Chapter 11
There Are No Intermediate Stages: An Organizational View on Development

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Abstract Theoretical accounts of development exhibit several internal tensions and face multiple challenges. They span from the problem of the identification of the temporal boundaries of development (beginning and end) to the characterization of the distinctive type of change involved compared to other biological processes. They include questions such as the role to ascribe to the environment or what types of biological systems can undergo development and whether they should include colonies or even ecosystems. In this chapter we discuss these conceptual issues, and we argue that adopting an organizational approach may help solve or clarify them.

While development is usually identified with the achievement of an adult form with the capability to reproduce and therefore maintain a lineage, adopting the organizational approach may provide a different strategy, which focuses also on the maintenance of the current organization of the organism. By doing so an organizational approach favors a switch in perspective which consists in analyzing how organisms maintain their viability at each moment of development rather than considering them as going through intermediate stages of a process directed toward a specific goal state. This developmental dimension of biological organization has yet to be given a general and detailed analysis within the organizational theoretical perspective, apart from some preliminary attempts. How a biological organization is maintained through a series of radical organizational changes and what these changes are issues that still require clarification. In this chapter we offer the beginnings of such an analysis of developmental transitions, understood as changes in functionality brought forth by regulatory mechanisms in the context of the continued maintenance of organizational viability at every step.

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11.1 Introduction

Accounts of development are characterized by a common focus on changes taking place during the lifetime of a biological system, usually centered on multicellular organisms. These accounts may address how complex forms are generated, the origin of differentiation and morphological variation, growth, regeneration, metamorphosis, and other related phenomena (see, e.g., Muller & Newman, 2003). In some cases, development is identified with any changes taking place throughout the entire life cycle of an organism, including phenomena such as the production of new blood cells or senescence (Gilbert & Barresi, 2018).

Yet, while differing on the type of change involved, development is usually identified with a process that gives rise to a complex multicellular organism (Barinaga, 1994; Martinez-Arias & Stuart, 2002; Wolpert & Tickle, 2011), more specifically with the achievement of an adult form with the capability to reproduce (Minelli, 2011; Griesemer, 2016). As explicitly stated by Griesemer (2016): "Development is the recursive acquisition, refinement, or maintenance of a capacity to reproduce"; and "development can be seen as relatively continuous growth and differentiation of shapes and sizes of parts along with the maturation necessary to reproduce." On these views, development is considered part of a larger life cycle defined by reproductive events. As a consequence, explanations of change across whole life cycles are usually focused on evolutionary considerations at the scale of lineages. This directionality of developmental processes from the zygote to an adult form capable of reproduction underlies these characterizations of development. By doing so, developmental biology has become a field in which scientists and theoreticians (implicitly or explicitly) face the issue of biological teleology and employ a teleological terminology.

Accounts of development face several internal challenges or puzzles. We introduce some of them in Sect. 11.2. These challenges include issues deriving from adopting notions of directionality and potentiality, especially if cases of reversible and multidirectional development are considered. Further tensions concern the problems of identifying the boundaries of development, i.e., the start and end points of development. An important issue in this respect is identifying the distinctive character of developmental change compared to other changes that living systems undergo during their lifetime, such as individual adaptivity, growth, regeneration, plasticity, acclimation, etc. Development is commonly defined in terms of the organism. It is the history of a particular organism from its earliest form, e.g., egg, seed, or clone, to its end, usually either reproductive maturity or death. Another important question is what are the types of systems that can develop and whether those systems should include unicellular organisms, colonies, superorganisms, symbiotic associations, or ecosystems.

In Sect. 11.3 we argue that the organizational framework may provide a shift in perspective that may be helpful in relieving these tensions and contribute to a better understanding of development by complementing existing accounts. A deep change in strategy concerns how to pick out the relevant system. We decenter the organism to focus on living systems characterized by organizational closure and regulatory mechanisms. Focusing on a wider phenomenon realized on a longer time scale – the reproductive cycle or the lineage – misses the importance of the explanation of development from the point of view of the organization of the system undergoing processes of change. The organizational approach accounts not only for the maintenance of the lineage through reproduction and selection but also of the organization of the system.

Adopting an organizational approach means switching focus to how organisms – and possibly other biological systems – maintain their viability at each moment of the developmental process instead of considering them as going through intermediate stages of a process directed toward a predetermined goal state. How an organization is maintained through a series of radical changes and what types of changes are involved are issues that still require clarification. We argue that from an organizational perspective, development is a regulatory process that changes the number or types of functions of a regime of closure of constraints. The reasons why we recommend this conceptual switch is because it resolves some of the outstanding tensions or problems of generalization emerging in comparative work that tries to circumscribe developmental phenomena across the entire tree of life. These are the challenges we take up in Sect. 11.4. In Sect. 11.5 we conclude by summarizing the main conceptual points of our proposal for an organizational view of development and some remaining open questions for future work.

