The Organism in Developmental Systems Theory

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Abstract

In this article, I address the question of what Developmental Systems Theory (DST) aims at explaining. I distinguish two lines of thought in DST, one that deals specifically with development and tries to explain the development of the individual organism, and the other that presents itself as a reconceptualization of evolution and tries to explain the evolution of populations of developmental systems (organism–environment units). I emphasize that, despite the claim of the contrary by DST proponents, there are two very different definitions of the "developmental system," and therefore DST is not a unified theory of evolution and development. I show that DST loses the most interesting aspects of its reconceptualization of development when it tries to reconceptualize evolutionary theory. I suggest that DST is about development per se, and that it fails at offering a new view on evolution.

From a general perspective, what does Developmental Systems Theory (DST) seek to explain? While being very sympathetic to DST, one can see a tension here. The problem can be expressed in this way: Is DST's aim to explain the characteristics of the individual organism? Or, in more concrete terms, and following the example taken by Griffiths and Gray (1994), should DST explain *both* Griffiths's having a thumb on each hand and his having a scar on his left hand? The DST proponents have given two strongly different answers to this question. One choice within DST, best illustrated by Oyama's *Ontogeny of Information* ([1985] 2000a), is to answer that DST's aim is indeed to explain the characteristics of the individual organism. The second choice within DST, which appears in Oyama's *Evolution's Eye* (2000b: 28–29), but is best illustrated in several papers by Griffiths and Gray (1994, 1997, 2001, 2004), is to answer that the first aim of DST is to explain not the characteristics of the individual organism but the coevolution of organisms and their environments (that is, evolution of organism–environments, or Œs, the symbol proposed by Griffiths and Gray 2001—discussed further below—for evolution of developmental systems or DSs).

In this article, I present these two answers, and then try to show that with the second one both the uniqueness and the unity of the organism are lost. I claim that the adoption of this second answer leads to the loss of the main conceptual gains of the first, without being compensated by a true profit in the reconceptualization of evolution by natural selection. I conclude that DST is a radically new vision of development, but not of evolution by natural selection.

First Answer: The Characteristics of the Individual Organism as the Explanandum of DST

Explaining Individual Characteristics

According to this first answer—best expressed by Oyama ([1985] 2000a), but that also appears in Lewontin's writings on development (1994, 2000a, 2000b),[1] in Gottlieb (1992),[2] and in some texts by Griffiths and Gray[3]—the general task of the biologist involved in developmental issues is to account for the construction of the characteristics of an individual organism throughout its life. In other words, it is to account for the individual development (individual ontogeny) of an organism, with the idea that development lasts from conception to death. Here (and throughout this article), *individuality* must not be confused with *uniqueness*: an individual organism is *one* (isolable) organism,[4] characterized by both common (sometimes species-typical) and unique traits. According to the first answer we are examining now, biologists should account *both* for the unique traits of an organism and for the traits that it shares with others. Oyama ([1985] 2000a: 137) quotes Lewontin (1983: 27) on this matter: "[developmental biologists are]

so fascinated with how an egg turns into a chicken that they have ignored the critical fact that every egg turns into a different chicken and that each chicken's right side is different in an unpredictable way from its left."[5]

In this first answer, the stress is put on the development of the individual organism. Indeed, the expected influence on biology is a reconceptualization of development. The developmental point of view comes first, even though, secondarily, it can have consequences on evolutionary issues.[6]

The explanandum, then, is the characteristics of the individual organism. The explanans is the *individual* DS. What does the individual DS contain? It is an *epistemological* notion: it contains all the resources that *explain* why this organism is as it is. The consequence is that explaining the individual traits of an organism implies taking into account many things, i.e., all the "developmental resources" that contribute to explaining the characteristics of this individual organism. As we see, this epistemologically defined DS is quite big.

