

The Organism in Developmental Systems Theory (DST)

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Abstract

In this paper, I address the question of what the Developmental Systems Theory (DST) aims at explaining. I distinguish two lines of thought in DST, one which deals specifically with development, and tries to explain the development of the individual organism, and the other which 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 claiming 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 the 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.

Keywords

Development; Organism; Developmental System Theory; Evolution and Development

1. Introduction

As 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* Paul Griffiths’s having a thumb on each hand and having a scar on his left hand? DST people have given two strongly different answers to this question. One choice within DST, best illustrated by Oyama’s *Ontogeny of Information* (2000a [1985]), is to answer that DST’s aim is indeed to explain the characteristics of the individual organism. A second choice within DST, which appears in Oyama’s *Evolution’s Eye* (2000b, e.g. pages 28-29) but which is best illustrated by 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 co-evolution of organisms and their environments (that is, evolution of CEs [GG 2001], or, in other words, evolution of developmental systems).

In this paper, I present these two answers, then I 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 one, 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.

2. First answer: the characteristics of the individual organism as the explanandum of DST

2.1. Explaining individual characteristics

According to this first answer – best expressed by Oyama (2000a), but which also appears in Lewontin’s writings on development¹, in Gottlieb (1992)², and in some texts by Griffiths and Gray³ – 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 paper), *individuality* must not be confused with *uniqueness*: an individual organism is *one* (isolable) organism⁴, 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 which it shares with others. Oyama (2000a: 137) quotes Lewontin 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 left⁵

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 issues⁶.

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

But isn’t it *too* big? Indeed, it seems that the DS includes many resources (all those which are relevant to explain the characteristics of the individual organism), and therefore, possibly, too many resources. For example, to take up an 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 which *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, Smith and Dickison (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 which explain why Dickison is like he is (let’s say, a rock-lover). The fact that the DS is big is not a problem, for two reasons. First,

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 references cited by DST proponents.

³ For example the section ‘Taking development seriously’ in Griffiths and Gray (1994), but also many arguments of Gray (1992) and Gray (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).

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 Which, again, includes both unique and common characteristics.

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 is organisms and what evolves is populations of organisms. Second, it should be clear that in this first option the DST does not state that the task of each biologist is to explain *all* the individual traits of *all* organisms. DST people are much more down-to-earth than it is usually said: they consider that a biologist starts with a well-defined question. For example, her question can be: 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 in the size of the DS.

2.2. 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 determinism⁸, internalism and preformationism⁹. As Godfrey-Smith (2000 and 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 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 less generally admitted by biologists:

1. Genes do not play a central, not even a privileged role, in development (that is, genes are not controllers of development).
2. Factors which 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 ridden of.

In order to show how strong and original these points are, I would like to contrast what DST people say with what someone as sympathetic to DST views as Peter Godfrey-Smith (2001) says. 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). But 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. This implies first 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 DNA¹⁰ 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

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 sometimes coexistent in one mind or one book, are logically very different.

⁹ Which does definitely 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 Because DST people 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 Susan 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

words, nothing becomes a developmental cause without interacting with other interactants. It is a point which is much more original and much stronger than it is usually thought. The consequences are that there is no 'nature', there is no nature/nurture dichotomy as usually conceived. This thesis has enormous developmental implications, and also important social, political, etc. implications (see in particular Oyama 2000b and Oyama, 2009).

3. Second answer: the co-evolution of organisms and their environments as the explanandum of DST

3.1. 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 of (2000b: 28-29; see also Chapter 3, 'Ontogeny and the Central Dogma'). Two important sources are Lewontin on co-construction (1978; 2000; etc.) and Odling-Smee, Laland and Feldman on niche construction (2003). In this second option, the enemies of DST are genic selectionism and all forms of externalism (usually under the metaphor of 'adaptationism'¹²). This option being mainly illustrated by Griffiths and Gray, here I will focus on their writings.