11.2 Puzzles and Challenges Within Theories of Development

There are a cluster of phenomena related to development that make the boundaries of this phenomenon difficult to define. Here we introduce a set of puzzles regarding development and development-like phenomena. They constitute challenges for any unitary theory of development. Few, if any, of these challenges are new, but neither are they universally accepted. The purpose of addressing them is not to provide a definition of development through a definitive set of necessary and sufficient conditions, which may not be desirable given the breadth and variety of work on development. Our aim is to build a conceptual account able to provide a different, theoretically coherent perspective from which it may be possible to better understand the implications of these puzzles and address them. We take as a starting point the work of Alessandro Minelli (especially Minelli, 2003, 2011, 2014). Minelli presents a definition of development that he thinks is often taken for granted: "development is a sequence of changes through which a multicellular adult is produced, through an increase in complexity more or less strictly programmed in its genes, starting from a single cell which in most instances is a fertilized egg" (p. 5). He uses this definition as a jumping off point for showing how inadequate it is and to further argue for "what development is not" (Minelli, 2011, p. 6). Minelli argues that the given notion of development is inadequate in five ways, because "development (1) is not restricted to the multicellular organisms, (2) does not necessarily start from an egg, (3) does not necessarily start from a single cell, (4) does not necessarily imply an increase in structural complexity, and (5) does not necessarily end with the achievement of sexual maturity" (p. 5).[1] We agree that these five points present contentious problems for a comprehensive theory of development and will use them as a starting point, taking and expanding on them one-by-one. We also introduce two more problems for the given definition of development: development (6) can proceed across complex life cycles punctuated by multiple reproductive events, and (7) does not necessarily exclude multispecies complexes (e.g., lichens) and host-microbe systems (e.g., aphids, corals, cows, or humans).

11.2.1 Challenge 1: What Is Developmental Change, and Is It Restricted to Multicellular Organisms?

Development is some sequence of changes, but what kinds of changes can count as development? Organisms, for example, are constantly going through metabolic changes in order to maintain themselves from moment to moment. However, metabolic change is not sufficient on its own to count as development if development is to retain any specialized meaning. To differentiate developmental changes from metabolic changes, development is usually restricted to changes that have to do with growth or a change in morphology or function. Acquiring new functions or changing the function of existing structures is especially central. The first challenge is to establish whether or not single-celled organisms go through the right kinds of changes to count as development. The answer might not be univocal due to the diversity of organisms under consideration. Asexually reproducing bacteria might only go through metabolic changes, some growth, and then reproduction, whereas many parasitic eukaryotes have complex life cycles transiting through very different morphologies. In these latter cases, the border between reproduction and development gets fuzzy. We will return to this in challenge 6.

[1] An additional source of inadequacy may be constituted by the idea that development is programmed in the genes. For criticisms of this idea, see Sonnenschein and Soto (1999) and Veloso (2017).

11.2.2 Challenge 2: Does Development Necessarily Start at Fertilization?

Pregnancy is a challenge when trying to draw clear cut lines between biological individuals (Grose, 2020; Kingma, 2020; Nuño de la Rosa et al., 2021). A fertilized egg makes for a clear starting point in the life cycle of a sexually reproducing species and is perhaps the obvious choice for where to pin the start of development. But this is clearly a byproduct of focusing on development in sexually reproducing organisms, primarily animals. It doesn't work for a general account of development because it ignores vegetative reproduction (e.g., cloning, budding) in plants, fungi, and many animals (Minelli, 2011). It doesn't even work for paradigmatic cases like humans because of monozygotic twins that develop from the splitting of a single embryo. Even more challenging is the case of the armadillo, which almost always produces four identical quadruplets, splitting at an even later developmental stage (Enders, 2002). Cases like these complicate drawing the line between developmental processes. For example, in the case of monozygotic twins, it seems like there are two equivalent interpretations of the developmental process: (1) there is one developmental process, and it is split between two separate entities, and (2) new developmental processes split off from an ongoing developmental process, but that splitting is not reproduction. Either interpretation produces a problem. In the first option, there is an apparent contradiction, as one and the same (token) developmental process is carried out within two distinct organisms. The second option undermines the initial claim that development necessarily starts at fertilization. Such claim is also undermined by phenomena such as parthenogenesis (Sonnenschein & Soto, 1999). There is a third option: the development of each twin starts at a stage later than fertilization. We will explore this option in Sect. 11.4.

11.2.3 Challenge 3: Does Development Always Start at a Unicellular Bottleneck?

This question is related to the previous one or is perhaps an expansion of it. Identifying the initiation of development requires identifying a new individual that is about to undergo development. A single cell that multiplies and transforms into a multicellular organism is a good candidate. Such a cell, especially when it is at least partially independent, is easier to delineate. Citing a multicellular clump as the start of development raises a few questions: (1) what is the origin of the clump, and what changes did it undergo to get to the multicellular stage?, (2) what kinds of changes did it undergo, if they were not developmental changes?, and (3) are there bounds on the size and complexity of an entity that both counts as a new individual and is able to undergo development?

In principle, is there a restriction on the types of mereological structures that can serve as starting points for developmental processes? The case of the armadillo, for example, seems to point to a later beginning of the development of distinct embryos. One possible restriction is that a system must be unified as an individual whole, as opposed to a colony or a collection of individuals. Furthermore, such a system must not have yet started to undergo changes in the functional/structural relations of its parts since its formation as a new and discrete individual whole.

If it were the case that the formation of a new cell through the fusion of sperm and egg marks the beginning of development, as is commonly assumed, then what does that leave out? One possibility is asexual reproduction through budding or parthenogenesis, which are both common in multicellular systems. A second is symbiotic associations such as biofilms, holobionts, lichens, or other multispecies systems that seemingly fuse to form new individuals (Skillings, 2016). The symbiotes don't fuse into a new single cell that then begins development. The creation of these entities happens when the cells of different species join together. Thus, the initial condition of the association is multicellular.

Challenges 2 and 3 can then be generalized: instead of looking for specific structural features, is there a common functional starting point for every possible developmental process?

