead solved by cybernetics and systems biology (Varela and Weber, 2002). Autonomous Systems Theory (AST) is a recent framework that integrates these developments into a systematic account of teleology, drawing on a long Kantian tradition (Desmond and Huneman, 2020; Gambarotto and Nahas, 2022). In contemporary philosophy of biology, the dominant naturalization of teleology operates at the physiological scale and is exemplified by AST. Without surveying its internal diversity, I briefly introduce its core commitments.

The central concept in AST is *self-maintenance*. Goal-directedness, normativity, and functionality are analyzed in relation to self-maintenance. The guiding question is: what is to be maintained? According to AST, the answer is the system’s identity, understood as a network of operational constraints that constitutes an organized structure. The notion of constraint has a specific technical meaning (Montévil and Mossio, 2015; Moreno and Mossio, 2015), referring to components that enable particular processes while remaining unchanged by their local effects. A key idea—absent from Kant’s scientific context—is that system components are mutually dependent: cause and effect are intertwined within a circular causal regime in which “the effects of its activity contribute to determining its own conditions of existence” (Mossio and Bich, 2017, 1089). Building on and refining earlier cybernetic models, the concept of *closure of constraints* characterizes an organized system as a set of operational relations that self-determine its identity, generating the energy and

matter required for persistence. A self-maintaining autonomous system thus preserves its topological organization of constraints despite ongoing change and transformation (Ruiz-Mirazo and Moreno, 2004).

AST successfully captures key characteristics of living systems, from unicellular (Ruiz-Mirazo et al., 2004) to multicellular forms (Arnellos and Moreno, 2015): *thermodynamic openness* and *operational closure*. Living systems are organized entities distinct from their environment and capable of maintaining their identity despite external fluctuations. Yet they are not closed systems, since they must exchange matter and energy with the environment to remain viable. Autonomy consists precisely in enabling the coexistence of these *interactive* (transformative) and *constitutive* (constraint-closure) dimensions: organisms cannot be thermodynamically closed if they are to survive, but they must be operationally closed in order not to vaporize (Moreno and Mossio, 2015).

Within AST, the *telos* of a living system is self-maintenance (Mossio and Bich, 2017). Function and normativity are therefore defined in relation to a system's capacity to maintain itself. On the organizational account (Mossio et al., 2009), function is grounded in the interdependence of system components required for self-maintenance (Barandiaran and Moreno, 2008). Division of labor is essential: an organized system comprises distinct parts with distinct causal roles (Bich, 2024b, 6). A functional criterion is thus defined by the successful performance of the causal role required for self-maintenance. Similarly, drawing on Christensen and Bickhard's (2002) account of normativity, system components presuppose specific causal contributions from one another. A trait fails to function properly when it does not perform the causal work expected by other parts of the system, and such failures may compromise the system's self-maintenance (Barandiaran et al., 2009; Saborido and Moreno, 2015).

Where do the norms and goals come from in AST? They arise from the current organization of the living system itself. The account is *synchronic*: it concerns the system's present organization and its constitutive and interactive dimensions, without appealing to past evolutionary or developmental history. The analysis proceeds by examining how a system maintains its organization and arguing that the system does so *because* its goal is self-maintenance. Accordingly, norms and goals are *self-established* by the system in virtue of its current conditions of viability (Barandiaran and Egbert, 2014).

This is a well-developed account of teleology, both philosophically robust and scientifically grounded, despite having attracted some criticism (Corti, 2023; Cusimano and Sterner,

2020; García-Valdecasas, 2021; Artiga and Martínez, 2016; Garson, 2017). It is important to note, however, that AST is primarily designed to explain organic processes at the physiological scale, such as metabolism and behavior (for example, Moreno and Mossio's (2015) central work does not address autonomy in development). This limitation is unproblematic insofar as AST aims to account for teleological physiology. Difficulties arise, however, when AST is extended to explanatory tasks that fall outside its proper scope.

4. Mixing and Separating *telos*

4.1 Mixing *telos*

The motivation of this article is that the distinction between developmental and physiological goals has not yet been examined in sufficient depth. Even if no such distinction ultimately holds, there is little critical discussion of why the goals of developmental teleology should be identified with those of teleological physiology, apart from a few explicit treatments (Bich and Skilling, 2023; Arnellos et al., 2014; Jaeger, 2024). The problem is that many authors and research programs—often outside AST—invoke an autonomous framework to explain development without addressing whether development can be accounted for solely in terms of self-maintenance. These are typically the same approaches that treat teleological development as a central *explanans* of evolution (Section 2). As a result, teleological physiology is repeatedly imported to explain development on the implicit assumption that a single set of organismal goals and norms suffices to explain everything organisms do or regulate. AST has flooded development as if such a theory had been constructed in the niche of developmental theory.

The degree of commitment to AST may vary, and since autonomy is thought to play a major role in development, the problem is all the greater. Recent work reveals a spectrum of positions: some explicitly defend an autonomous account of development, others draw on AST to analyze particular developmental aspects, and still others merely cite key AST contributions when invoking goals or agency in development (e.g., Rosslensbroich, 2024; Walsh, 2015; Jaeger et al., 2024; Virenque, 2024; Fulda, 2023; Roli et al., 2019; Miller, 2018; Desmond and Huneman, 2020; Heylighen, 2023; Mossio et al., 2016; Montévil et al., 2016; Montévil and Soto, 2023; Newman, 2023; Jaeger, 2023, 2024). The central issue is the conflation of scales of analysis. This problem extends beyond explicit commitments to AST and concerns, more generally, the application of physiologically oriented theories of agency and teleology to development. A common pattern—often independent of AST—is the uncritical shift between temporal scales in defending an agent-based view of development:

development is characterized as purposive and agential, yet the supporting examples are drawn from the physiological scale, such as metabolic or behavioral processes (e.g., Rosslenbroich et al., 2024; Kohn, 2024; Fulda, 2017; Švorcová, 2024b; Calvo et al., 2020; Jaeger, 2024).

Moreover, although my primary target is AST, a distinct ecological and behavioral account of teleological development has recently gained traction, drawing on the concept of *affordances* from Gibsonian ecological psychology (Nahas and Sachs, 2023; Fulda, 2017; Segundo-Ortín and Raja, 2024). On this view, organisms' responsiveness to affordances renders development central to adaptive explanation: "Agency is the gross dynamical capacity of a goal-directed system to bias its repertoire to respond to its conditions as affordances" (Fulda, 2023, 1). Its evolutionary significance has been extensively developed within Walsh's *Situated Adaptationism* (Walsh, 2012, 2013, 2015). The difficulty, however, is that the role affordances play in goal-directed development may differ from their role at the physiological scale. Like AST, ecological psychology was primarily devised to explain physiological processes, including behavior. Applying it to development, therefore, requires an explicit account of the goals proper to developmental systems, rather than assuming continuity across scales.

