

An Enactive-Developmental Systems Framing of Cognizing Systems

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Abstract

Organisms live not as discrete entities on which an independent environment acts, but as members of a reproductive lineage in an ongoing series of interactions between that lineage and a dynamic ecological niche. These interactions continuously shape both systems in a reciprocal manner, resulting in the emergence of reliably co-occurring configurations within and between both systems. The enactive approach to cognition describes this relationship as the structural coupling between an organism and its environment; similarly, Developmental Systems Theory emphasizes the reciprocal nature of structurally coupled systems in its analysis of organisms as developmental processes embedded within a developmental system. Through an enactive-developmental systems framing, this paper identifies the organizational features of cognizing systems in order to motivate a picture of how organism and environment co-determine and co-construct one another. I argue that organisms can be characterized as self-organizing, operationally closed, plastic systems ecologically embedded within a developmental system. In virtue of this organizational makeup, organisms actively engage in the modulation and assessment of their coupling with their environment: cognitive strategies that entail contextualized responses to variations across the web of interactions that comprises the developmental system.

1. Introduction

All organisms, from bacteria to trees to human beings, are situated in an environmental setting. Engaging in some form of activity to utilize resources within that setting is necessary for survival and maintenance. Yet this activity is highly specific—only some resources or properties of resources can be acted upon by only some organisms. The basis of this specificity can be said to lie predominantly in the history of interactions between an organism and its environment as well as between populations of organisms and their environments. Organisms live not as discrete entities on which an independent environment acts, but as members of a reproductive lineage in a continuous series of interactions between members of that lineage and a dynamic ecological niche. The series of interactions between members of a reproductive lineage and the influences within that lineage’s environmental setting continuously shape both systems in a reciprocal manner. Interactions of this kind result in the emergence of reliably co-occurring configurations within and between both systems.

According to the enactive approach to cognition (e.g., Varela, Thompson and Rosch 1991; Thompson 2007; Di Paolo, Buhrmann and Barandiaran 2017), this relation can be described as the *structural coupling* between an organism and its environment. A history of structural coupling specifies how an organism brings forth or “enacts” a world with a particular valence for that organism. Some resources are perceived as food, for example, in virtue of an organism’s capacity for sensing that such a resource affords nourishment. On this view, enaction is identified with cognition. An organism’s cognitive capacities, and thus the sort of activities it engages in, are the result of a specific history of structural coupling between features of the

environment and an organism's embodied action. Cognition is grounded in this coupling; cognitive capacities are "inextricably linked to histories that are *lived*, much like paths that exist only as they are laid down in walking" (Varela, Thompson and Rosch 1991, 205, original emphasis).

Developmental Systems Theory (DST) (e.g., Oyama 2000 [1985]; Oyama, Griffiths and Gray 2001) follows a complementary line of thinking in describing the organization of organisms as living systems. From a DST perspective, organisms can be defined as developmental processes—more precisely, life cycles (Griffiths and Hochman 2015)—embedded within a broader developmental system containing resources for the construction of a life cycle. Like the enactive approach, DST emphasizes the fundamentally reciprocal nature of organism and environment. The organism-environment system is not merely a dyad consisting of two discrete entities, but rather is a system comprised of dynamic processes that extend over many interwoven biological scales. This conceptualization of living systems rejects the commonly held view of organisms as relatively passive entities on which an independent environment acts. Instead, it motivates a picture on which an organism both actively shapes and is shaped by its environment, thereby playing a central role in its own development and evolution.

DST conceives of development and evolution as "processes of construction and reconstruction in which heterogeneous resources are contingently but more or less reliably reassembled for each life cycle" (Oyama, Griffiths and Gray 2001, 1). Through this shift in conceptualization of the organism-environment relationship, DST serves as a tool for reinterpreting key claims about biological systems. Its analysis of organism-environment

dynamics and multiscale explanatory mechanisms provides a more comprehensive and nuanced view of organismal development and evolution. It also points the way forward for how to structure new research questions and programs in light of such a view, including support for the integration of subfields (such as ‘ecological developmental biology–’ see Gilbert and Epel 2009).

This paper weaves together these two perspectives—the enactive approach to cognition and developmental systems theory—to provide a characterization of cognizing systems *qua* living systems. By drawing on theory from enactive cognitive science and developmental systems thinking, I aim to show how concepts from both areas can, upon integration, compose a rich account of the nature of cognizing systems (see Thompson 2007, 193 for a convergent view). An enactive-developmental systems framing illustrates how organisms and their environments co-construct one another. This relationship, I argue, entails that there is no strict separation to be made between organism and environment; rather, taken together, they comprise a developmental system. In ‘The organization of living systems’, I describe scientific and philosophical research on the conceptualization of organisms as developmental systems with a particular set of features. This characterization entails that organisms can be thought of as developmental processes themselves rather than discrete entities on which the environment acts. In ‘Plasticity as structural flexibility’, I suggest that this characterization illustrates how organisms are fundamentally plastic. As thermodynamically open systems situated in dynamic environments, organisms undergo changes via mechanisms of plasticity in order to maintain themselves in the face of perturbations and to persist over time. In ‘Acting on plasticity’, I

suggest that through plasticity, organisms alter both themselves and their environments through their dynamic interactions with elements within the developmental system. These interactions result in an emergent pattern of alterations (for both the organism and its environment). The concept of *structural modification* of the developmental system captures the process and effects of such active reshaping. I argue that modulation and assessment, as forms of structural modification, are cognitive strategies that bring about contextualized responses to variations across the web of interactions that comprises the broader developmental system. A key observation from this account is that structural modification can be thought of as forming the basis for cognitive acts. Through an enactive-developmental systems framing, this paper provides a conceptual framework on which we can understand and appreciate the deeply reciprocal nature of the organism-environment relationship.