According to the second answer, what DST seeks to explain is not anymore the characteristics of the individual organism, but the co-evolution of organisms and their environments. In other words, the explanandum is the co-evolution of organisms and their environments, that is, the evolution of populations of \mathbb{C} s (an \mathbb{C} is a unit made by the organism and its environment), that is, the evolution of populations of evolutionary DSs. The explanans is historical-adaptive explanations (Griffiths and Gray 1994).

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)¹³. So the developmental resources which explain traits that an organism has but that its descendants do not have are *not* part of the evolutionary DS. The evolutionary DS is obtained by *abstraction* from the individual DS¹⁴: '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'¹⁵. The result is an 'idealized DS of a particular lineage' (Griffiths and Gray 2001: 207)¹⁶.

3.2. 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 of evolutionary individuals¹⁷. 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 became the *explanandum*, it is not anymore the *explanans* of DST.

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).

¹³ The same idea appears in (Griffiths and Gray 2001): 'all the resources which produce those developmental outcomes that are reliably reproduced in a lineage'.

¹⁴ 'Just as a traditional model of evolution abstracts away from the unique features of individual phenotypes', as Griffiths and Gray say in (Griffiths and Gray 2001: 207).

¹⁵ Note that "contains" differs from "is". The question is : does it contain only that, or more than that ?

¹⁶ Word for word the same idea is expressed in (Griffiths and Gray 2004: 12).

¹⁷ 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.

3.3. Consequence: the two different definitions of the ‘developmental system’

The evolutionary DS is clearly different from the DS as defined in the first option. Indeed, from this evolutionary DS, Griffiths and Gray 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 (Griffiths and Gray 1994: 286). Griffiths and Gray themselves contrast this definition of the DS 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”. For their part, by ‘individual’, they mean idiosyncratic, unique (e.g. Griffiths and Gray 1994: 286: ‘The scar is an individual trait’). In (1994: 287), Griffiths and Gray write: ‘For other explanatory purposes, such as the study of developmental abnormalities, a different system must be delineated’.

Thus, we do have *two* developmental systems:

- i) The individual DS, that is, all the resources which explain why this organism is as it is (with *both* unique and common traits). It is the DS as Oyama (2000a) defines it.
- ii) 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 and 1997) define it.

It is noteworthy that Susan Oyama admits that there are two possible definitions of the DS, and that the one which is preferable is the individual one, *even when evolutionary questions are being asked*. See (Oyama 2000a: 141, in the section called “DS in ontogeny and phylogeny”)¹⁸:

“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.”¹⁹

The table below sums up the differences between the two answers we have examined.

Strategies	Individual DS	Evolutionary DS
<i>Explanandum</i>	Traits of an individual organism	Co-evolution of O and E (= evolution of populations of DSs)
<i>Explanans</i>	Developmental system	Historical-adaptive explanations ²⁰
People	Mainly Oyama	Mainly Griffiths and Gray
Sources	Gottlieb, Lewontin on development, etc.	Lewontin against adaptation; Odling-Smee et al.; etc.
Enemies	Preformationism, internalism, genetic determinism	Genic selectionism, all forms of externalism
Biological entities	Organisms	Developmental systems

¹⁸ Susan Oyama also confirmed this idea in a personal communication.

¹⁹ Here we see clearly the filiation between Lewontin (e.g. in the quotation given above) and Oyama.

²⁰ An ‘etiologial solution’ (Griffiths and Gray 1994: 278). And on page 287: ‘adaptive-historical explanation’.

4. 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:

i) 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 variations²¹, 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).

ii) 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 O-E system which evolves, *i.e.* the D.S. (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: 207), they suggest to use the symbol ‘Æ’ in models of evolution, and write ‘we claim that there is no distinction between organism and environment’. The same idea appears 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. There is, here, a parallel with Richard Dawkins²². 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 developmental systems in evolution, Oyama 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 analysed here shows that there is no real unity of the theory (the DST), because we have different *explananda* in the two different strategies. In recent writings, Griffiths and Gray claim²³ that there is only *one* DS, but in fact there are two very different DSs, doing very different things.