The references cited in this section are not intended as an exhaustive survey of works that conflate different kinds of *telos*. They are merely recent examples in which theories developed to explain physiological-level processes are extended beyond their proper explanatory scope. To my knowledge, only Nuño de la Rosa (2010; see Cuciniello, 2026, for analysis) has explicitly questioned the applicability of AST to development, arguing that in vertebrates, full functional integration of the system is achieved only at late developmental stages. Related concerns have been raised by Artiga and Martínez (2016), who emphasize difficulties in applying AST to cross-generational functions, and by Garson (2017), who highlights problems in forward and backward functional analyses when these are disconnected from development. Is this not remarkably little attention for such an important issue?

4.2 Separating *telos*: change ≠ maintain

If "phylogeny is the derivational history of developmental systems" (Oyama, 2000, 179), is it the case that "evolution by natural selection is always the evolution of autonomous, self-determining agents" (Jaeger, 2023, 176)? If we want to explain how developmental changes have adaptive evolutionary consequences, should we focus on processes at the physiological level? So are developmental histories explained by AST? I argue that

maintaining an identity is not the only goal in town, and development continuously constructs and dismantles identities. This is not a defect, but its defining feature—development is precisely about the ongoing destruction and construction of identities.

All living systems must be preserved in order to exist—an almost trivial point. In a broad sense, “maintenance” can be extended to other living entities such as populations, societies, or lineages, and in an even looser sense to any entity whatsoever, from the moon to a hurricane, even when no full-fledged autonomy is involved. Self-maintenance exists across the life cycle too: as Gilbert and Barresi (2016, 1) note, “[o]ne of the critical differences between you and a machine is that a machine is never required to function until after it is built.” However, explaining “how a biological organization is maintained through a series of radical organizational changes” (Bich and Skillings, 2024, 241) *does not entail that organizational changes at one ontogenetic stage are explained by the self-maintenance requirements of a previous stage*. There is a crucial difference between showing that a system can maintain an organization and claiming that changes in that organization are themselves explained by the goal of maintaining it. The issue is not merely that organization changes across ontogeny, but that such change cannot be accounted for by the norms and goals posited by AST—a point developed in the next section.

Why is the self-maintenance of an organization insufficient to explain ontogenetic change? Although detailed arguments follow in the next section, the core idea is that the requirements of self-maintenance do not *specify* which developmental outcome should be produced. AST examines an organized autonomous system and identifies what it must do to preserve its organization, but these requirements cannot account for the drastic and rapid transformations that the organization undergoes during development. Consider distinct ontogenetic stages such as the morula and the blastula: can the transition to the latter be explained by the self-maintenance of the former? Their organizational properties differ so radically that it is implausible to identify shared maintenance requirements across such transformations. As Levin (2023, 180) observes, “from the perspective of each embryonic stage, the prior stage has incorrect anatomy.” When development involves the emergence of a new organization that is decoupled from the demands of maintaining the previous one, AST fails to capture what drives these changes. This motivates the central thesis of this article: the goals and norms of self-maintenance do not determine ontogenetic change, because development does not preserve a fixed organization and cannot be explained by its maintenance requirements.

The thesis of this article gains further significance when considered in relation to evolutionary theory. As noted in Section 2, the gene-centered, preformationist view leaves no room for developmental teleology in identifying a “guide” of development. This highlights a crucial difference between developmental teleology and teleological physiology: AST is, in principle, compatible with genetic preformationism. On such a view, genetic preformationism would explain how autonomy is generated, while AST would explain how it is preserved. To be sure, most proponents of AST would reject genetic preformationism, since self-maintenance presupposes a systems view of gene expression (as discussed in Section 4.3). Still, if we consider preformationism as a theory about the *genesis* of form and functions, the relevant point is that AST is not a theory of how the system is constructed: it is not a solution to the problem of development, nor does it aspire to be one, and it can operate independently of how the system is built. If organismic agency and teleological explanations are to challenge the tenets of the MS, it is development—not physiology—that “restores purpose to evolutionary biology” (contra Noble and Noble, 2023b). Physiological agency certainly affects evolution, for instance, through relocational niche construction, but physiological agency as such is not necessarily incompatible with the MS. As Baedke and Fábregas-Tejeda (2023, 131) note, the MS “was not completely inimical to animal agency.” The Baldwin effect, for example, concerns whether *new* behaviors can alter evolutionary trajectories—that is, the *development of behavior* and the *emergence of autonomous agency*. The real challenge posed by agential perspectives lies at the developmental scale, in the generation of adaptive variation (Rama, 2025b). For this reason, explaining the origin of phenotypes requires recognizing goals beyond self-maintenance; without them, the agential view of evolution remains incomplete.

5. Tracking the difference

Let us now turn to a more detailed analysis. I examine several explanatory features common to both levels—constraints, repertoires, regulation, and self-production—and argue that AST’s treatment of these notions is inadequate for explaining their features in development. The reason, I suggest, is that the goals involved differ across scales. I advance that no theory of developmental goals is presented here. Nonetheless, for explanatory purposes, I appeal to notions that plausibly relate to developmental goals—such as “change,” “adaptive development,” or the “construction of autonomy”—even though these concepts are not articulated within a full-flagged theory of teleological development.

5.1 Constraints

Constraints play central roles at both developmental and physiological scales. In development, constraints are typically understood as factors that limit and enable the emergence of particular phenotypic variants (Amundson, 1994). In AST, the self-determination of an autonomous organization is grounded in the closure of constraints, which likewise function as “limiting and enabling” factors (Bich, 2024b, 17). The question, then, is whether constraints play the same theoretical and causal role at both scales—whether the elements that define organization are comparable in developmental and physiological scales. If, as AST maintains, constraints define organization at the physiological scale, do they do so in the same way at the developmental scale? I argue that they do not. Developmental organization emphasizes a systems perspective on elements that confer *specificity*, whereas AST’s organizational account rests on the closure of constraints that generate *efficiency*. The following discussion examines this contrast more closely.

Building on Rosen’s insight into self-organization, Montévil and Mossio (2015, 2, emphasis added) articulate the notion of closure of constraint by asking: “what entities actually play the role of *efficient causes* in a biological system?” and “how should the relevant level of causation at which self-determination occurs be characterized?” As noted above, a constraint is a system component that enables a given process while remaining unaffected by that process’s local effects. A paradigmatic example is an enzyme that catalyzes a reaction while itself being conserved, thereby enabling a specific cellular function. Within AST, therefore, the causes relevant to self-maintenance are precisely those that self-determine the organization’s identity: efficient causes. At the physiological scale, organization is thus characterized as a system closed under causal efficiency: a network of interdependent constraints whose mutual relations enable the system’s self-maintenance.