However, isn't it *too* big? Indeed, it seems that the DS includes many resources (all those that are relevant to explain the characteristics of the individual organism), and therefore, possibly, too many resources. For example, to take up again the example of Griffiths and Gray (1994), is the scar on Griffiths' left hand part of his DS? Precisely because the DS contains all the resources that *explain* why this organism is as it is, within this first answer, Griffiths' scar is to be explained. The DS accounts for *ontogenetical individuality*.[7] So, the "surgeon's knife," which Griffiths and Gray exclude from the DS, is in fact part of it, because it is an explanation of an individual trait—which happens to be unique. Similarly, though Sterelny et al. (1996) tend to make fun of this idea, in this first strategy, Elvis Presley is clearly part of Dickison's DS, because Presley is one of the resources that explains why Dickison is like he is (let's say, a rock-music fan). The fact that the DS is big is not a problem, for two reasons. First, in this first option, there is no ontology of the DSs, contrary to what we will see with the second option. The DS is epistemologically, and not ontologically, defined. In other words, the DS is indeed huge, with many resources overlapping with other DSs, but the size of the DS is not a problem because the biological entity is the *organism*, not the DS itself. What develops are organisms and what evolves are populations of organisms. Second, it should be clear that in this first option DST does not state that the task of each biologist is to explain *all* the individual traits of *all* organisms. The DST people are much more down-to-earth than is usually stated: they consider that a biologist starts with a well-defined question. For example, her question can be the following: Why does this particular fly have eyes with many facets? She will not need to resort to all resources to explain what she seeks to explain: she will choose what is relevant. Thus, we cannot say that there is an epistemological problem with the size of the DS.

Aim of This First Option: A Reconceptualization of Developmental Causality

The aim of this first option is to reconceptualize the causality of development. Here, the enemies of DST are genetic determinism,[8] internalism, and preformationism.[9] As Godfrey-Smith (2000, 2001) showed, the best way to define DST is to present it as a strong anti-preformationism. He also clearly demonstrates that the reconceptualization of developmental causality is a key element of DST, as is obvious in Oyama ([1985] 2000a). Here are the key points of the reconceptualization of developmental causality that she offers (followed by Griffiths and Gray, and others), hierarchically organized from the most to the least generally admitted by biologists:

1. Genes do not play a central, and not even a privileged, role in development (that is, genes are not controllers of development).
2. Factors that play a role in development are not separate channels; they become causally relevant only by their interaction.
3. The nature/nurture dichotomy should be got rid of.

In order to show how strong and original these points are, I would like to contrast what the DST proponents say with what someone as sympathetic to DST views as Godfrey-Smith (2001) explains. After conceding that genes do not code for phenotypic traits, he claims that genes certainly code for proteins (and that proteins make a critical contribution to the characteristics of an individual organism). However, here, DST makes, I think, a strong point, by refusing this claim. For DST, genes are only *necessary conditions* (among others) for the synthesis of an organism's proteins. First this implies that there are (many) other necessary conditions; and second that even if material DNA (i.e., some material "stuff") is present in the egg cell, the *causal* power of DNA[10] in development only arises through the interactions with other factors. A very simple (but very convincing) example is the demethylation of some parts of DNA according to the local environment of the cell (e.g., Reik 2007). According to this environment, proteins "choose" which genes will be activated. This is the crux of the matter in Oyama's demonstration: *things* are "already here" in a sense (genetic things, but also other things—that is, all the developmental resources upon which the DS depends), but these things become *information*[11] only through the interactions of many different elements. In other words, nothing becomes a developmental cause without interacting with other interactants. It is a point that is much more original and much stronger than is usually thought. The consequences are that as there is no "nature," there is no nature/nurture dichotomy as usually conceived. This thesis has enormous developmental implications,

as well as important social and political implications (see in particular Oyama [1985] 2000a, 2009a).

Second Answer: The Coevolution of Organisms and Their Environments as the Explanandum of DST

Explaining the Evolution of Organisms and Their Environments

The people involved in this second answer are mainly Griffiths and Gray, but also, as we said, Oyama in some texts (2000b: 28–29, 44–76). Two important sources are Lewontin on co-construction (1978, 1994, 2000a) and Odling-Smee et al. (2003) on niche construction. In this second option, the enemies of DST are genic selectionism and all forms of externalism (usually under the metaphor of "adaptationism"[12]). Since Griffiths and Gray mainly illustrate this option, I will focus here on their writings.