2. The organization of living systems

It is standard practice to characterize living beings by the sort of things that they do. Living beings take in resources from the environment, convert those resources into energy, release waste products, produce new cells, move around in and respond to their environment, and reproduce by various means. This characterization tells us what kinds of activities all living things engage in. In studying living beings, we are also interested in how it is that they are able to engage in these kinds of activities. In other words, we might want to know: in virtue of what can living things take in resources, utilize them, and release them as waste? This is a question about the *organization* of living things. In order to understand what distinguishes living things from non-living things, we can investigate how they are organized such that they are able to do the sort of things by which we characterize them.

Some enactive theorists (e.g., Varela, Maturana and Uribe 1974; Maturana and Varela 1987; Varela, Thompson and Rosch 1991; Thompson 2007) claim that a defining feature of living things is a particular kind of *self-organization*. In this section, I introduce the enactive concepts of autopoiesis as self-organization and autonomy as operational closure to describe the organizational makeup of living things. I then integrate the enactive concept of structural coupling with the DST concept of a developmental system to show how systems organized in this way develop over individual life cycles. Additional concepts from the literature on self-organization and complexity science, namely autocatalysis and dissipative processes, provide a fuller picture of the self-organizing nature of living systems. Theoretical claims from DST describe how living beings, as particular kinds of self-organizing systems, undergo change and variation on developmental and behavioral timescales.

2.1. Organizational attributes of living systems

The term *autopoiesis* (from Greek *auto-*, self, and *poiesis*, production) refers to a system's capacity for maintaining itself as an entity persisting through time. Enactive theorists Humberto Maturana and Francisco Varela claimed that what defines living beings as their own class of entities is their continual self-producing, or autopoietic, nature (Maturana and Varela 1987, 43). On this view, the organizational pattern that living beings exhibit is one of self-production. Maturana and Varela refer to this pattern as *autopoietic organization*.

Autopoietic systems are specified as networks of processes where those processes are linked to one another by enabling relations. A system is classified as autopoietic when its processes form a network of continual, dynamic interactions and in doing so produces its own

components. Cell metabolism serves as a straightforward example of autopoietic organization. The chemical transformations that take place during cell metabolism constitute a dynamic, self-referential network of interactions that, in their activity, create a boundary for that network. An autopoietic system is thus a unity that undergoes dynamic, self-referential interactions (such as metabolism) while creating a boundary (such as the cell membrane) (Maturana and Varela 1987, 46). According to the enactive approach put forth by Maturana and Varela, this organizational pattern describes all living things, from individual cells to multicellular, complex life. Autopoiesis is central to an enactive understanding of life as it specifies the kind of organizational pattern that living beings exhibit.

In addition to being autopoietic unities, living beings are *autonomous*, or self-governing, unities. They are autonomous in virtue of their autopoietic organization: they continually produce themselves, and so are unities that exist as a result of their own internal processes. Maturana and Varela state that autopoiesis is the mechanism by which living beings are autonomous systems (Maturana and Varela 1987, 48). The relation between self-regulatory processes that comprise an organism's internal dynamics is captured in the enactive concept of *operational closure*. Operational closure describes the "network of processes whose activity produces and sustains the very elements that constitute the network" (Di Paolo et al. 2017, 112). Enabling relations between these processes serve as anchors for the system, ensuring the system's integrity. Because enabling relations effectively produce the network, the breakdown of an enabling relation will result in the network's disintegration.

Living systems take in material from the external environment and convert those resources into viable sources of energy, thereby maintaining the system's integrity. They are thus *thermodynamically open*: they actively exchange energy with their environments. This exchange highlights how living systems are in constant flux, with energy stores depleting and being restored continuously throughout their life cycles. Prigogine's analysis of living systems engaging in continuous cycling between dissipative states and structural states illustrates the effects of energy flow through the system (Prigogine 1980). A system is in a dissipative state if it is destabilizing in the absence of energy resources flowing into the system. Conversely, a system is in a structural state if it is regenerating as a result of an influx of energy resources. A system at a state of thermodynamic equilibrium, whereby there is no further exchange of energy, is stable. Living systems are, as highlighted above, in constant flux, and in self-maintenance continuously exchange resources between internal processes and external processes. Therefore, they cannot, operationally, persist at thermodynamic equilibrium. Living systems continuously cycle between dissipative and structural states, as new resources are taken in and used resources are expelled. Being far from thermodynamic equilibrium, dissipative states occur regularly in living systems as resources are exhausted through normal activity. A dissipating system is a failing system, however, and so living systems must continually work to replenish resources and keep from breaking down completely. Prigogine thus refers to organisms as a form of "dissipative structures" (Prigogine 1980).

One distinctive feature of organisms as dissipative structures is that they have the capacity for efficient regeneration in the constant face of dissipation. *Autocatalysis* describes a

type of chemical reaction that results from reaction products being utilized in the same catalytic reaction. DST proponents Weber and Depew (2001) note that this organizational pattern of chemical activity is tightly linked with the same system exhibiting a dissipative structure, and that it follows from the notion of self-organization as a kind of self-production that autocatalysis and dissipative states should be seen in living systems as self-organizing systems. Put concisely, if organisms are self-producing, whatever mechanisms they employ must enable them to maintain themselves far from thermodynamic equilibrium (where the system will fail). They are dissipative structures in virtue of their being thermodynamically open. And it is autocatalysis which serves as a way to efficiently maintain this organization.