11.2.4 Challenge 4: Does Development Imply an Increase in Complexity?

There are two different ways the answer to this question is no, or at least ambiguous. The first answer is that different kinds of complexity can appear during a life cycle, and it is unclear how to compare them. For example, in species that go through metamorphosis, organisms will often lose some functions while gaining others. Through metamorphosis an organism might lose the capacity to feed but gain the capacity to sexually reproduce, such as in mayflies (Skillings, 2019), or behavioral complexity found in the larvae might be lost while structural complexity increases in the sessile adult form, such as in tunicates (Holland, 2016). Tunicates lose complex and energetically expensive structures like a head/brain that become unnecessary once they transform into sessile adults. In cases like these, it is unclear if there has been an overall increase in complexity.

The second, more definitive, answer to the question of whether development implies increase in complexity appears to be a straightforward no. Parasitic rhizocephalan barnacles transform from a free-swimming larval stage to a larval "injection" stage, where the organism essentially acts as a giant hypodermic needle. This stage then injects a small group of poorly differentiated amoeboid cells into the hemolymph of a crab host. Those cells later metamorphose into the adult form, which does not inherit any organs from the larval stage and consists of two parts: an interna, which is a system of ramifying rootlets spanning the body of the host, and an externa, which is a structure containing the reproductive system (Høeg et al., 2012; Miroliubov et al., 2020). In a more extreme case, the immortal jellyfish *Turritopsis dohrnii* (see Matsumoto et al., 2019) is able to reverse its developmental trajectory from medusa back to polyp in response to stress without going through the whole cycle (i.e., through reproduction and the unicellular stage). It does so by going through a different intermediate stage, the cyst, constituted by a cluster of poorly differentiated cells. Is rejuvenation, with or without simplification, a kind of development? If it were the case, it would put into question the very idea of development as a unidirectional or irreversible process (of which an increase in complexity is one example).

11.2.5 Challenge 5: Does Development End at Reproductive Maturity?

According to Griesemer, development is intrinsically related to reproduction "Development is the recursive acquisition, refinement, or maintenance of a capacity to reproduce. Reproductive capacity is realized in diverse ways and modes of development in extant lifeforms on Earth" (Griesemer, 2016). He writes elsewhere that "reproduction involves the conveyance or conferral of developmental capacities. Not every mereological change achieves that. Moreover, since development is the acquisition of a capacity to reproduce, only lineage- forming (or terminating) mereological changes in development count" (Griesemer, 2016). It appears that Griesemer is using reproduction to explain development.

This focus on reproductive maturity as the endpoint of development can lead to a kind of "adultocentrism" (Minelli, 2011). This adultocentrism is an improper fixation, or essentialization, of the adult form of an organism as the true or proper form. This can create the view that the adult form is the form the "organism works toward," injecting a kind of teleology or forward-lookingness into all developmental processes. This risks overlooking the importance and distinctive features of other non-terminal forms, especially when studying organisms that are not amniotes (reptiles, birds, mammals). Let us think of organisms that have different free-living forms and may undergo metamorphoses, or that go through complex life cycles, where it is not clear if there is even an adult or terminal form.

It is not hard to find examples of adultocentrism; it is rooted in our language and maybe even our psychology. Picture a sea star, butterfly, or frog. It is probably the adults, not the larvae or juvenile forms, that come to mind. This is also the case for how organisms like mayflies are characterized, where the adult form is present for only a fraction of the life cycle. This is all fine for everyday use. It is the adult forms that we are most likely to encounter, because they are either larger or more active and consequently easier to see or come across. But this becomes misleading when thinking about the development or evolution of an organism. The organism has evolved to maintain itself at every point of the life cycle, and the maturation process (developing into an adult) constitutes an important part (and often a major one) of the whole life cycle. The question (for development) isn't only how did these features evolve in order to increase future reproductive function or output but how/why did these features evolve in order to maintain the organism at that stage of the life cycle. The proximal selection pressure is at the maintenance of the organism at that stage, not some future reproductive stage that isn't realized at that point. The tadpole is an adapted self-maintaining organization subject to selection and lives freely as an agent in its environment. In the case of the axolotl, a pedomorphic salamander, it can even undergo reproduction. So, the tadpole's tail is just as important as the frog's four-legged form.

11.2.6 Challenge 6: Are the Transitions Between Multicellular and Unicellular Forms in a Complex Life Cycle Development or Reproduction?

Complex life cycles are probably the most common type across the spectrum of life. This includes sequences of forms that are divided by metamorphosis (like between the caterpillar and the butterfly), by both asexual and sexual reproduction (e.g., corals, and parasitic flatworms, etc.) and transitions between multicellular and unicellular forms (e.g., algae, ferns). Let us think of a life cycle with multiple stages divided by reproduction, where the same type of form doesn't come back until it has gone through different stages separated by reproduction. It is hard to parse a life cycle like this on an account of development that focuses on development as a unitary process that moves solely toward reproduction. Moreover, it makes it extremely problematic to distinguish development from reproduction. Is a single life cycle – say from haploid form to sexual reproduction to diploid form to asexual reproduction with multiplication at each step – made up of multiple and vastly different, reproductive and developmental cycles attached end to end? Or is it a single developmental process measured by one turn through the entire cycle but punctuated by "minor" forms of reproduction along the way? There isn't a knockdown argument for either interpretation (Godfrey-Smith, 2016). But there needn't be. What is needed is a conception of development that can make sense of this problem and the rest of the other problems.