However, what are the relevant elements at the developmental scale for an organizational account of development? Drawing on the work of Griffiths, Stotz, and collaborators (Calcott et al., 2020; Griffiths, 2016, 2017; Griffiths et al., 2015; Griffiths and Stotz, 2013; Stotz, 2006; Stotz and Griffiths, 2017), the answer lies in elements that provide *causal specificity*—those that help determine which developmental trajectory is realized. Briefly, these authors define developmental specificity through an account of biological information that combines mathematical information theory with Woodward’s (2003) interventionist conception of causation. A factor provides specificity if interventions on it yield different developmental outcomes. The degree of specificity of one variable over another is assessed in terms of

control, measured via conditional mutual information. A factor is not a source of specificity if interventions, under appropriate background conditions, fail to generate distinct outcomes. In this view, biological information in development is just causal specificity. This framework explains the role of developmental constraints as *limiting* the range of possible outcomes that a given factor can *produce*, quantified by changes in the entropic distribution of outcomes under intervention.

Reductionist accounts of development typically treat specificity as entirely reducible to gene sequences. Crick's sequence hypothesis, for example, attributes developmental specificity to protein-coding sequences, making nucleotide variables central to developmental explanation. By contrast, once *distributed specificity* is acknowledged (Stotz, 2006; Griffiths and Stotz, 2013), an organizational view of development emerges in which multiple non-genetic sources jointly contribute to phenotype construction. Griffiths et al.'s account generalizes the notion of information implicit in Crick's hypothesis, showing that epigenetic marks, transcription factors, cytoplasmic states, intercellular interactions, and ecological signals can all function as causal specifiers. Developmental organization is thus constituted by *networks of interacting sources of specificity—a form of organization fundamentally different from that described by AST*.

Crucially, the distinction between efficiency and specificity in development is not unique to organizational accounts. In both reductionist and organizational approaches, specificity remains the explanatorily relevant cause in accounts of development. Whatever is taken to explain development—Weismannian determinants, protein-coding sequences, or distributed networks of causal specifiers—the relevant variables are those that determine the specificity of phenotypic outcomes. This is precisely the intended role of information in development: “the cause that imparts order and form to matter” (Oyama, 1985, 3). By contrast, physiological constraints that secure the efficiency of self-maintenance are not sources of developmental specificity. Metabolic states and functional requirements undoubtedly influence development, but when they enter developmental explanations, they do so by functioning as sources of specificity—that is, as developmental constraints that channel development toward particular trajectories.¹ Although AST allows for a minimal

¹ Arnellos et al.'s (2014) comparative analysis of autonomy and multicellular development implicitly supports this conclusion, even if it is not stated explicitly. Unlike the other cases they examine, in *S. purpuratus*, the developmental process involving complex multicellular integration is decoupled from metabolic demands. Their account does not explain development in terms of the organizational requirements needed to maintain each

notion of closure of constraint in terms of metabolic self-maintenance (Bich, 2024b), this does not preclude metabolic factors from also functioning as sources of developmental information. As Waddington already emphasized, the physiological and developmental scales are deeply intertwined, and developmental processes are themselves connected to evolutionary dynamics.² Even so, it follows that the kinds of causes relevant to biological organization differ across developmental and physiological scales. Development concerns the construction of phenotypes, and thus foregrounds causes that shape phenotypic formation. By contrast, at the physiological scale, processes are oriented toward maintenance, and the explanatorily relevant causes are those that sustain an existing phenotype. Whereas physiological teleology is defined in terms of self-constraints (Mossio and Bich, 2017), developmental teleology involves a distinct kind of constraint. Clarifying the relations among specificity, organization, and teleology in development—beyond self-maintenance—remains a central challenge for any attempt to naturalize teleology in development.

5.2 Repertoires

Repertoires—and related notions such as spaces or landscapes—are central at both developmental and physiological scales (as well as at the evolutionary scale, exemplified by Wright’s adaptive landscape). At the physiological scale, repertoires comprise the processes a system can perform to sustain itself, such as motility, catalysis, or synthesis. A *viability space* thus represents a repertoire of possibilities evaluated against a normative criterion (Barandiaran and Egbert, 2014): some possibilities support viability, others increase precariousness, and still others lead to system death. This distinction is crucial for teleological explanation, since not all actions are possible, and among those that are, not all equally serve the system’s goal. Selecting one possibility over another is therefore a defining feature of goal-directedness.

Repertoires are likewise central to development, from Alberch’s (1991) morphospaces and Waddington’s (1957) epigenetic landscape to Walsh’s (2013) more recent affordance landscape. These representations depict either the range of phenotypic outcomes that can be produced or the developmental trajectories that can be followed. Developmental repertoires are inherently linked to goal-directed development: variation is constrained, yet among the available possibilities, some outcomes are more adaptive than others. The capacity of

embryonic stage. Rather, it focuses on the multicellular organization of causal specificity in development, not on causal efficiency.

² I thank an anonymous reviewer for pointing this out.

developing systems to realize adaptive outcomes within this space is a hallmark of agential accounts of development and underlies plasticity-first views of evolution (West-Eberhard, 2003; Levis and Pfennig, 2016). As Gilbert (2016, 415) puts it, “developmental plasticity enables the genome to generate a repertoire of possible phenotypes, and environmental cues are often used to select the phenotype that appears most adaptive at that time.”

However, a crucial difference emerges, closely tied to the preceding analysis of constraints. Physiological repertoires consist of actions an organism can perform, some of which are more or less conducive to *maintaining* the organism. Even when repertoires are defined in terms of regulatory regimes (Bich, 2024a), the available options concern what an organism can do to sustain itself. Developmental repertoires, by contrast, concern *the possible organizations* that can be realized through different processes. At the physiological scale, repertoires are possibilities within a given autonomy, whereas at the developmental scale they are possible autonomies—or of properties that constitute autonomy, such as morphology. Consequently, analyzing goals and norms in developmental repertoires requires recognizing that the relevant possibilities differ across scales: maintaining an existing autonomy versus generating new forms of autonomy.

The notion of repertoires thus reveals both the distinction and the connection between these scales of analysis: each possibility within a developmental repertoire corresponds to its own physiological repertoire (see Figure 1). This relation serves as a proxy for the link between developmental and physiological goals. Developmental processes aim to construct an adaptive, autonomous system; developmental teleology therefore yields a specific organization endowed with its own physiological repertoire (without implying an adult-centered perspective; see Section 6.2). Development can thus be understood as the construction of autonomy. If physiological norms arise from the demands of self-maintenance within a given organizational closure, development determines which organizational closure is to be established. It functions as a second-order process that selects among possible physiological repertoires. In this sense, developmental repertoires represent alternative autonomies, and realizing one of them generates a corresponding physiological repertoire. A viability analysis at the developmental level therefore amounts to a higher-order normative assessment: a norm-establishing account of possible norm-establishing systems.