To summarize: as dissipative, autocatalytic systems, living beings are in a constant state of flux. They maintain themselves as a unity in virtue of their organizational makeup, which can be conceived of as a complex network of interacting processes, with enabling relations between processes essential for the system's integrity. They are operationally closed in virtue of their capacity for generating and maintaining their own internal processes. At the same time, they are thermodynamically open, taking in resources from the environment and releasing consumed resources into the environment. These processes are repeated throughout the life cycle of the system, until a point when they can no longer operate sufficiently, and the system dissipates.

A similar account of the organization of living systems has been developed by Mossio and Moreno (2015), with a focus on the notion of the biological autonomy of such systems. In this paper, I will be exploring a complementary trajectory, but one that frames the question of the organization of cognizing systems qua living systems partly in the language and theorizing of

DST. This perspective, I suggest, directs our attention to the mutually enfolding, reciprocal nature of organism and environment. While there may be points of overlap along the way, my philosophical goal is to weave together insights from theories of enaction with those from DST in order to motivate a picture of organism and environment as co-determining one another. This paper is therefore framed with this motivation in mind. The next section sets this project in motion by developing a DST-guided position on autopoiesis and autonomy in the context of ontogeny.

2.2. Structural coupling over ontogenetic time

Organisms change as they develop, undergoing cell differentiation and maturation as a result of interaction between developmental resources over time. Organisms exhibit variation as well, with individual differences arising in members of the same population. Developmental Systems Theory (DST) (Oyama 2000; Oyama, Griffiths and Gray 2001) was formulated as a response to commonplace views on development that were seen as failing to capture the complexities and nuances of ontogenetic processes. Instead of viewing the organism as a template onto which genetic information is read out, DST conceives of organisms as developmental processes in themselves. As Weber and Depew note, DST's proponents describe organisms as "self-organizing processes rather than as discrete, hard entities on which 'forces' impinge" (Weber and Depew 2001, 242).

The broad web of interactions in which an organism is embedded is defined as a developmental system. A developmental system is comprised of a matrix of resources, processes, and interactions between developmental features (Griffiths and Hochman 2015) and includes the

organism itself. Each organism has a unique ontogenetic history as a result of the interactions of developmental resources both internal and external to the organism.

A unique ontogenetic history entails that no two organisms will be exactly the same; each organism has a distinctive structural makeup in virtue of its ontogenetic history. While organisms may differ in their structural makeup, they do share a common organizational makeup as autopoietic, autonomous systems. Maturana and Varela distinguish between *structure* as the individual formation of a living system and *organization* as specifying the types of relations necessary for a system to be classified as a particular kind of system (Maturana and Varela 1987, 47). For example, a keyboard's organization is specified by its capacity for typing, but whether the keyboard is made of plastic, metal, projected onto a surface, and so on, does not matter for its organization. Individual keyboards may differ in their structural (here, material) makeup, but fall under the same classification of 'keyboard'. In this sense, structure realizes organization; individual systems or entities are realizations of a particular kind of organization.

Differentiation in structure, on both a DST account and an enactive account, results from the innumerable dynamic interactions between organisms as living systems and the developmental systems in which they are ecologically embedded. Maturana and Varela define structural coupling as "a history of recurrent interactions leading to the structural congruence between two (or more) systems" (Maturana and Varela 1987, 75). An organism's ontogenetic history can be thought of as mapping onto a pattern of interactions between processes in a developmental system. Some of these interactions may be highly conserved, occurring with regular frequency. Maturana and Varela offer the example of the continuous active transport of

certain ions through a cell membrane such that the cells can in turn interact regularly with these ions (Maturana and Varela 1987, 76). The structure of each system is thus shaped by continued reciprocal interactions with the system(s) with which it is coupled.

Structural coupling scales up to the whole organism as well, and the concept can help to make sense of what both enactive theorists and proponents of DST mean when they talk about organisms and their environments being tightly interwoven. A species-typical ontogeny requires structural coupling between the organism and the developmental resources reliably recurrent for that species. Variation occurs when there are shifts in structural coupling. Shifts may be due to new resources entering the system (such as novel food types), extant resources being removed (such as loss of typical habitat), and differentiation in how individuals interact with resources (such as the implementation of tool use). Other sources of variation are possible as well, namely in terms of feedback effects accumulating from previous interactions. As Sultan (2015) points out, “[t]hrough these interactions, ontogeny becomes a Markovian process—a sequence of events where each determines the starting point for the next—in this case, a chain of complex feedbacks between the organism’s previous state and its current environmental experience” (Sultan 2015, 20). Variation can be understood in the context of the ongoing and perpetual cascade of interactions between the organism as a developmental process embedded within a web of developmental resources. Reliably recurrent patterns of interaction may initiate a new configuration of structural coupling between an environmental resource and an organism which

exploits it¹. Novel kinds of food resources, for example, may cause physiological shifts over an individual's lifetime, with the potential for more dramatic effects over evolutionary time if regularly exploited.

One way in which the enactive concept of structural coupling can shed light on the ontogenetic process is in specifying what constitutes an individual life cycle. An individual life cycle can be thought of as a temporal pattern in structural coupling between processes in a developmental system. These processes form a self-organizing network on a larger scale, with constant, dynamic interactions between developmental resources resulting in the formation of a complex, spatially-bound cluster of operationally closed interactions – an individual organism. While this conceptualization may be abstract, it highlights the fundamental processes that are at play in any ontogenetic cycle. Within a complex web of dynamic interactions between variable resources, an individual organism materializes as a locus of order, maintaining itself as a unity over time and dissipating only when met with significant perturbation from interacting forces within the developmental system.