11.2.7 Challenge 7: Can Multispecies Assemblages Develop as One System?

The deeper question behind this challenge asks what kinds of systems can develop: Is it only organisms that develop? Do symbiotic associations like lichens develop at the level of the whole? Can ecosystems develop?

Accounts of development focused on achieving reproductive capabilities as the end point of the process fail to be satisfactory when dealing with integrated symbiotic assemblages. These are systems where developmental phenomena appear to be present in the more comprehensive system (the assemblage) but that do not reproduce at the level of the comprehensive system. Examples include symbiotic assemblages like lichens, biofilms, and holobionts. Lichens don't reproduce to form new lichens; the algal and fungal partners reproduce separately and then disperse and rejoin to form new lichens. Yet they undergo developmental changes at the level of the system as a whole. These systems are contradictory for developmental accounts focused on reproduction. Moreover, the boundaries might be drawn in the wrong places, because the overall developmental process of the assemblage would be overlooked. To address the question whether these associations undergo development, one needs to focus on how they change as integrated entities and abandon the idea of development as a tendency toward reproduction.

11.3 Gestalt Switch: Adopting the Organizational Perspective

The challenges discussed in the previous section put into question accounts of development as a progressive irreversible process directed toward the production of an adult organism capable of reproduction. They bring to the surface the need for a gestalt switch: development needs to be addressed also from a different point of view, one that is not directed toward some defined state in the future. A possible way of answering these challenges is through a change in perspective that centers on the maintenance of the living system from the very beginning of development. Such an account should be able to provide a general characterization of what development is, what type of changes it implies, and when development starts and ends. At the same time, it should be precise enough to address the challenges posed by phenomena such as rejuvenation, complex life cycles, and multispecies assemblages. Moreover, it needs to distinguish development from other types of change taking place during the life of an organism. By this, we do not claim that a different approach should replace those currently available but provide a complementary coherent theoretical perspective.

In the second part of this paper, we argue that this gestalt switch can be accomplished by adopting an approach focused on organization. We sketch a proposal of an organizational account of development, and we discuss how it can address the challenges presented in Sect. 11.2. The central idea is to focus on how the organization of living systems is maintained during the transitions that characterize development. This is a radical shift from a view of development as a process aiming toward a final state, or as an actualization of an intrinsic potentiality. Our focus is on what is maintained and on the developmental changes occurring at each moment, rather than interpreting them as early stages work toward constructing the adult form and achieving reproductive capabilities. According to the organizational approach, there are no intermediate stages, ones defined by their relation to some future goal state.

Every stage is equally important, because the system must build and maintain itself at every point of its existence.[2]

The organizational framework was built upon pioneering work on biological autonomy carried out by Jean Piaget (1967), Robert Rosen (1972), Humberto Maturana and Francisco Varela (Varela et al., 1974), and Howard Pattee (1972), among others. More recently it was further developed by Stuart Kauffman (2000) and by Alvaro Moreno and collaborators (Ruiz-Mirazo & Moreno, 2004; Moreno & Mossio, 2015), among others. The organizational account characterizes a biological organism as an autonomous system capable of producing its own components and maintaining itself in far from equilibrium conditions while interacting with its environment. To explain this capacity, this tradition appeals to the internal organization of the organism, which is maintained despite the continuous transformations that the organism undergoes at the level of its components. The core feature of this approach is the focus on the organization of the system: the identification of topological relations between the operations of components and between processes of transformation within a system. Organization refers to the way production and transformation processes are connected so that they are able to synthesize the very components that make them up, by using energy and matter from the environment. In this view, the fundamental feature of the organization of biological self-maintaining systems is its circular topology as a network of processes of production of components that in turn realize and maintain the network itself. This distinctive type of generative circularity that characterizes biological systems is known as "organizational closure." The basic capability of a biological organization to self-produce and self-maintain has been explained in terms of closure of constraints (Moreno & Mossio, 2015; Montevil & Mossio, 2015). Constraints are characterized as material structures that harness processes and that by doing so specify part of the conditions of existence of those processes. According to this framework, living systems are capable to generate a subset of the constraints acting on their internal processes and realize a distinctive causal regime by which these constraints are organized in such a way that they are mutually dependent for their production and maintenance and collectively contribute to the maintenance of the conditions in which the whole network can persist.

The notion of closure of constraints focuses on the distinctive capability of living systems to contribute to their own conditions of existence and to the existence of their parts. This basic idea grounds two important biological notions: function and teleology. Within the organizational framework, a biological function is understood as a contribution of a part to the maintenance of a self-maintaining organization (e.g., a living cell) that, in turn, contributes to producing and maintaining the part itself (Mossio et al., 2009). Functional parts coincide with the constraints subject to closure. The *telos* of the system is understood in terms of

[2] It is important to make clear that considering different stages as equally important does not mean that they are all the same. On the contrary, it means that their distinctive features and how they are maintained should not be overlooked or interpreted in terms of a future state. However, some stages might be more relevant in relation to specific research agendas.

self-maintenance (Mossio & Bich, 2017). The focus of the organizational account of teleology is on how the activity of a biological system contributes to determining its own conditions of existence. The organization of a living system is characterized as an intrinsically teleological causal regime where the conditions of existence on which the organization exerts a causal influence are the goal (*telos*) of the system. Other accounts of biological functions and teleology centered on evolution differ from the organizational one in that (1) they take the lineage rather than the current system as the grounds of intrinsic teleology; (2) they characterize functions of traits etiologically, as contributions to the survival of the ancestors of those organisms that currently carry those traits; and (3) the goals of the system are characterized in terms of adaptation by natural selection (inasmuch as they contribute to maintain the lineage). An important implication of adopting the organizational account is that it entails this distinctive teleological framework that is focused on the maintenance of the system. Applying this framework to development means identifying the *telos* of the developing system in its current organization, rather than in a future state that contributes to the maintenance of the lineage (i.e., the adult form and reproduction). As such, it provides a different theoretical perspective which is not based on a future-oriented directionality and is not subject to the issues discussed in the previous section.