According to the second answer, what DST seeks to explain is not the characteristics of the individual organism any more, but the coevolution of organisms and their environments. In other words, the explanandum is the coevolution of organisms and their environments, that is, the evolution of populations of Œs (an Œ is a unit made by the organism and its environment), or the evolution of populations of evolutionary DSs. The explanans is a historical-adaptive explanation (Griffiths and Gray 1994).[13]

What is an evolutionary DS? It is "the resources that produce the developmental outcomes that are stably replicated in that lineage" (Griffiths and Gray 1994: 278).[14] So the developmental resources that explain the traits an organism has but its descendants do not have are *not* part of the evolutionary DS. The evolutionary DS is obtained by *abstraction* from the individual DS[15]: "In evolutionary terms the DS contains all those features which reliably recur in each generation and which help to reconstruct the normal life cycle of the evolving lineage."[16] The result is an "idealized DS of a particular lineage" (Griffiths and Gray 2001: 207).[17]

Aim of This Second Option: A Reconceptualization of Evolution

The aim of this second option is to build an entire reconceptualization of evolutionary theory. It implies a redefinition of key evolutionary concepts and evolutionary individuals.[18] According to Griffiths and Gray (1994: 304), evolution should be redefined as "the differential replication of developmental processes/life cycles." In Griffiths and Gray (2001: 207), they suggest, "evolution is change in the nature of populations of DSs." Thus, in the second option, the DS becomes the *explanandum*; it is not anymore the *explanans* of DST.

Table 1. Summary of the differences between the two views of the aims of DST.

Strategies	Individual DS	Evolutionary DS
Explanandum	Traits of an individual organism	Coevolution of O and E (= evolution of populations of DSs).
Explanans	Developmental system	Historical-adaptive explanations.
People	Mainly Oyama	Mainly Griffiths and Gray.
Sources	Gottlieb, Lewontin on development, etc.	Lewontin against adaptation; Odling-Smee et al. (2003) etc.
Enemies	Preformationism, internalism, genetic determinism	Genic selectionism, all forms of externalism.
Biological entities	Organisms	Developmental systems.

Consequence: Two Different Definitions of the "Developmental System"

The evolutionary DS is clearly different from DS as defined in the first option. Indeed, from this evolutionary DS, Griffiths and Gray (1994) explicitly exclude Griffiths's scar—or, to be more accurate, they exclude from the evolutionary DS the *interactions* that produced Griffith's scar, because there is no evolutionary explanation of this scar, for the scar is not stably replicated in the lineage (p. 286). Griffiths and Gray themselves contrast this DS definition with the individual DS: "The DS of an individual organism contains all the unique events that are responsible for individual differences, deformities, and so forth" (Griffiths and Gray 2004: 420). For their part, by "individual," they mean idiosyncratic, unique (e.g., p. 286—"The scar is an individual trait"), contrary, then, to the definition I have adopted in this article. They further write: "For other explanatory purposes, such as the study of developmental abnormalities, a different system must be delineated" (p. 287).

Thus, we do have *two* DSs:

- The individual DS, that is, all the resources that explain why this organism is as it is (with *both* unique and common traits). It is the DS as Oyama ([1985] 2000a) has defined it.
- The evolutionary DS, that is, all the resources that produce the developmental outcomes that are stably replicated in that lineage. It is the DS as Griffiths and Gray (especially 1994, 1997) define it.

It is noteworthy that Oyama admits that there are two possible definitions of the DS, and that the preferable one is the individual one, *even when evolutionary questions are being asked*. See Oyama ([1985] 2000a: 141, in the section called "DS in ontogeny and phylogeny")[19]:

. . . but to restrict the term [system] to species-typical developmental pathways and structures would defeat the purpose of the conceptual organization being attempted here. . . . Scientists are usually interested in common and/or enduring interactional networks, but one might want to investigate rare or transient ones as well. A unique historical sequence or an individual life may be worth our attention.[20]

Table 1 sums up the differences between the two answers that we have examined.

The Loss of Two Key Aspects in the Second Answer

Adopting the second option (that of the evolutionary DS) leads to the loss of two key aspects of the first option:

- The loss of the uniqueness of the organism: In the second answer, one must explain the maintaining of biological forms through time, of course with some minor variations,[21] and to do so one must isolate among developmental resources those (and only those) "whose presence in each generation is responsible for the characteristics that are stably replicated in that lineage" (Griffiths and Gray 1994: 286).
- The loss of the unity of the organism: One loses the idea that it is the organism which evolves when one says that it is the organism-environment, or O-E, system which evolves, i.e., the DS (or the life cycle). The DS fuses the organism and the environment. Indeed, Griffiths and Gray claim that there is no meaningful distinction between the organism and the environment: "Perhaps the most radical departure [from the classical evolutionary theory] is that the separation of organism and environment is called into question" (1994: 300). Griffiths and Gray are even clearer in two later texts. In 2001 (p. 207), they suggest using the symbol "Œ" in models of evolution, and write as follows: "We claim that there is no distinction between organism and environment." The same idea also appears elsewhere in Griffiths and Gray (2004: 11–12, section "Fitness and adaptation"). This loss of the unity of the organism is related to what I take as an implicit aim of Griffiths and Gray, that is, an ontological revision about the living world. Here, there is a parallel with Richard Dawkins.[22] As Dawkins says that the biological world is better seen as made, not of organisms, but of genes having extended phenotypes; Griffiths and Gray say that the biological world is better seen as made, not of organisms, but of DSs. If one follows their demonstration, the organism is not a theoretically justified entity. Gray (1992: 199) strongly emphasizes that his view is not a "return to the organism." It contrasts with Bateson (2005) and, even more

importantly, with Oyama (2000b: 30–31): at the very moment when she defines DSs in evolution, she explains that her aim is to "put the organisms back" in evolution, and to "restore the organism."

Now, one may ask, what is the problem? After all, isn't it natural that the unique traits of the individual organism are lost, and that the organism itself tends to disappear as the main biologically relevant unit, since we are talking about evolution? The problem is that this issue about the role of the organism in DST that I have analyzed here shows that there is no unitary DST because we have different *explananda* in the two different strategies. In recent writings, Griffiths and Gray (2004) have claimed[23] that there is only *one* DS, but in fact there are two very different DSs, doing very different things. This very fact challenges the claim made by the DST proponents that they have offered an *articulation* of development and evolution or "a general account of development and evolution" (Griffiths and Gray 1994: 278). If the view presented here is correct, then DST has not (yet) completed an original "evo-devo" program,[24] because the individual DS and the evolutionary DS receive strongly different definitions. It is noteworthy that in recent conversations and a paper Oyama (2009b) admits that there is a gap between the two different strategies within DST.

What exactly is lost in the second option, the one represented by Griffiths and Gray? The loss of the individual organism is in fact the loss of key aspects of development: as the first option shows, the biologist (especially the developmental biologist) must explain the traits of individual organisms because all organisms are different, especially—but not exclusively—those that sexually reproduce (see Lewontin's quotations above). It is what research on developmental noise (see Lewontin 2000a) and phenotypic plasticity (West-Eberhard 2003) shows. In fact, we could claim that very few "characteristics" or "outcomes" are stably replicated in one lineage. Of course, they may be very important from the point of view of natural selection, but my claim is that so few resources involved in individual development are stably replicated that, with such a definition of the DS, most of the development (as understood in the first answer) is lost.

Moreover, the vast majority of examples used by the DST proponents (both Griffiths and Gray, and Oyama) to justify their thesis about an "extended inheritance" are problematic from the point of view of evolution by natural selection. Many (e.g., antibodies transmitted from mother to child; cell membranes; most cytoplasmic elements—but not mitochondria, of course) are transmitted over only one generation, which will not be sufficiently significant for a lineage explanation. For other resources, the DST proponents speak of a "stable replication" or "reoccurrence." However, it is certainly not true that "reoccurrence" is sufficient for evolution by natural selection to occur. For example, if there is no differential fitness con-

cerning the trait under consideration, as seems to be the case with gravity or sunlight (see, e.g., Griffiths and Gray 2001), then no selection occurs. In other words, if one follows the traditional "recipe" for evolution by natural selection (variation, heritability, differential fitness, as in Lewontin 1970, or, more specifically, in Lewontin 1985), it is clear that many resources important for *development* will not be a part of an *evolutionary* explanation.

The consequence of all that has been said here is that the evolutionary DS has lost the great majority of its developmental characteristics: it has lost not only its unique traits but also traits that are certainly important for survival, and are not inherited and associated with differential fitness. Thus, contrary to what the DST proponents claim, they have not offered a theory that succeeds in *articulating* development and evolution.

Two points follow from what has been said here:

1. We really have two very different definitions of the DS.
2. The second DS has lost most of its developmental traits.

Therefore, I think that, thanks to the analysis of these two different definitions of the DS, the unity of DST is lost, or at least deeply threatened.