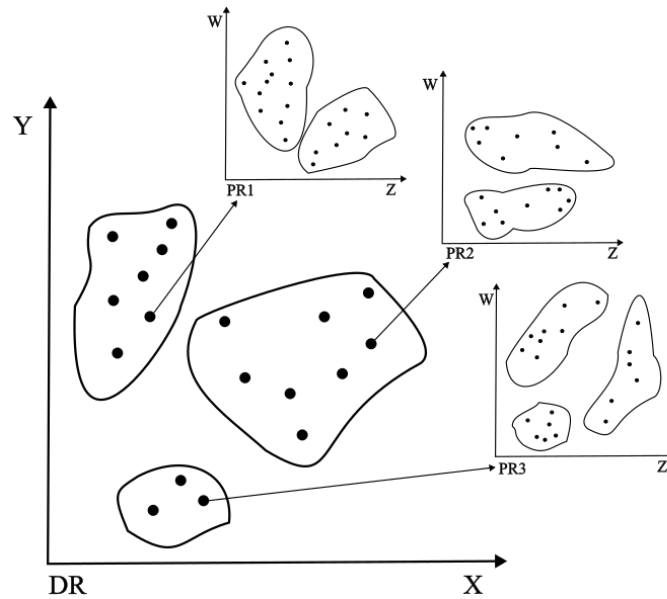


Figure 1: Developmental repertoires and physiological repertoires. The developmental repertoire (**DR**) represents a space of possible autonomies that can be constructed (black dots in the DR). Each autonomy has its own physiological repertoire (PR). **PR1**, **PR2**, and **PR3** merely illustrate three different physiological repertoires, each with its own possibilities for action (black dots in PR). DR and PR are defined by certain parameters, **X** and **Y**, and **W** and **Z**, respectively.

Waddington’s classic experiments with *Drosophila* fruit flies provide an illustrative case. Under experimentally induced thermal conditions, different phenotypic variants emerged. Waddington’s epigenetic landscape represents the alternative developmental paths available under these conditions: some trajectories lead to the normal (species-typical) phenotype, while others lead to abnormal ones. Each resulting phenotype, moreover, is associated with distinct viability conditions for self-maintenance and therefore with a different physiological repertoire. For instance, an abnormal phenotype may have greater difficulty finding food in the wild than the normal phenotype. In this sense, the phenotypes instantiate different autonomies: they regulate their self-maintenance under different environmental conditions, and the range of actions available to them differs accordingly.

5.3 Regulation

Regulation is central to both physiology and development, but the two must be distinguished. If regulation is explained teleologically, it must be tied to a goal—and the relevant goals differ by scale. Different goals might require different theorizing about regulatory processes. At the physiological scale, regulation is oriented toward maintaining an organization. In AST, this is explained by how processes are modulated and integrated

within a heterarchical organization to secure self-maintenance (Bich et al., 2016; Bich, 2024a, 2024c; Bich and Bechtel, 2022b; Bechtel and Bich, 2021, 2024). Developmental regulation, by contrast, is not about stabilizing an organization but about producing a new one. Developmental regulatory processes coordinate and deploy developmental resources to construct a novel organization.

The distinction between regulatory systems at different scales is also important for clarifying the previously explained difference between specificity and efficiency. Bich (2024a) has attempted to construct a “teleology 2.0” by incorporating *control regulatory processes* over self-maintenance regimes. This approach is central to explaining how a system can, for example, switch between different metabolic pathways depending on living conditions and thus maintain its stability by different means. Control is also important at the physiological level, as physiological control mechanisms regulate specific physiological processes: “What they [control mechanisms] do is to selectively shift between different available regimes of self-maintenance, in such a way as to contribute to the viability of the system” (Bich et al., 2016). This represents an improvement over a purely constraint-based and static view of autonomy and shows how autonomous systems can change within their own physiological viability space. However, physiological regulation does not contradict the previous point, namely that the specificity of physiological regulatory mechanisms is always tied to the self-maintenance of the system, whereas this is not the case for specificity in development. Therefore, when changes are analyzed at the physiological scale, they remain relative to self-maintenance: changes serve to keep the system alive. Developmental specificity, by contrast, is conceptualized as being directed not toward self-maintenance but toward developmental products. While Bich’s advance toward a dynamic view of self-maintenance is pertinent and well justified, it still falls short of grounding teleological development: physiological changes remain relative to goals defined by self-maintenance, and the kinds of changes that a dynamic perspective within AST can explain are not developmental changes, but rather physiological ones. Physiological change must therefore be distinguished from the construction of autonomy. Physiological control and developmental control are different.

Let us analyze this problem in the context of gene expression. At each point in the life cycle, a cell must produce new proteins. Regulation of gene expression is central at both the physiological and developmental scales. However, it is possible to distinguish between regulated gene expression aimed at the production of a new cellular (or multicellular) organization and gene expression aimed at the self-maintenance of an existing cell (or multicellular system). Let us take the *lac operon*, an often-cited example in AST (Bich et al., 2016; Bich, 2024b; Bich and Bechtel, 2022a; Moreno and Mossio, 2015). Its historical

importance lies in the fact that it shows a way in which genes can be regulated and their expression controlled. This is the first step towards solving the problem of development. However, the *lac operon* itself is not a process of developmental regulation, but a metabolic regulatory system of gene expression. It operates according to the *metabolic needs* of the cell (see Figure 2). It shows how cell regulation is linked to the homeostatic and conservative capacities of cells. This is not a solution to the problem of development *per se*. Compare the *lac operon* with developmental regulatory mechanisms of gene expression, such as the regulatory mechanisms of *Notch* signaling in vertebrate eye formation (Gibert and Berrasi, 2016, 138, 139). Through a process of conditional specificity via juxtacrine factors, the Notch pathway is central to determining which retinal precursor cells become optic neurons and which become glial cells (Figure 2). Is this process controlled by the self-maintenance of retinal precursor cells? Not at all. The goal is the construction of traits, and the regulation of cell differentiation is not about self-preservation but about self-construction processes.