A further aspect of the organizational approach needs to be taken into consideration before building an organizational framework of development. The idea of closure alone is insufficient to ground a theoretical understanding of this biological phenomenon. There are two primary reasons. The first is an intrinsic limitation of the very notion of closure alone in providing an understanding of biological organization. The second is the limitation of the notion of closure in accounting for change in general and, therefore, even more so for developmental change. Both limits can be overcome by employing the notion of regulation. Regulation is carried out by mechanisms realized by sets of constraints that are sensitive to internal and external variation and are capable of changing their activity accordingly. Regulatory mechanisms operate as higher-order constraints in the sense that they act on other constraints in the system. What they 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).

Let us consider the first limitation. The capability to produce their own functional components (i.e., constraints) is not enough to understand how biological organizations maintain themselves and actually realize closure. The basic biological constraints involved in a regime of closure are not always functioning or functioning whenever their substrates and energy are available. Their activities are constantly controlled (inhibited, activated, modulated) by other constraints on the basis of the state of the system and the environment:

> Cells, for example, engage in division, but they are not constantly dividing (when they do, the result is a pathology such as cancer). Cells metabolize glucose to produce ATP, but they only do so when ATP levels drop and energy is needed. Otherwise, they convert glucose to glycogen. Protein synthesis is another process that is inhibited or activated on the basis of the needs of the cell. Neurons generate action potentials, but either do so only when they receive an appropriate stimulus or change the rate at which they generate action potentials in response to stimuli. (Bich & Bechtel, 2022a).

To maintain itself, an organism needs to *continuously* modulate and coordinate the activities of its basic functional constraints, which directly harness thermodynamic processes, in such a way that they can realize a viable regime of closure (Bich, 2018). Equally important, an organism must interact with a changing environment, which is the source of matter and energy for its internal processes. To do so, the internal organization of an organism must manage adaptively the dynamical variability available within it. As argued elsewhere, this is achieved by means of regulatory mechanisms (Bich et al., 2016, 2020; Bich, 2018; Bich & Bechtel, 2022a, b). They continuously exert a fine-tuned functional control over the exchanges of matter and energy of the system with its surroundings and over the activity of the internal constraints in such a way that the system is able to bring forth different viable responses to environmental perturbations and internal needs.

The second limitation of an account of closure without regulation concerns the capability to account for change in biological systems. This is particularly relevant because development is a specific type of change. As argued in the previous paragraph, living systems do not only and simply produce, repair, and maintain their components. Such activities are continuously undergoing regulation. Importantly, on this view the basic regime of closure does not operate in a regular manner: an organism needs to constantly change in order to maintain viability. However, as argued by Bich et al. (2016), closure alone would account only for a very limited type of change, one understood in terms of a dynamic stability that is realized as a passive network property. The basic regime of closure simply "absorbs", as a network, the effects of a limited set of perturbations or internal variations. The system compensates for perturbations by means of reciprocal adjustments between tightly coupled internal subsystems. The dynamics of the whole system are maintained in the initial attractor state or are pushed by the perturbation into a new stable attractor state. In living organisms, instead, regularity and stability in the activity of components are exceptions. A living system coordinates the activities of its components, modulates internal processes, and responds adaptively to environmental variation. The activity of each basic constraint is controlled according to the needs of the organization, starting from those basic constraints involved in transcription, translation, and protein synthesis. The system changes what activities its constraints perform in ways appropriate to the circumstances it faces and its internal state. On this view, active change is controlled by regulatory mechanisms (see Bich et al., 2016, 2020). Regulation is therefore a crucial notion to understand the organizational approach and its application to development.

In sum, adopting an organizational account implies focusing on how a living organization is currently maintained and on the functional contributions of its different components. Change, in this perspective, is understood as the result of the action of regulatory mechanisms which, on the basis of the state of the system and the environment, modify what functions are realized and modulate how they are performed.

11.4 Toward an Organizational Account of Development

What can an organizational approach say about development and its teleological dimension? As a starting point, this approach has a distinctive focus on developmental processes: on the system's current organization rather than on the realization of potentialities or the achievement of reproductive capability. The organizational account provides a conceptual framework which can be applied to development by accounting for how organisms, or biological self-maintaining organizations in general, maintain their viability at each moment of the developmental process. On our view it allows characterizing development as a regulatory process that changes the number and type of functions available to the system at a given moment while the system itself maintains its viability. From this perspective, development is not addressed as an adult-oriented process. Instead, the telos of the system is grounded in the maintenance of the viability of the organism at each stage of development, rather than in a future state.