In this section, I have outlined a first step in understanding the organization of cognizing systems by describing the organizational makeup of living systems. Enactive theorizing defines autopoiesis as a type of self-organization that captures how living systems maintain themselves as autonomous unities over time. Organisms, as living systems, are structurally coupled with

¹ Significant variation reoccurring in multiple generations, on which selection can then act, may result in evolutionary change. Similarly, new patterns of coupling (such as a new or drastic shift in ecological niche) can result in macroevolutionary change, such as in the case of speciation events. Conceiving of both organismal and environmental variation as being effects of shifts in structural coupling between those systems can help to make sense of the relationships between processes in each system. If a process in one is linked to a process in another, it may be possible to explain variation in one by pointing to variation in the other. Analyzing relationships of structural coupling can thus aid in understanding the mechanisms at play in the evolutionary effects of variation.

their environments such that an organism and its environment together form a complex web of dynamic interactions. The DST concept of a developmental system characterizes this web of interactions. Developmental systems are comprised of an organism as a kind of developmental process—specifically, a life cycle—and the developmental resources which construct that life cycle. With a picture in place of how living systems are organized, I next address how living systems have the capacity for undergoing alterations in structure in virtue of this organizational makeup.

3. Plasticity as structural flexibility

Organisms undergo structural changes as a result of multifarious interactions with developmental resources within the broader developmental system. In this way, they are structurally flexible, not following a linear ontogenetic path but rather developing through a dynamic constructive process. This *plasticity*² enables organisms to undergo change and variation in structure, in turn giving rise to both variability and stability of form and of traits (West-Eberhard 2003). In this section, I suggest that, in addition to the attributes identified in the previous section, this flexibility in structure captures how living systems are essentially plastic, actively constructing and reconstructing structural elements as a result of their dynamic interactions with their environments.

3.1. An array of possibilities

² West-Eberhard (2003) defines plasticity as environmental responsiveness. While a distinction can be made between adaptive and nonadaptive plasticity, West-Eberhard suggests a fitness-neutral description of plasticity is most practical (noting Schlichting and Pigliucci 1998). How fine-grained a definition is necessary will be context-dependent. Phenotypic traits that are plastic in nature, captured by the notion of phenotypic plasticity, enable an organism to respond differentially to environmental stimuli.

A plastic, non-linear system can undergo a wide array of structural alterations. A conceptualization of living systems as plastic invites a discussion of how such systems undergo both change and variation. The DST concept of an “array of possibilities” (Oyama 2000, 68)—a dynamic landscape upon which a wide variety of developmental trajectories may be taken as a life cycle progresses—can form the basis for this conceptualization. It is important to note that the proper locus of an array of possibilities is the developmental system, comprised of both the organism and its environment, rather than the organism alone. This is because possible trajectories are determined not solely by an organism’s genome but rather by the elements which constitute the developmental system. Griffiths and Hochman (2015) identify this landscape as a ‘matrix of developmental resources’. These resources constitute the materials needed to construct a life cycle (i.e., a living being) and extend beyond typical notions of what is required to do so (e.g., genetic material). Griffiths and Hochman (among other DST thinkers) emphasize that, contra commonly held notions regarding development and evolution, the matrix of developmental resources forms a wide range and includes factors and interactions that are underemphasized or overlooked in more traditional accounts.

Oyama introduces the notion of an array of possibilities in an analysis of Konrad Lorenz’s discussion of innate and learned behaviors as being both ultimately determined by innate genetic mechanisms. On Lorenz’s view, regardless of whether stimuli resulting in an adaptive response result from the organism or its environment, the organism’s genome must be structured in such a way to enable the development of such a response. In other words, only what is genetically possible can be actualized; whether or not a particular response is possible will depend on an

organism's genomic structure. Oyama, comparatively, stresses the importance of mutual selectivity between factors within the developmental system, noting that

The selection from the array of possibilities cannot be an exclusive function of the array itself. Nor, and this is an important point, can the array, the "potential", be strictly defined apart from the array of selecting influences ... A structured system selects its stimulus—indeed, defines it and sometimes produces it (the state of the system determines the kind and magnitude of stimulus that will be effective, and intrasystemic interactions may trigger further change)—and the stimulus selects the outcome (the system responds in one way rather than another, depending on the impinging influence). (Oyama 2000, 68)

An organism's genomic structure places constraints on what is developmentally possible, and so ontogenetic outcomes are in some sense contingent upon genetic architecture. What Oyama stresses, however, is that selective influences originate from the broader developmental system; the array of possibilities spans both organism and environment and thus spans developmental resources throughout both systems. The reciprocal selectivity between both illustrates the importance of the mutuality between influences in a developmental system. Selection of an influence is a function of the interactions within the entirety of the system.

Here I want to suggest that for a developmental system, movement through the dynamic array of possibilities is possible due to plasticity on behalf of the organism. Traits undergo structural alterations over developmental time as a result of movement through an array of possibilities within the matrix of developmental resources. A focus on plasticity as

movement through the array of possibilities emphasizes how developmental systems are in constant flux, with multifarious influences morphing the structural landscape over time. A rich understanding of organismal change and variation therefore requires an account of what allows for such change and variation, and plasticity is well suited for the role.