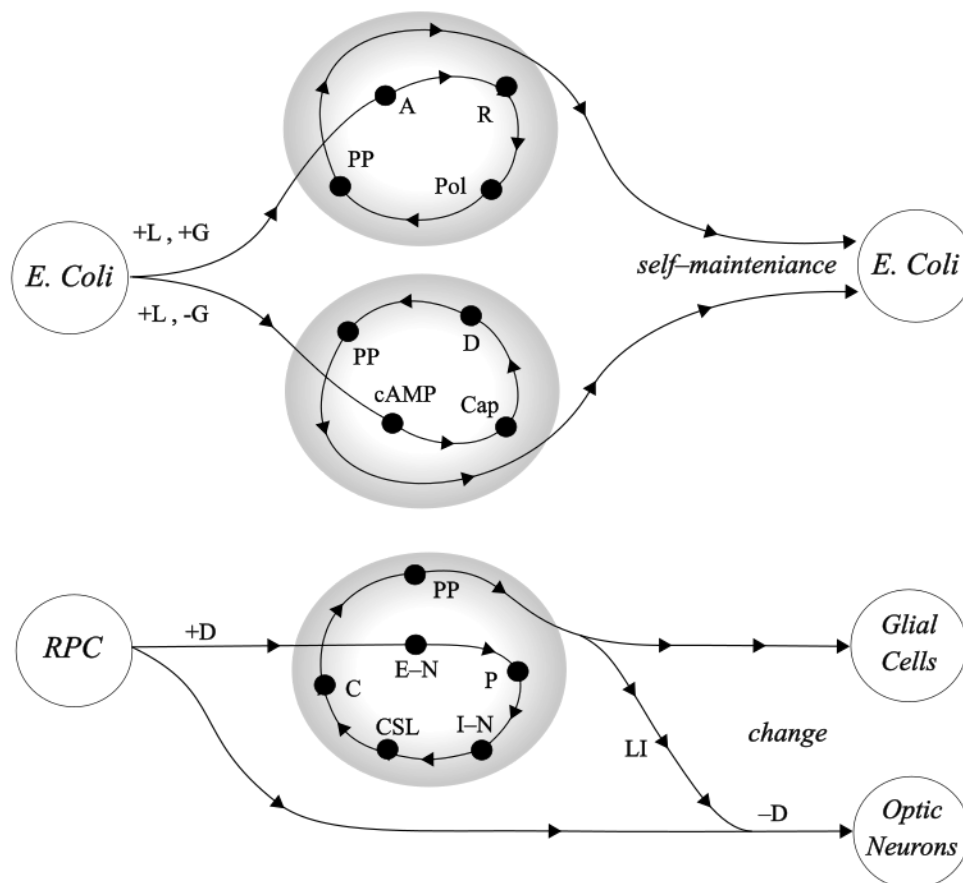


Figure 2: Physiological and developmental regulation. (Top) Two mechanisms of lactose metabolism in *E. Coli* enable the production of energy and the maintenance of the system. First, by substrate induction in the presence of lactose (+L) and glucose (+G), allolactose (A) is

produced, which inactivates the repressor (**R**) in the promoter region and allows RNA polymerase (**Pol**) to transcribe polygenic (*lacZ*, *lacY* and *lacA*) mRNA to produce the protein products (**PP**; B-galactosidase, permease, transacetylase) required for lactose digestion. However, under lower levels of glucose (**-G**), the **cAMP** concentration increases and binds the catabolite activator protein (**CAP**). The cAMP-CAP complex works as a dimer (**D**) near the promoter zone and synthesizes more protein products (**PP**) for more efficient lactose digestion. (Bottom) Instead, the fate of retinal precursor cells (**RPC**) is not linked to maintenance but to change. When Notch signaling is inactive, a repressor binds the transcription factor **CSL** in the enhancer of the target gene and blocks its transcription. During the formation of glial cells, the neighboring cell interacts with the Notch receptor at the extracellular domain (**E-N**) via a juxtacrine ligand (Delta; **+D**), which activates the Notch pathways inside the cell. The protease (**P**) cleaves the Notch receptor, allowing the intracellular domain of the Notch protein (**I-N**) to enter the nucleus, where it binds to the CSL transcription factor, displaces the repressor, recruits other transcription factors (such as p-300) and forms the complex (**C**) for transcription of the target gene in the protein product synthesis (**PP**). Feedback regulation by lateral inhibition (**LI**) means that the active state of the Notch pathway in a cell reduces the Delta concentration (**-D**) and thus induces the formation of optic neurons in the neighboring cells, thereby succeeding in controlling the amount of production of each cell type in eye formation.

5.4 Self-production: two interpretations

Self-production (sometimes equated with self-construction, self-organization, self-building, or self-manufacture) refers to the production of the elements that make up a living organization. At one point, what made us was outside of us. However, the concept of production can be interpreted in two different ways, depending on the scale of analysis. At the physiological scale, self-production is interpreted in accordance with AST: it is the production of the elements that an organism needs, given its current organization. Following Bechtel and Bich, *production mechanisms* consist of “components that constrain free energy and use it to perform work,” and they are central to regulation oriented toward physiological goals. As they put it, “maintaining the viability of the internal environment, or homeostasis, requires control mechanisms to detect conditions that require a response and to activate appropriate production mechanisms” (Bechtel and Bich, 2024, 6014). At the developmental scale, however, self-production refers to a different process: the production of the elements required to build an autonomy that does not yet exist. Here, self-production takes on a different—and more intuitive—connotation, namely that of *creation*. Just as there

are important differences between control mechanisms in development and in physiology, the production mechanisms operative at each level are conceptually distinct.

Let us analyze self-production in the context of cell fate and cell differentiation. In cell specification, potency is progressively reduced, from the totipotent cells of the morula to the multipotent stem cells involved in organogenesis. If we contrast ontogenetic stages before and after differentiation, how can the purposeful construction of new cell types be explained solely by appeal to the self-maintenance of cell identity? The relevant difference between the two scales is not quantitative but qualitative—it is not merely that blastomeres are pluripotent whereas bone marrow cells are multipotent; rather, cell specification differs across scales because different goals are pursued. Consider stem cells. At the physiological scale, somatic stem cells subordinate their own self-preservation to the production of required cells according to the viability conditions of the organization in which they are embedded. Here, self-production is analyzed at the multicellular level, and differentiation is explained in terms of how tissue components are produced to meet systemic needs. The *production* of erythrocytes, leukocytes, and platelets by hematopoietic stem cells (HSCs) in the bone marrow is regulated according to requirements for maintaining viability. Erythropoietin drives the differentiation of HSCs into erythrocytes and is produced by the kidneys in response to low blood oxygen levels. Cytokines such as IL-3 commit HSCs to leukocyte production in response to immunological needs. Platelet production is regulated by thrombopoietin, produced in the liver, through feedback mechanisms tracking circulating platelet levels. This simplified account of hematopoiesis shows that, at the physiological scale, cell specification is regulated by control mechanisms that ensure the appropriate production of cells for functions contributing to self-maintenance.