Conclusion

Developmental Systems Theory is a radically new vision of development, but not a fruitful reconceptualization of evolution by natural selection. Griffiths and Gray say that they want to "bring out the radical implications of the new approach to development for the theory of evolution" (1994: 278), but I do not think they succeeded in doing so. If the argument developed here is correct, DST is a fascinating and very productive account of development, centered on the individual organism—and, again, I want to insist that this view is expressed both by Oyama and in some of Griffiths and Gray's texts. I believe that what the DST proponents suggest about development is fascinating and that *it is enough*, and therefore need not offer in addition to that a reconceptualization of evolution.

Acknowledgments

Notes

1. Though Lewontin is a population geneticist, many of his points are about development, and more precisely about our understanding of what causes *this* development in *this* organism (Lewontin 1994, 2000a, 2000b).

2. Lewontin and Gottlieb are two of the major authors cited by the DST proponents.

3. For example, the section "Taking development seriously" in Griffiths and Gray (1994), as well as many arguments given by Gray (1992, 2001).

4. As difficult as delineating the organism may be, on this question (which is different from that of delineating the developmental system), see Oyama (2006) and Pradeu (2010).

5. Same idea in Lewontin (1994: 11): "Developmental biologists concentrate on the question of how lions give rise to lions and lambs give rise to lambs, but they never ask the question, 'Why are all lambs not identical?' "

6. In fact, Oyama started with the nature/nurture question, which led her to developmental issues, and subsequently to evolutionary issues.

7. This, again, includes both unique and common characteristics.

8. The term "genocentrism," though widely used, should be avoided: it can refer both to genetic determinism and to genic selectionism. These two ideas, though they sometimes are coexistent in one mind or book, are logically very different.

9. This definitely does not imply that DST proponents argue in favor of an environmental determination of individual characteristics: they reject all forms of simple determinism. Nevertheless, the view against which they struggle the most is genetic determinism.

10. Or "genes" in an informational (not material) sense.

11. Since the DST proponents are often suspicious about the notion of "information," it is probably more accurate to say, "things become causally relevant" or "play a causal role." Contrary to what Godfrey-Smith (2001) says, I think Oyama's argumentation is: (i) I don't really like informational language, and (ii) if you really want to talk about information, then you cannot consider genes as the only source of information in the construction of the individual organism.

12. Lewontin (1978); Gould and Lewontin (1979). Instead of "adaptation," the appropriate metaphor is said to be "construction" (Lewontin 1978; Odling-Smee et al. 2003). This influence is acknowledged, for example, in Griffiths and Gray (2005).

13. An "etiological solution" (Griffiths and Gray 1994: 278), and "adaptive-historical explanation" (p. 287).

14. The same idea appears in Griffiths and Gray (2001): "All the resources which produce those developmental outcomes that are reliably reproduced in a lineage."

15. "Just as a traditional model of evolution abstracts away from the unique features of individual phenotypes," as Griffiths and Gray say (2001: 207).

16. Note that "contains" differs from "is." The question is, does it contain only that, or more than that?

17. Word for word the same idea is expressed in Griffiths and Gray (2004: 12).

18. See Griffiths and Gray (1994: 300): "Taking developmental processes, rather than genes or traditional phenotypes, to be units of evolution requires a substantial reformulation of evolutionary theory." See also the last two pages of Griffiths and Gray (2001).

19. Oyama also confirmed this idea in a personal communication.

20. Here we see clearly the filiations between Lewontin (e.g., in the quotation given above) and Oyama.

21. "The theory aims to provide an explanation of transgenerational stability" (Griffiths and Gray 1994: 286).

22. In a section called "DSs and extended phenotypes," Griffiths and Gray (1994: 288) write as follows: "The idea of a DS has certain parallels with Richard Dawkins's notion of the extended phenotype." The same idea appears in Gray (1992: 195).

23. See Griffiths and Gray (2004). In another paper, they say that their "main aim" was "to make the idea [of a DS] precise" (1994: p. 304), but they have dealt with only *one* definition of the DS.

24. I am talking here about the general aim of articulating evolution and development. It is important to emphasize that Griffiths and Gray have explained the similarities and the differences between DST and "evolutionary developmental biology" as it has been elaborated in the last 30 years (Griffiths and Gray 2004, 2005; see also Robert et al. 2001).

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