This picture of structural change is not to suggest that there are no “fixed” elements in organismal development, nor that such elements cannot arise. Indeed, rigidity of certain traits, captured by Waddington’s notion of canalization, is a key aspect of developmental regulation, defined as “the tendency for similar results to appear despite some variation in developmental conditions” (Oyama 2000, 109). The canalization of such traits illustrates a frequency measure of them, but not that they are predetermined. Rigidity of canalized traits reflects their developmental regularity. They are subject to constraints as any traits are, but they are identified by their tendency to produce the same or a similar outcome despite perturbations from these constraints. One way to conceive of developmental regularity is to consider the structural coupling relation identified with the canalized trait to be deeply entrenched—highly reliably recurrent over many cyclic iterations. While the system itself remains flexible, in that with enough pull from developmental influences they may be altered, high frequency, canalized traits should be expected to develop under typical conditions. They are “resistant to variation” (Oyama 2000, 110) but not impervious to it.

A similar way of conceptualizing resistance to variation is to consider it in the context of what Griffiths and Gray (1994) refer to as the ‘transgenerational stability’ of factors interacting within a developmental system. Organisms utilize resources across each resource domain

depending on a shared history of interaction and with regard to individual needs (further discussion on this in the following section). What is relevant for the sake of providing an explanation of this stability is identifying recurrent interactions between resources and multiple generations of organisms with the capacity to access and act on those resources (typically via sensory modalities). Variation arises when, for example, resources are utilized in a new manner, new resources are introduced or extant resources are removed, the relationship with resources is altered, or the timing of interaction with resources is altered.

Plasticity and flexibility, while both capturing the means by which organisms may change, are not identical phenomena.³ A plastic system is a system that can undergo alterations that in turn shape the structure of the system as a whole. General flexibility, on the other hand, refers to the capacity of a system to respond differentially to particular contexts. Plasticity is thus a process which occurs over a longer timescale, such as in the development from a neonate to an adult. The changes that occur over this timescale shape and direct the development of the individual, and in turn have lasting effects throughout the remainder of the individual's life. They mold the individual uniquely, depending on the particular set of interactions undertaken throughout development.

A developmental system is not merely comprised of an individual organism interacting with an environment over the course of its life cycle. Rather, it extends over both the organism as a developmental process and the developmental resources with which it is coupled such that interactions with those resources constitute a species-typical life cycle. Phenotypic traits that

³ I thank an anonymous reviewer for bringing this important distinction to my attention.

emerge on a consistent basis obtain stability through the recurrent interactions that are responsible for bringing them about. Importantly, transgenerational stability is dependent upon reliably consistent recurrent interactions; the dissipation of such a relationship would likely result in the dissipation, in turn, of the phenotype arising from that interaction.

3.2. Controls and constraints

Some type of constraint must be in place in order for phenotypes to form, as evidenced by the above discussion on loci of stability. Oyama outlines three ways in which *control* emerges as a result of the organization of developmental systems: through interaction, hierarchical levels, and time. Rather than thinking of genes as ultimately controlling developmental outcomes, DST specifies the interaction between elements across the developmental system, noting the context of the interaction, as being the locus of control. Oyama states:

Every developmental interaction, and therefore the entire norm of reaction, is jointly determined. To question the notion of genetic constraint or potential is not to deny limits to variability, flexibility, or adaptation. It is simply to give all developmental interactants comparable theoretical status, to recognize the importance of levels of structure above (and below) that of the genes, to insist that the significance of an interactant must be discovered by investigating the roles it plays in ongoing processes, and to point out that phenotypic potential cannot be said to be limited in any practical sense until we know what the limits of genotypic and environmental variation *and interactions* are. (Oyama 2000, 132, original emphasis)

Control also emerges as a result of the relationship between various interactions within sub-structures of the organism. Processes at the scale of the organs, for example, will be affected

by processes at the scale of the cells as well as processes at the scale of the whole organism. The extent to which certain processes maintain control over others will vary, with feedback between outcomes from interactions potentially generating greater variation.

Importantly, developmental systems have a history; life cycles are played out in a temporal context such that events preceding the enactment of a life cycle will impact elements of that life cycle. Phylogenies, in part, illustrate the temporal aspect to developmental systems by situating them historically. These histories are contingent upon factors across all scales, not merely major events. Small events may have generative effects if reconstructed reliably in each life cycle (Wimsatt 2001) just as large, constant events (for example, exposure to elements that comprise the wider environment) place conserved constraints on both development and evolution.

As Oyama centrally claims, studying differentiation as a function of variation in interactions over time dissolves concerns over whether genetics or the environment is responsible for a given trait, and “[u]nderstanding ontogeny thus becomes partly a matter of charting the shifts from one source of change (including intraorganismic processes) to another, as one interaction alters the developmental system in a way that provides transition to the next” (Oyama 2000, 161). This conceptualization motivates a view not of genes and environment as separate forces acting in distinct ways, nor simply the interaction between the two. Instead, the focus is on dynamic movement through the developmental state-space. This focus allows for comparison between developmental states at differing times, which can provide a clearer picture of how organisms undergo both change and variation over time.

In this section, I have discussed the impact that a capacity for plasticity has on living systems. Phenotypic traits can vary as a result of complex interactions between features of the developmental system. The developmental system encompasses both the organism as a developmental process and the resources within its niche that shape and are shaped by its development over time. Relatedly, traits can be stabilized through reliably recurrent interactions within the developmental system, and this stability can both control and constrain the structural makeup of a system.