Cell differentiation in development is instead directed toward producing cells that do not yet exist, and that play a central role in constructing an organization that also does not yet exist. These processes are not oriented toward maintaining an organization in which the cells are already embedded. From both empirical and conceptual perspectives, it makes little sense to claim that the fate of embryonic stem cells is governed by the needs of embryonic self-preservation. As Davidson (1991, emphasis added) noted, the “function of embryonic cells is to interact in specific ways, to generate morphological structure.” Consider the development of the notochord in the amphibian *Xenopus laevis* (Gilbert and Berrasi, 2016, chapter 11). Starting from a fertilized egg, the notochord is *produced* in a specific region of the blastula through processes that define axes, regions, and layers, and commit cells to specific lineages. High concentrations of the transcription factor Vgt in the vegetal pole *generate* Nodal protein; the Nodal pathway induces the mesoderm layer; in the dorsal mesoderm, the

Spemann organizer is *produced* by high concentrations of β -catenin *synthesized* from maternal mRNA; and the notochord is *constructed* through a series of BMP inhibitors (noggin, chordin, and follistatin) *manufactured* by the organizer. All of these processes (in italics) involve self-production of the notochord. However, unlike hematopoiesis, cell specification here cannot be explained in terms of blastula self-maintenance—not only because the blastula is not maintained by these processes, but also because the functions of the organizer, the Nodal pathway, or maternal mRNA are not related to self-maintenance (Gilbert and Berrasi, 2016, 335). Rather, their effects are directed toward producing a new organization: “to bring inside the embryo those areas destined to form the endodermal organs; to surround the embryo with cells capable of forming the ectoderm; and to place the mesodermal cells in the proper positions between the ectoderm and the endoderm” (Gilbert and Berrasi, 2016, 227).

To sum up, the analysis in this section shows that the naturalization of teleology at the physiological scale is not adequate to account for the naturalization of teleological development. Further argumentation and open questions may also support separating AST from developmental teleology: Are embryos metabolically autonomous? Are embryos functionally organized as a whole, exhibiting the properties of an autonomous system? Are embryos individualized in the sense AST requires? These questions will be left for future work. Rather than further arguing for the distinction between teleological development and teleological physiology, my aim now is to highlight specific problems that arise when teleological development is treated as our *explanandum*.

6. The riddles of teleological development

If teleological development is not explained within the domain of AST, then what fundamental questions remain open? What is special about the teleological explanations that makes it a hard problem? In Section 6.1. I will present two *desiderata*—Bernard’s *desideratum* and Baer’s *desideratum*—that are connected with the place of time in teleological explanations of development. In Section 6.2, I introduce specific philosophical issues in which treatment is different at distinct time scales. The analysis of the issues treated here will also illustrate the limits of AST to solve them, but my main purpose is to introduce these problems and philosophical questions to, hopefully, stimulate the search for a teleological view of development.

6.1 Distant and close: subdividing teleological development

Karl Ernst von Baer's reflections on developmental teleology emphasized that developmental changes occur for a purpose revealed in distant ontogenetic stages: "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 [...] 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, 1886, 4, 55). This is Baer's *desideratum*: how is it possible for an ontogenetic change to occur for its distant effects? The term "distant" is inherently fuzzy, as its scope is not easy to specify. We can formalize it as follows: a change is distant in terms of its effect if its consequences are functional under different environmental and internal conditions from those in which the change occurs. For example, how can traits produced at the embryonic stage be useful for cutting leaves during the larval stage? The challenge is that the environment and internal conditions are constantly changing. One way to define "different" environments and conditions is to consider those that the developmental system *cannot perceive or respond to*. Changes at the embryonic stage cannot be explained as responses to conditions that do not yet exist—those of the larval stage. In this sense, developmental changes occur because of their effects at *distant* ontogenetic stages. Baer's *desideratum* thus calls for a naturalized teleological explanation of *developmental trajectories across temporally distant stages*. It highlights key features of developmental trajectories that motivate the concept of goal-directed development, namely robustness and plasticity.

Claude Bernard stated that "all morphological change is contained in the previous state [...] there is no morphology without predecessors" (1878, 2; quoted in Minelli, 2021, 21). Bernard's *desideratum* is not about trajectories but about the *transitions* between states of the system. It concerns ontogenetic changes produced by the regulation of the various sources of developmental specificity available to developing organisms. In other words, it asks how we can define the goal involved in regulating development from one stage to the next. This view does not presuppose future-oriented changes in conditions that are not yet "perceived." Instead, it focuses on transitions between ontogenetic stages as a result of the organism's perceptually mediated abilities and its capacity to regulate developmental resources according to its developmental goal. Bernard's *desideratum* thus highlights a central feature of goal-directed development: the need to explain how a system adaptively integrates different sources of developmental specificity to respond to particular conditions.

Each desideratum manifests in different developmental phenomena that exhibit a teleological profile—namely, transitions and trajectories. This implies a subdivision of

temporal scales within the developmental domain (see Figure 3): some teleological explanations concern close ontogenetic stages (transitions), while others concern distant ontogenetic stages (trajectories). This subdivision is *organism-dependent*: X and Y are considered *close ontogenetic stages* if the change from X to Y can be explained based on the system’s “perceptual capacities” at X, whereas X and Y are considered *distant ontogenetic stages* if the change from X to Y cannot be attributed to such perceptual capacities. “Perception” is used here in an informal sense, but it has many interpretations in developmental theory, including “experienced niche” (Sultan, 2015), “ecological information” (Stotz, 2017), “affordance” (Walsh, 2015), “environmental cues” (Sultan, 2015), “signaling systems” (Gilbert and Epel, 2015), “Umwelt” (Rama, 2024c), and other concepts that operationalize development as a response to particular internal or external conditions.

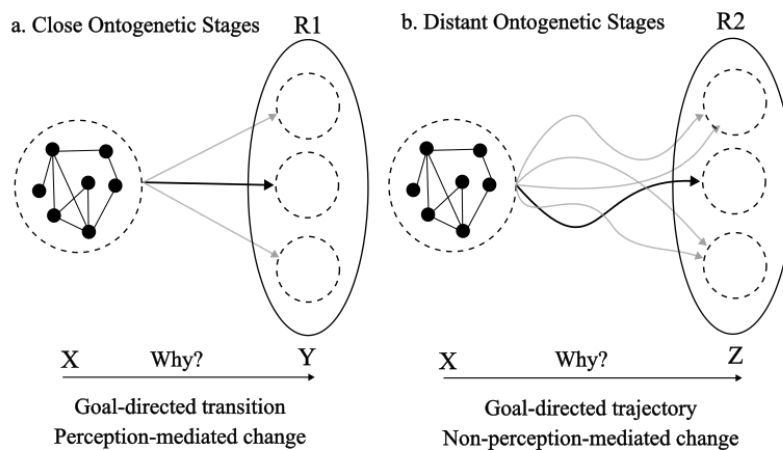


Figure 3: Temporal subscales in development. A system at ontogenetic stage **X** consists of an organized network of causal specifiers (black dots). 3a: Transitions (straight arrows) from stage X to stage **Y** are explained by perceptually-mediated responses that produce a particular outcome (black line) within a repertoire (**R1**) of possibilities. 3b: Trajectories (curved arrows) from X to **Z** are explained in a goal-directed way by showing a chosen trajectory (black line) that leads to a specific outcome in a repertoire (**R2**).