To date, few contributions belonging to the organizational framework have addressed aspects of developmental processes. Arnellos et al. (2014) and Veloso (2017) focus on the role of intercellular signals and constraints in cell differentiation at early stages of development as an important factor to achieve integration. They contrast it with accounts of cell differentiation processes focused on intracellular factors such as genetics. Bich et al. (2019) point out the limits of cell differentiation alone to address multicellularity and development.[3] They focus on what is a minimal multicellular organization capable of maintaining itself as an integrated system and what are the types of mechanisms that control individual cells and ensembles of cells to realize tissues and organs. They emphasize the importance of the control of spatial organization and the role of the extracellular matrix (ECM) in development.

The only work entirely centered on development within an organizational perspective is by Nuño de la Rosa (2010). She focuses on vertebrate development. She characterizes development as the generation of a fully-fledged autonomous organization, which happens in the later stages of this process. According to this view, development is considered as the *explanans* for biological autonomy.

This pioneering and detailed work has the merit to be the first and only to fully focus on development. However, it exhibits some features that make it incompatible with current organizational accounts. Moreover, it shares some of the limits exhibited by the other accounts of development discussed in the previous sections. In the first place, it focuses on a small subset of vertebrates: mammals and more specifically humans. Therefore, it might not be representative of development as a general biological phenomenon. In the second place, it focuses on autonomy considered as a form of independence from the mother organism, rather than a general form of self-maintaining organization characterized by a regime of organizational closure.

[3] Moreover, cell differentiation itself, is determined by the surrounding ECM and by tissue in which cells reside (see Sonnenschein & Soto, 1999).

The problem is that biological autonomy does not imply independence. In principle, closure is not incompatible with forms of dependence, and a system can be autonomous in the sense that it realizes closure even though it is not independent from other systems. Examples are symbiotic associations, multicellular organizations, and, possibly, ecosystems (see Montevil & Mossio, 2015; Nunes-Neto et al., 2014, Bich, 2019). This is an important aspect of the organizational framework and allows it to account for forms of nested closure. In the third place, this account is in tension or even in contradiction with organizational approaches. Nuño de la Rosa's view is explicitly Aristotelian: development is characterized as a process of progressive actualization of autonomy. This account is characterized by a future-oriented teleology incompatible with the teleology that is characteristic of the organizational framework, based on current contributions to the persistence of an organization.[4] Like other accounts, here again the goal of development is producing the adult organism. Finally, an implication of this focus on the progress from potency to actuality is that this account assumes change as an *explanans* of autonomy instead of an *explanandum*: on this view developmental change is what bring forth and explains the origin of an autonomous system. It is not the object of analysis.

The developmental dimension of biological organization has yet to be given a detailed analysis within the organizational theoretical perspective. The idea that an organization is maintained through a series of radical changes or transitions, such as those that take place in developmental processes, is an issue that still requires clarification. The application of this idea faces several internal tensions, insofar as the organizational approach is mainly focused on what is currently maintained – the whole organization – rather than what changes over a long sequence of often radical transitions. The first conceptual problem is determining what kinds of organization can undergo development as opposed to mere change. The second problem is how to account for the specificity of developmental change. It consists in distinguishing developmental changes from the other types such as metabolic changes. The third problem concerns the boundaries of development. To address it requires establishing when development starts within an organizational framework by identifying what is the initial self-maintaining organization that undergoes developmental change. It also requires establishing whether and when development stops and why. Common options have it ending with the realization of the adult form versus continuing through ageing or senescence.

The organizational approach can provide a principled way to address these problems and helps refocus those tensions and puzzles discussed in the previous sections. We offer here the beginnings of a supplementary analysis of development that

[4] The criticism of future-oriented approaches and potentialities is shared also by early work on the organizational framework, such as the autopoietic theory, which is explicitly focused on the current system (Maturana & Varela, 1980). Change is understood in terms of "structural determinism," that is, all changes a living organization undergoes at a given moment are determined by its structure at that specific moment. It is important to mention that autopoietic theory rejects teleology insofar as in the interpretation of Maturana and Varela teleology is future or past oriented (see Mossio & Bich, 2017).

focuses on the continued maintenance of organizational viability at every step. The starting point is the idea that during the life of an organism, what is maintained through the deep and continuous changes of its components is the organization of the whole. The conservation of organization unifies the biological processes an organism undergoes, which includes development, growth, senescence, etc. This idea has been expressed by Di Frisco and Mossio (2020) through the notion of organizational continuity, that is, "the presence of a continuous causal process linking successive organizational regimes, irrespective of material and functional changes." This is the foundational assumption that it is to be adopted in order to understand biological phenomena from an organizational perspective. However, it is a very general notion. Alone, it does not provide conceptual tools to distinguish between development and other phenomena such as reproduction and aggregation. To do so it requires additional assumptions such as on the necessary variation in the number of organizations.[5] Even more importantly, it does not provide an account of change. It focuses on what is maintained. Understanding development exactly requires understanding change, a specific type of change, within a scenario of organizational continuity.