4. Acting on plasticity

Through plasticity, an organism can undergo alterations in response to changes in conditions. This modification occurs over developmental, behavioral, and, for populations, evolutionary time. Interactions within the developmental system result in an emergent pattern of alterations. These alterations can be thought of as the *structural modification* of the developmental system. Organisms, as developmental processes themselves, undergo change in structure, as does their developmental niche, either as a result of organisms directly imposing alterations to their environments or as an indirect result of organismal activity. Relations between processes in the developmental system are thus subject to structural modification over time in a way that is significant for understanding the reciprocal nature of the organism-environment relationship.

There are two main methods of structural modification: *modulation* and *assessment*. Modulation is the active modification of the relations between coupled processes in a developmental system. Assessment refers to “adaptive switching between phenotypes” (West-

Eberhard 2003, 440). I argue that one way in which organisms cognitively engage with the world is through modulation and assessment. These forms of modification are cognitive strategies in response to fluctuations across the web of interactions that comprises the developmental system.

4.1. Modulating coupling with an environment

Recall that living systems can be thought of as self-producing systems that are operationally closed while remaining thermodynamically open. In this way, a living system maintains its organizational makeup while making adjustments in response to the flow of resources both into the system and out of the system. As enactive theorists Di Paolo et al. (2017) note, however, living systems do not merely passively exchange resources in the form of energy and materials. Rather, they make specific, context-dependent alterations based on the status of their metabolic needs at a particular time (see also Di Paolo 2005). One way to frame this is to suggest that the system has a particular manner of behaving such that it exhibits a type of agency—it acts so as to produce a particular effect. For Di Paolo et al., the goal in characterizing living systems in this way is to identify what makes this type of system an agent⁴. In order to describe how it is that living systems exhibit active evaluation of their conditions, it is necessary to describe the sort of organizational features they have that allow for such behavior.

On Di Paolo et al.'s account, organism and environment seem to stand in a symmetrical relation to one another, as one is co-determined by the other as a result of their structural coupling. They suggest that conceiving of an organism as an agential system, however, highlights a fundamental asymmetry between organism and environment. Agents behave in

⁴ While agency is not my focus here, the discussion is helpful for understanding the factors involved in the modulation of coupling with an environment.

response to a valenced aspect of the environment; organisms act on the environment in a self-interested manner, whereas the environment acts on organisms according to constraints but without this aspect of self-interestedness. Di Paolo et al. spell this distinction out further:

...acts have the property of being asymmetrical in terms of the relation between agent and environment. Because the idea of coupling is symmetrical, one way to introduce an asymmetry in it is to go one level up and propose that an agent is sometimes able to *modulate* its coupling with the environment (i.e., to modify the way its own processes and those of the environment relate). (Di Paolo et al. 2017, 117, my emphasis)

What Di Paolo et al. highlight is an organism's capacity for modulation as a way of relating to the environment in an active, responsive, self-interested manner. Modulation, then, is the way in which an organism modifies the relationship between its internal processes and environmental processes, or in other words, its coupling with its environment. By making these kinds of adjustments, organisms engage in structural modification in response to changing conditions both internally (within the organism) and externally (within its niche). As Di Paolo et al. note, not all modulation will result from organismal initiation, as some alterations will be necessitated by the environment. But as a general capacity of living systems, modulation is central in adequately responding to environmental changes across developmental, behavioral, and evolutionary timescales.

Modulation is also central in maintaining homeostasis in the face of environmental perturbations. Organisms with homeostatic physiology must maintain their internal environment in response to fluctuations within that environment and external forces responsible for variable

effects on the internal environment (Nijhout 2001, 138). Temperature regulation is one such example: behavioral thermogenic strategies include huddling together for warmth, actively seeking out warmer locations, or enhancing one's body with insulating material. Modulation of effects on thermoregulation processes can serve as an important adaptive strategy, especially in cases of survival in challenging environments.

4.2. Assessing environmental conditions

As a technical term, *assessment* refers to the evaluation of environmental circumstances that “occurs whenever a particular response correlates consistently with some environmental variable” (West-Eberhard 2003, 442). Environmental features, in the form of resources, conspecifics, predators, and so on, vary across niches, and organisms that engage in assessment of those features will vary in their responses to them. Selective responses are made when there is a “differential response to stimulus differences associated with the alternatives” (442). The evaluation of these stimulus differences, captured in the notion of assessment, is a way of initiating structural modification in virtue of the evaluative acts serving as action-guiding cues. Avoidance of a predator-inhabiting patch of forest, for example, might lead animals to seek out new and safer habitats. A novel habitat might bring along with it new developmental resources and therefore, over time, alter the structural coupling between a reproductive lineage and its broader developmental system. An alternative strategy might be to develop a suitable defense against said predators. A strategy such as this would have consequences for structural coupling as well, in that a novel capacity might, inadvertently or not, bring about novel ways of interacting

with environmental resources. The active assessment of these factors enables organisms to respond differentially and in turn develop adaptive strategies.

Di Paolo et al. also draw attention to the active modification of traits and behaviors in response to environmental conditions. They use the term *normativity* to refer to a system's modulation of interactions with respect to norms (Di Paolo et al. 2017, 120). Drawing on Merleau-Ponty (1963), they suggest that organisms have a suitable way of being and sustaining themselves in their environmental niche. Some actions are, in a sense, purposeful, such as searching through a sparse environment for food or singing to draw the attention of potential mates. According to Di Paolo et al., these actions have a biological normative dimension to them, and this sense of normativity fills out their account of agency⁵.