Mainstream biology has solved both *desiderata* by invoking a preformationist view. Inherited information determines developmental outcomes and any change in the course of ontogeny. In Mayr’s teleonomic view, for example, development is “guided by ‘a program’ and it depends on the existence of some end point, goal, or terminus” (Mayr, 1992, 127), and the transitions toward that end are a matter of running the program. Nonetheless, the motivation of this paper comes from those views that neglect gene-centered, evolutionary

views of function (Nenader, 1991; Millikan, 1989) and agency (Okasha, 2018; Gardner and Welch, 2011). The conundrum, however, is that we cannot fall back on the physiological scale either. Teleological development is cornered. It seems that developmental goals and norms cannot be set evolutionarily—“develop as your replicators say”—nor can they be set physiologically—“develop to maintain organization”. A further puzzling point is that developmental goals and norms are related to the evolutionary scale in very important ways. Developmental systems follow the developmental pathways inherent in their lineages. Developmental biologists speak of *normal* development from the perspective of the lineage that is *extrinsic* to the individual. From an agential view, however, normativity is usually explained by holding an *intrinsic* view of the organism. Moreover, phenotypic novelties or monsters are evaluated externally, while the concept of *monster* itself makes no sense from an intrinsic point of view. Variation is not even an intrinsic property of organisms. How can these normative attributions be reconciled? This question must be answered if development is to regain the explanatory role in evolutionary theory that genes have usurped. All the talk about agency, teleology, and norms in organism-centered approaches is meant to show that phenotypic outcomes result from adaptively oriented developmental processes so that variation and novelty, for example, are explained by an adaptive cause: development. However, if we take an extrinsic view of what is normal—i.e., a phylogenetic, species-specific perspective—variation would always be abnormal. If individual development is an adaptive force, the norms underlying both *desiderata* must be intrinsic.

6.2 Open questions for a theory of teleological development

Let us conclude with some programmatic questions that arise from these desiderata concerning i) developmental agency, ii) developing organisms, and iii) adultocentrism.

AST has developed its own theory of biological agency (Barandiaran et al., 2009; Arnellos et al., 2010; Virenque and Mossio, 2024; Pickering, 2024). But when it comes to understanding agency specifically in development (Brooks and Baedke, 2023), is there any difference at all between the agency of organisms at different temporal scales? At least two differences can be suggested. First, what are the elements that agents regulate or “take care of”? If organismal agency involves the ability to “enlist the causal capacities of its parts and direct them toward the attainment of a robustly stable end-point” (Walsh, 2015, 195), what are the relevant causes in development? As we have seen, developmental agents operate with a set of constraints distinct from those in physiological processes. How do developmental agents “enlist” causal specificity to achieve their goals? How is this developmental capacity related to developmental goals? The role of agency in *self-determination* at the physiological scale may

differ from its role in *self-differentiation* at the developmental scale. Second, and related to Baer's *desideratum*, developing agents are invoked in explanations for which it is difficult to understand how they could perform the alleged explanatory role. How can an agent be oriented toward an end state that it cannot perceive? AST explains agency in the context of the system's perceived internal and external conditions. Yet many teleological explanations in development—analyzing plasticity and robustness of trajectories—seem to extend agential explanations beyond what a system can perceive; adult morphospaces are not afforded during gastrulation, nor is the ecological role of each variant fully accessible in future environments. How, then, does agency fit into teleological explanations of *distant* change? How can an agential view of development account for the equifinality of sea urchin development that so impressed Driesch?

Moreover, if “agency is intrinsic to living organisms” (Rosslénbroich et al., 2024, 1), understanding agency in development requires careful reflection on what constitutes a *developing organism* (Smith, 2017). Considering the entire life cycle, as Minelli (2009, 67) has done, “one could ask how many different ‘lives’ an animal may fit into its cycle.” Organisms experience different organizational closures throughout their life. The complexity of life cycles thus demands conditions that allow us to track the system's identity across stages without relying on any single organizational closure (Griesemer, 2014, 2016; Balari and Lorenzo, 2018). There are at least “two ways of being in living organisms,” as Nuño de la Rosa (2010, 295) notes: one defined by the current organizational identity—synchronous identity—and another defined across different synchronous identities—diachronic identity (Minelli, 2021). If causal specificity—or information—constitutes the central variable in development, should developing organisms be defined in terms of causal specificity? Is a developing system “closed under causal specificity”? DiFrisco and Mossio's (2020) recent analysis of diachronic identity from an organizational perspective represents an important advance. According to them, closure of constraints (as described in Section 3) must be present at all stages to define diachronic identity. Yet this position assumes that, during developmental stages, a developing organism collectively implements closure of constraints. Is a developing system “collectively closed under causal efficiency” at all stages of life? Likely not (Nuño de la Rosa, 2010), although detailed analysis is required to determine whether an embryo is collectively self-maintained by the coordinated functioning of its parts or resembles more an aggregate of autonomous systems (individual cells) lacking collective action, structure, or functioning.³ Be that as it may, the relevant point is that, as Nuño de la

³ Some clarifications are necessary. DiFrisco and Mossio (2020) do not assume that AST can explain the change in development. They are worried about the organism's diachronic identity and not explaining change teleologically—indeed, the words ‘teleology’, ‘goals’ or

Rosa (2010, 291) observes, “developing organisms are not explicitly discussed as exemplars of the concept of organism,” unlike accounts at evolutionary (Godfrey-Smith, 2009) or physiological (Moreno et al., 2008) scales.

Finally, an important issue in developmental theory, closely related to the previous discussions, is that of *adultocentrism* (Minelli, 2011, 2021; Bich and Skillings, 2023; Rama, 2022): the common assumption that development is directed toward an adult form. On one hand, Baer’s *desideratum* seems to presuppose the existence of an adult form toward which the developmental system is oriented. Many teleological explanations of development that describe goal-directedness in terms of dynamic systems (Heylighen, 2022) may also implicitly assume an end-(adult) state (an attractor) toward which the system is progressing (e.g., Sultan et al., 2022). Developmental explanations addressing robustness and plasticity likewise often frame outcomes of developmental trajectories in an adult-centered way. For example, Alberch’s morphospace portrays adult forms rather than intermediate embryological forms. Moreover, both the practice and theory of development typically distinguish between the construction of form and function via cell differentiation and the subsequent growth of the body through cell division.