What exactly is lost in the second option, that 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 which sexually reproduce (see Lewontin’s quotations above). It is what research on developmental noise (see Lewontin 2000) and phenotypic plasticity (West-Eberhard 2003) show. In fact, we could claim that very few ‘characteristics’ or ‘outcomes’ are stably replicated in one lineage. Of course, they are definitely important, because natural selection acts on traits which last across generations (varying only slightly), but my point is that so few resources involved in individual development are stably replicated that with such a definition of the DS most of development (as understood in the first answer) is lost. Griffiths and Gray

²¹ (Griffiths and Gray 1994: 286): ‘the theory aims to provide an explanation of transgenerational stability’.

²² In a section called ‘DSs and extended phenotypes’ (Griffiths and Gray 1994: 288), Griffiths and Gray write: ‘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 their 1994 paper, Griffiths and Gray say that their ‘main aim’ was ‘to make the idea [of a DS] precise’ (page 304), but they have dealt with only *one* definition of the DS.

say (1994: 278) they want to produce ‘a general account of development and evolution’²⁴. I think they fail, because they lose most of development.

Moreover, if we turn to evolution, we realize that the vast majority of examples used by DST people (both Griffiths and Gray, and Oyama) to justify their thesis about an ‘extended inheritance’ are in fact not ‘inherited’ in a strong ‘natural selection’ sense. To understand inheritance, we need a proper concept of *replicator*. Griffiths and Gray make a critique of the replicator concept (1994: 299-300)²⁵, but I do not think they use a proper definition of the replicator. In my view, a replicator is something which fulfills *three criteria*: i) faithful transmission; ii) differential transmission (most often, individual transmission); iii) transmission correlated to the expression of traits which themselves are correlated with better survival and/or reproductive success. The replicator is *not* the key controller of development, that’s beside the point (at least in the view defended here). With these three criteria, examples like cell membranes, most of cytoplasmic elements (but not mitochondria, of course), etc. have to be excluded. They simply do not pass the test. Some of these traits are, like antibodies transmitted from the mother to the child for instance, *necessary conditions for survival*, but they are *not* relevant from the point of view of natural selection. Indeed, antibodies transmitted from mother to child are probably indispensable for the child’s survival, but this child will not transmit these antibodies to the next generation, so the ‘success’ of a lineage cannot be due to the ‘quality’ of its antibodies. Kim Sterelny seems right when he says that what is needed is an extended replicator conception, even though I prefer the conception of a replicator defended here than the one presented, for instance, in Sterelny et al. (1996). I also agree with Sterelny that endosymbionts pass the test and therefore are very good replicators (see also Sterelny, 2001).

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 its unique traits, but also traits which are certainly important for survival, but which are not replicated in a strong sense.

Hence, 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.

So I think that, thanks to the analysis of these two different definitions of the DS, we see that the unity of the developmental systems theory is lost, or at least deeply threatened.

5. Conclusion

My conclusion is that DST 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 Susan Oyama and by some Griffiths and Gray’s texts. Thus, I would like to tell DST people that what they suggest about development is fascinating and that *it is enough*, and therefore that they need not to offer in addition to that a reconceptualization of evolution.

Acknowledgments

²⁴ And section II of their 1994 paper is entitled : ‘Taking development seriously’ (page 283).

²⁵ 1) ‘If the replicator is something that self-replicates’: but it is not! – at least, it is not a necessary component of a replicator ; 2) If a replicator is ‘anything that is reliably replicated in development, there will be many replicators’. But it is not: a replicator is reliably and *differentially* replicated (and also correlated with survival and/or reproductive success). Few things, in fact, fulfill these three criteria of being reliably and differentially replicated, and correlated with survival and/or reproductive success.

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