On West-Eberhard's account of assessment, normativity appears in the notion of adaptive switching between phenotypes. For example, *Daphnia* that evaluate predator-indicating chemical cues and modify their morphological structure to be able to defend themselves against potential predators make an adaptive switch in phenotypes. A bluehead wrasse (*Thalassoma bifasciatum*) male, rather than facing competition with other territorial males, can take on a smaller, female-like form, allowing them to intrude on occupied territories unnoticed (West-Eberhard 2003, 458). The selection of criteria in adaptive switching may occur with respect to individual organismal norms. Making an adaptive switch in morphological traits requires both the capacity for assessing environmental conditions and the capacity for initiating changes in form in response to those conditions.

⁵ The "joint conditions" of self-individuation, asymmetry, and normativity make up their full account of agency (Di Paolo et al. 2017, 120).

Bechtel and Bich (2021) suggest that the sort of activities organisms undertake in order to maintain viability displays their capacity for decision making, which is typically considered to be a key aspect of cognition. Therefore, even individual cells engaging in this type of behavior can be thought of as cognizers to some degree, providing support for the view that living systems are manifestly cognizing systems. While my focus here is not explicitly on agency or agential behaviors such as decision making, such views are complementary to the overall picture I am putting forth regarding the factors involved in the realization of such behaviors. Assessment and modulation provide a foundation for decision making in that they inform and guide behaviors and behavioral traits in light of changing conditions.

The set of developmental resources accessible throughout an individual life cycle fluctuates across time. Thus the organism's developmental niche, while perhaps more stable at coarse-grained scales with regard to some environmental features, is likely to fluctuate at the scale of individual organismal activity. In order to cope with a dynamic environment, an organism acts on plasticity by modulating the relationships within the developmental matrix via assessment and modification. Because an organism *qua* developmental process is ecologically embedded in within a developmental system, the changes it makes can initiate additional changes in that system; feedback loops between components of the system warrant that a change in one place can potentially initiate changes at many other places. To put the relationship more concretely, examples from niche construction theory (Odling-Smee, Laland and Feldman 2003) illustrate how this structural coupling can be enacted. Through continued interactions with their niches, organisms shape and are shaped by the niches they inhabit. The reciprocal nature of this

interaction is mirrored in the analysis of the relationship between processes within a developmental system.

5. Life and cognition

Modulation and assessment, as methods by which structural modification occurs, are cognitive strategies undertaken by organisms. A central focus of the enactive approach to cognition is on the notion that organisms enact a world through active engagement with the environment, where patterns of engagement are constructed through recurrent interactions between elements of, to borrow from DST language, the developmental system. Similarly, from a DST perspective, an organism's ontogeny is the result of these interactions; individual life cycles are (re)constructed through an organism's activity within the developmental system.

Enaction — the active construction of an organism-specific world, and the activity in which cognition is grounded — happens in part through modulation and assessment as forms of structural modification, which, I have argued, is possible in virtue of the organizational makeup of living beings. Structural modification can thus be thought of as forming the basis for cognitive acts, as it is the result of organismal activity within a developmental system. In this way, life and cognition are bound up in one another; through the act of living, organisms engage in cognitive activity, an insight enactive theorists refer to as the 'continuity between life and mind' (Thompson 2004). Living systems are cognizing systems in virtue of such a continuity.

The deep continuity between life and mind requires a theoretical framework furnished with the tools necessary for investigating both phenomena. While the enactive approach has its roots in biological theory (see early work by Maturana and Varela, both of whom were

biologists), its focus is more so on characterizing mind and cognition than on biological systems *per se*. Similarly, DST was initially developed by Oyama partly in reaction to the nature-nurture debate and views endorsing genetic determinism in biology; while DST perspectives certainly have implications for understanding cognition, the issues such perspectives have addressed have typically been situated within evolutionary and developmental biology. The integration of concepts from each theory is necessary in order to elucidate the structural and organizational features of living systems *qua* cognizing systems. That said, their divergence in origins invites the question of in what ways these two theories may importantly differ, and precisely on what grounds they may enhance one another. As Oyama (2009) notes, theories may be friends (in that they share a common cause), or they may be merely neighbors—sharers of a boundary, but with no obligation to build closer relations. Complementarity is a starting point, but closer analysis is needed if the theories are to be successfully integrated.

As discussed in Section 4.1, some enactive theorists have argued for a fundamental asymmetry between organisms as *agents* and their environments. This asymmetry is necessary in order to make sense of how organisms respond differentially in the modulation of their coupling with the environment—in other words, what is entailed in organismal agency. Yet within DST, no causal primacy is given to the individual organism in its shaping of the interactions within the developmental niche. It is on this point where I believe there is the most divergence between the enactive approach and DST, and thus the greatest need for further analysis. An asymmetric relation between organism and environment highlights a potential tension in terms of boundaries: what, if any, distinctions we might draw between “internal” and “external” factors. Drawing a particular boundary may also have implications for what is considered the unit of evolution. Is it

the individual organism, or the broader developmental system? Lastly, especially for thinking about the nature of mind and mental phenomena, boundaries drawn farther away from the individual organism may have fairly radical implications for the mind. Views in 4E (embodied, embedded, enactive, extended) cognition posit that mental activity does not occur solely within the head (or brain). While 4E views differ in their commitments (and the degree of radicalness of their commitments), it may be easier to accept a picture of an organism being fundamentally intertwined with its environmental milieu than one of the mind being fundamentally intertwined with the environment. Arguably, there is thus more at stake for the enactive theorist, and a stronger impetus to provide a persuasive characterization of organisms as systems unified by their autopoietic organization, while still being thought of as fundamentally embedded within a developmental system. These kinds of boundaries may be drawn spatially (as in the example of a cell, through its autopoietic activity, constructing its own surrounding membrane), but this may be unsatisfying to some DST thinkers, coming too close to privileging internal factors.