The first problem to face in order to address development is how to pick out the relevant system. Focusing on a system realized on a longer time scale than the organismic organization – the reproductive cycle or the lineage – would miss the importance of the explanation of development from the point of view of the organization of the system undergoing a process of change. The organizational approach focuses on the organization of current biological systems capable of maintaining themselves. In this context the relevant system is a functionally integrated self-maintaining organization. Functional integration on this view consists in the degree to which the different components that collectively realize a biological regime of self-maintenance depend on one another for their own production, maintenance, and activity. In principle, an integrated system can be a unicellular or a multicellular organization (see Challenge 1 in Sect. 11.2) or even a symbiotic association if it satisfies the requirements (Bich, 2019; see Challenge 7 in Sect. 11.2). Let us focus on the second type of organization, given that it is the one usually discussed in relation to development. To achieve functional integration, a multicellular system requires some internal differentiation, the basic requirement for division of labor. For example, internal differentiation depends on the presence of components that contribute in different ways to the realization of the system, such as cells and an extracellular matrix (ECM). Through functional differentiation multicellular systems become, in principle, capable of harboring components that have different functional roles. Hence, functional differentiation realizes division of labor under certain conditions. Integration between these different tasks is achieved when functions are coordinated at the system level such that the differentiated components actively contribute to the maintenance of the system while their activities are being

[5] Counting the variation in number of organizations might be problematic as well. For example, it does not respond to the question whether the first steps of cell division in the embryo count as reproduction or development and why.

activated, inhibited, or modulated at different moments in time depending on the state of the system. This is achieved by means of mechanisms of control and spatial organization acting at different ranges or time scales. Examples include cell-to-cell interactions, an ECM dynamically constraining groups of cells, biomechanical forces, and long-range control exerted by the vascular, nervous, or immune systems (Bich et al., 2019; see also Sonnenschein & Soto, 1999; Montevil & Soto, this volume). To undergo development, this organization should also exhibit regulatory capabilities, that is, be able to determine its own processes of change. This means that it should be able to modify itself and modulate its internal dynamics in response to variation in internal and external conditions, rather than only passively undergoing change driven by perturbation (Bich et al., 2016).

The second problem faced by the organizational approach is that not all regulated change is developmental (see Challenge 1 in Sect. 11.2). Otherwise, development would include all possible biological dynamics. Let us sketch an account of developmental change. Regulation operates by sensing the internal and external conditions of the system. Most regulatory processes act upon available mechanisms and the processes responsible for energy production, synthesis of parts, and the like. Regulation in these cases consists in bringing forth change in the basic dynamics of the living system by selecting between available mechanisms, via activation or inhibition, or by modulating mechanisms already in operation. An example is the activation and inhibition of genes responsible for the synthesis of enzymes specific to the presence of variable food sources, as in the case of the *lac operon* in bacteria.[6] In these cases, regulatory mechanisms select between available functions or functional regimes.

Development is qualitatively different from other regulatory processes because it does not operate only on available functions but also changes the set of functions available to the system. At each developmental step, some new functional traits are generated, such as in the appearance of new tissues, organs, or limbs. In unicellular systems development might include the production of new organelles or other functional supramolecular structures. Functional traits might also be shed. Think of the transition between tadpole and frog, with the appearance of legs and lungs and the disappearance of gills and tail. These changes are different from the activation or inhibition of mechanisms which are already present in the system, and they affect the way the multicellular organization maintains itself in its new regime of closure.[7]

[6] While the case of the lac operon is well-known and illustrative of regulatory mechanisms, self-maintenance and regulation do not only apply to metabolic processes. Many other types of processes that are not metabolic contribute to self-maintenance and are strictly regulated: for example, behavior, movement, perception, or the activity of an organ or an organelle.

[7] This notion of developmental change has interesting implications. At a first approximation, it does not seem to necessarily apply to growth, unless a change of size of the system, or of part of it, implies the realization of a new function instead of a change in the realization of function that is already available.

Developmental regulatory change on this picture is not necessarily irreversible.[8] Nor does it imply that development necessarily tends toward some future adult state. There are cases that contradict the idea of development as either an irreversible adult oriented process or the actualization of a potentiality (see Challenge 4 in Sect. 11.2). The "immortal jellyfish" *Turritopsis dohrnii* can return to the juvenile polyp stage from the adult medusa stage through the action of regulatory mechanisms that kick in as a response to adverse conditions or damage (Matsumoto et al., 2019). It does so while maintaining its multicellular organization, that is, without going through the whole life cycle and passing through a unicellular form. On our account of development, there is no conceptual problem in including cases in which changes are reversed, if these changes contribute to maintaining organizational closure. Therefore, an organizational approach to development can go beyond the biology of vertebrates and account for controversial cases such as rejuvenation or reverse development.

Adopting a regulatory framework to understand development also addresses issues such as the role of environmental factors. On some accounts, these factors are viewed as directly regulating development (Gilbert & Epel, 2015). On our view, what triggers developmental transitions is the sensing of environmental conditions by regulatory mechanisms and the consequent changes they trigger, not the direct action of the environment. We do not deny that environmental factors modify regulatory mechanisms. But even in these cases, environmental factors engage regulatory mechanisms which then bring forth developmental change.[9] Direct change from environmental causes, such as the loss of a limb to a predator or an accident, would not count as developmental.

Let us focus now on the third problem: identifying the boundaries of development. Regarding the starting point of development, some approaches, such as Minelli (2011), have questioned the idea that development begins with the egg (see Challenges 2 and 3 in Sect. 11.2). Reproduction can be also vegetative or occur via budding, that is, through a system that is already multicellular. However, Minelli's focus is centered on reproduction and so implicitly adopts the directional teleological framework underlying the adultocentrism that he criticizes. Accordingly, when he criticizes the identification of the adult as the end point of development, he does so on the grounds that some species of animals undergo reproduction before reaching the adult form (Minelli, 2011). This doesn't alleviate the problem. The adultocentrism is just a symptom; the real issue is the directional teleology that underlies it – reproduction as the goal of development.