On the other hand, the constant changes inherent in complex life cycles pose difficulties in defining a clear state of the system as an adult (Minelli, 2009, 2021). Life cycles involving metamorphic transitions or scaffolding processes particularly illustrate this challenge (Griesemer, 2016). Systems undergo periods of drastic change as well as periods of stabilization and relative constancy, but these dynamics are trait- and subsystem-specific. For instance, morphological stabilization occurs at different stages than cognitive stabilization. Moreover, stabilization does not preclude future change; development appears

‘autonomy’ are not used in their text. However, analyzing their position can shed light on the limits of AST in explanations of development. One strategy for pointing out these limits is the one I pursue here: to argue that teleological development is something different from teleological physiology. Another strategy, pursued by Nuño de la Rosa (2010), is to argue that developing organisms are not in fact autonomous systems (at least not at all stages of the life cycle). This is related to DiFrisco and Mossio’s proposal, since it is necessary to analyze whether developing organisms are closed under constraints. Are embryos metabolically autonomous? What collective actions occur in a blastula to maintain its structure and function? These questions need to be addressed separately to provide further arguments against deploying AST in development. Furthermore, DiFrisco and Moreno (2020) propose some boundaries for defining diachronic identity (and for distinguishing development from reproduction), but it is unclear how these boundaries can accommodate cases of polyembryony.

to be an open-ended process (Balari and Lorenzo, 2015; Minelli, 2011). Plasticity can be observed at advanced stages, from morphological changes during puberty or metamorphosis in tadpoles, to cognitive changes, such as those experienced by a philosophy of biology student graduating as a doctor. Additionally, assuming that development is directed toward an adult form risks a form of preformationism, suggesting that the adult state is already present, represented, or encoded in earlier ontogenetic stages. To address this and related issues, Bich and Skillings (2023) propose a “snapshot” strategy: teleological development is analyzed as a series of snapshots rather than as a continuous trajectory through intermediate stages—to reduce teleological development to developmental transitions. Or as Veloso (2017, 84) also put it: “If [development is] seen as a motion picture in fast-forward, it intuitively appears teleological or end-directed,” but when the process is seen in slow-motion, no endpoint is strictly required

We might find a middle ground between adultocentrism and the snapshot strategy. Even if we reject “adult” as an idealized concept that cannot be operationalized across all species and life cycles, it seems inevitable that organisms experience phases of stasis and phases of change. Therefore, it may not be necessary to postulate a *single* adult state to satisfy Baer’s *desideratum*: a “distant” stage does not imply that the system at this stage is an adult—developmental trajectories do not need to culminate in ‘adult’ forms. The *desideratum* concerns connecting two temporally distant stages by explaining changes in one stage in terms of their effects on the later stage. Baer’s *desideratum*—and the teleological explanations it motivates—can accommodate multiple “adult” stages. The “adult stage” depends on the period of system stabilization toward which earlier ontogenetic changes are directed; endpoints are relative to the temporal scope of a given teleological explanation. While this mid-term position requires further elaboration, it acknowledges the complexity of life cycles and the open-ended nature of development, while permitting teleological explanations that go beyond the snapshot strategy (developmental trajectories).

7. Conclusion

I begin by highlighting the significant explanatory role of goal-directed views of development, that is, as *explanans*. After a brief introduction to AST, Section 4.1 examines various ways in which teleological physiology has been conflated with teleological development: explicit commitment to AST; the use of self-maintenance as the guiding goal of development; the application of physiological agency to explain developmental agency; and the adoption of other physiologically oriented theories—such as ecological psychology—to account for developmental phenomena, among other strategies. In Section

4.2, I present the central idea underlying the distinction between teleological physiology and teleological development: the goals and norms of self-maintenance do not determine ontogenetic change, because such change neither preserves a specific organization nor is explained by its maintenance requirements. Section 5 develops these differences with greater clarity and specificity, even though some arguments are left for future work. Key explanatory concepts—constraints, repertoires, regulation, and self-production—differ conceptually across scales, rendering AST inadequate for understanding them in development. Goal-directed developmental explanations are thus fundamentally distinct from the type of goal-directed explanations formulated within AST. Section 6 addresses programmatic questions specific to teleological development. I first outline two *desiderata* related to different temporal subscales in development: one concerning the teleological profile of trajectories, such as plasticity and robustness, and the other concerning the teleological character of transitions, namely the organismic regulation of its developmental conditions. I conclude by introducing and briefly discussing specific issues in developmental theory that cannot be addressed within the scope of AST. These *desiderata* and philosophical concerns are particular to the developmental scale and require taking it as the primary *explanandum*, avoiding reduction to the evolutionary scale or to the physiological scale.

One of the central aims of agential and teleological views of development is to explain how adaptive changes are generated by developing systems. Yet a crucial issue remains unresolved: we lack a normative, goal-directed criterion for describing developmental processes. The central philosophical insight of AST is that such a criterion is grounded in the maintenance of an organization. This functions as the “guiding principle” of the system and, correspondingly, of scientists and philosophers seeking to explain processes at the physiological level purposefully. However, at the developmental level, this principle loses its relevance: developmental changes are not guided by the needs of an organization, and thus development cannot be explained in terms of self-preservation (nor do developmental biologists attempt to do so). What goals, then, does a developing system pursue? On what properties of living systems are developmental norms based? I did not answer these questions here, but if development is going to be treated as an adaptive force in evolution, further research must address them, particularly their relationship to developmental agency, developmental information, and developmental repertoires.

This article does not aim to refute the agential and teleological view of development. On the contrary, it seeks to highlight an important programmatic challenge within this perspective and to call for a solution. Nor should it be read as a critique of AST, but rather as a critique of its application to development. I do not deny that autonomy has a place in development. The

issue lies in how we understand it. The organizational view of the AST needs to be reshaped or expanded to address developmental specificity, repertoires, regulation, and self-production, among other aspects. My commitment to a plurality of organismal goals rests on the fact that multiple goals are necessary to explain diverse biological processes. Development, maintenance, and reproduction can be considered central goals pursued by organisms—perhaps there are others. Reducing one to another risks producing explanations that fail to capture the phenomena adequately. The notion that an organizational framework serves solely to explain maintenance represents a theoretical and empirical mischaracterization, or at least an underestimated assumption. The organismic and agential perspective must be extended theoretically to encompass the full range of goals that living systems pursue.

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