While I have drawn on several DST perspectives in the constructing of this framing, it is important to note that there is not a single unified DST view (see Oyama 2009 for discussion). There is thus a question of which kind of DST approach may work best with the enactive approach. Given that the identification of autopoietic unities is a central aspect of the enactive approach, a DST position which builds on that account would be profitable. I have found Weber and Depew's focus on self-organization especially helpful here; other DST views that build on an account of organismic individuation, such as those of Griffiths and Gray, are also helpful in identifying developmental entities.

Both the enactive approach and DST have important implications for evolutionary theory. While I have here predominantly addressed phenomena at developmental and behavioral timescales, both perspectives argue for a reconceptualization of natural selection (see Thompson 2007, chapter 7; Oyama 2000, chapter 7). An enactive approach to evolution remains lamentably underexplored in the recent literature (but see Gallagher 2017, chapter 9), despite the approach's biological origins. A shared view could contribute valuable theoretical posits for current debates regarding the explanatory structure of evolutionary theory.

Despite their differing starting points, the enactive approach and DST share several fundamental commitments. The strongest point of convergence is on the deeply interwoven nature of organism and environment. Both the enactive approach and DST argue for no strict separation between organism and environment. As Thompson notes:

Developmental systems theory offers one of the most radical rejections of the separation of organism and environment. If the unit of evolution is the developmental system, and if inherited developmental resources include not only endogenous elements ... but also structured exogenous environments—environments structured into viable niches by the organisms themselves—then there is no basis for thinking that the environment is independent of the organism. On the contrary, organism and environment construct each other in development and evolution ... This co-determination of organism and environment is central to the concept of enaction. (Thompson 2007, 203-204).

Both theories reject a view of the environment as an external, independent realm of problems posed to organisms. For enactive and DST thinkers alike, the world is not pre-given: it is co-determined, co-constructed in the acting out of life cycles. The epistemic gain from a

shared enactive-DST perspective is thus that of a comprehensive theoretical understanding of how organisms and environments are mutually unfolded and enfolded structures (Oyama 2000, 199).

6. Concluding remarks

I began by working through what I take to be the organizational features of living systems. I then discussed the kinds of mechanisms that plasticity affords so as to bring about both variability and stability. This work serves as a basis for a discussion of specific forms of structural modification as cognitive strategies. Through their embodied activity, organisms shape and reshape the coupling relations between themselves and their environments. Modulation and assessment can be thought of as ways of responding to environmental variation. And it is the structure of the developmental system, comprised of an organism as a life cycle and the developmental resources which (re)construct that life cycle, which is modified as a result.

To be clear, I am not making any deeper claims about how to define cognition itself. Definitional claims about cognition, including those concerning the evolution of cognition itself, are outside the scope of this paper (but see Griffiths and Stotz 2000 for a discussion on convergences between DST and embodied cognitive science for the purposes of characterizing cognition). Rather, my more narrow goal is to identify the types of configurations that enable organisms to engage in the sort of behavior I am referring to as cognitive strategizing.

Differences in capacity for modulation and assessment can offer a starting point for drawing out distinctions in capacity for cognitive functioning. Being more structurally flexible and able to assess more conditions (perhaps by way of multiple sensory modalities, or

multimodal perceptual capacity) may lead to more complex cognitive ability. At the same time, being embedded within a richer (i.e., more complex or multivariate) developmental system may require greater responsiveness, and thus more complex cognitive functioning. This framing can serve as a fruitful way of understanding the complexity of human cognition in particular. Laland, Boogert, and Evans (2014) offer similar remarks on the immeasurable complexity of the human socio-cultural niche and the tremendous extent to which humans engage in various forms of niche construction. Complexity in environment arguably invites complexity in cognitive functioning, as evidenced by further discussions on cognitive scaffolding (Sterelny 2010). The complexity of these aspects can be investigated as a function of the contingent relations of an organism ecologically embedded within a developmental system.

My broader philosophical hope is to have shown that the weaving together of enactive theorizing and DST thinking is a fruitful project for understanding the nature of mind and life. To begin with, it provides us with a conceptual framework on which we can both understand and appreciate the reciprocal nature of the organism-environment relationship. It enables us to see how there is no strict separation to be made between organism and environment: each co-determines and co-constructs the other. This focus reveals valuable insights about the organizational makeup of living systems and the sort of features that identify them as cognizing systems. As raised by Thompson (2007) and Oyama (2011), there is a natural affinity between enactive cognitive science and DST, and their integration is worth investigating further. A project of this kind serves to direct our attention away from a gene-centered view of development and evolution and toward a view of organismal life that both shapes and is shaped by the environment (Sultan 2015; see also Jablonka and Lamb 2014; Laland et al. 2015). Similarly for

cognitive science, it supports a non-representational view of cognition whereby living beings themselves enact their own viable niches, rather than cognition being a matter of the representation of an independent, external environment.

One area for further analysis might be what account of agency the framework that I have proposed entails. In thinking about organisms as agents, highlighting the ways in which they are self-producing, operationally closed systems with the capacity for dynamic structural modification of their coupling with their environments helps in identifying what is fundamental to organisms as living beings, and what distinguishes organisms as agents. In addition to picking out these features as being facets of agency, a related claim can be made about them also being facets of cognition. The concepts of modulation and assessment are arguably key to understanding cognition, as they are ways in which living systems dynamically respond to variable conditions. Active regulation and response is the product of self-organization, operational closure, and plasticity in turn affording structural modification. Cognition emerges as a result of the architectural makeup of these types of systems. It is enacted in the reconstruction of each life cycle.

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