[8] Many, if not most physiological and behavioral regulatory processes, are reversible, starting from the simple case of the *lac operon*. However, it is important not to confuse thermodynamic reversibility with regulatory reversibility (physiological, behavioral, developmental, etc.). In a nutshell, the reversibility of regulatory processes requires energy, so it is a thermodynamically irreversible process.

[9] The only partial exception would be molecular compounds, such as, for example, hormones, released by other organisms and capable to operate in the receiving organism as if they were some of its own regulatory mechanisms.

Our organizational account questions the idea that the egg is the starting point of development but does so on a different basis. The egg cell divides into several cells when it undergoes cleavage. But this is not the growth of a single developmental system because these cells do not realize an integrated multicellular organization but several distinct unicellular organizations. These cells do not communicate among themselves, do not realize division of labor, and therefore do not collectively realize closure. On our organizational view, development starts when cells come together to form one integrated multicellular system – one organism – that then undergoes changes regulated at the level of the whole. So one system, the egg cell, reproduces to form multiple connected unicellular systems that only later come together as a single system with organizational closure. To illustrate an alternative trajectory, sometimes the aggregate of individual cells splits into two independent developing systems, such as in the case of monozygotic (identical) twins. Development does not start with the egg but with integrated organization capable of regulation.

What are the requirements for realizing an integrated multicellular organization? One might say when cells start signaling to one another (Arnellos et al., 2014), but this is neither necessary nor sufficient. What is needed is functional and spatial differentiation and integration, that is, a differential contribution to the maintenance of the organization. For example, when the ECM (a noncellular constraint) is deposited, it contributes to the maintenance of the system by controlling cell differentiation and behavior, cell migration, and spatial differentiation and subsequently allows different *groups* of cells to emerge that perform different activities (see Bich et al., 2019). When these functional changes taking place within an integrated multicellular organization are directed by regulatory mechanisms, development starts. These organizations need not have parts that all have the same origin (see Challenge 7 in Sect. 11.2). In principle, they can be realized also by symbiotic associations such as lichens or biofilms insofar as they satisfy requirements for integration and regulation.

When does development end? Not necessarily with the achievement of the adult form (see Challenge 5 in Sect. 11.2). Adult organisms can still exhibit functional changes, and in some cases they can undergo phenomena such as rejuvenation (reverting to a previous stage) or regeneration (reestablishing a lost function). According to the organizational view that we propose in this paper, development ends when regulated changes to the number or types of functions no longer take place.[10]

In this respect, it is important to distinguish development from senescence. Senescence is a process of loss or decrease of functionality due to a change in the properties of components (such as the ECM; see Moreau et al., 2017) or of the overall organization of the system. While development might also produce a loss of functions, the difference is that in the case of senescence the loss of functions is not

[10] On this view, whether and when development actually ends is an empirical question and might have different answers for different species.

determined by the action of regulatory mechanisms. It is rather a question of whether and how functions are realized, and therefore it could be fruitfully addressed in relation to the organizational view of malfunctions (Saborido & Moreno, 2015).

11.5 Conclusions

In this chapter we showed that from an organizational perspective, development is a process of regulated change in number or types of functions of a regime of closure of constraints. It starts when a functionally integrated multicellular organization endowed with regulatory mechanisms is realized, and it ends when there are no further regulated changes in functions. It is a goal-oriented process, but a special one that is focused on the present, in which at each stage the goal is to maintain a viable organization of the system.[11] Development does not aim at a future goal state, and therefore there are no intermediate stages. Each stage of a life cycle is equally important from a point of view that is focused on the persistence of that life over the life cycle. The *telos* can be found in the actual developing system at any point during the entire process. This approach does not characterize living systems as the result of development, but the system undergoing development is already considered a self-maintaining organized biological system. With respect to environmental factors, the organizational approach can explain their role in relation to the internal logic of the system that undergoes a regulatory transition in the presence of these environmental conditions. There are still several challenges that an organizational approach needs to face. Some, not included among those discussed in Sect. 11.2, concern the range of developmental systems and phenomena. They include questions such as whether biofilms or ecological systems – to which some argue it may be possible to ascribe a closure of constraints (see Militello et al., 2021; Nunes-Neto et al., 2014, respectively) – can undergo development or not. A fundamental challenge among those mentioned in Sect. 11.2, which is still open, is related to the type of organisms taken into account to explain development. Most work has been focused on metazoa and specifically on vertebrates. Vertebrates along with many other animals have the advantage of being easily individuated, often exhibiting a straightforward developmental pathway. However, they constitute only a small portion of the multicellular systems which undergo development. Some steps have been taken in this direction in this chapter. However, a sufficiently general organizational account of development needs to be able to handle a wide range of multicellular systems and provide the tools needed to address problematic cases such as facultative multicellular systems with life cycles composed of alternating and

[11] Focusing on the present does not mean ignoring phenomena happening in the past. A system undergoing development is the result of a reproductive event and of a history of evolution. However, here we have been focusing on the developmental process itself. A direction for future work to expand this approach within the organizational framework is to integrate development with heredity (Mossio & Pontarotti, 2019).

distinct life stages (e.g., multicellular and unicellular; see Challenge 6 in Sect. 11.2). These more basic, yet no less complex, cases constitute an important sample of all multicellular systems and might play an important role for our understanding the origin of multicellularity and development. However, they have been primarily explored only from a historical and evolutionary perspective (van Gestel & Tarnita, 2017). We have addressed this challenge by expanding the range of examples analyzed to include some of these organisms, but there is much more to do. This is surely a necessary and interesting avenue to be pursued in future work on development.

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