

Introduction: Reassessing Developmental Systems Theory

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The Developmental Systems Theory (DST) presented by its proponents as a challenging approach in biology is aimed at transforming the workings of the life sciences from both a theoretical and experimental point of view (see, in particular, Oyama [1985] 2000; Oyama et al. 2001). Even though some may have the impression that the enthusiasm surrounding DST has faded in very recent years, some of the key concepts, ideas, and visions of DST have in fact pervaded biology and philosophy of biology. It seems crucial to us both to establish which of these ideas are truly specific to DST, and to sift through these ideas in order to determine the criticisms they have drawn, or may draw (e.g., Sterelny et al. 1996; Griese-mer 2000; Sterelny 2000; Kitcher 2001; Keller 2005; Waters 2007).

Although DST can be considered as the continuation of an old tradition in biology, illustrated in particular by Lehrman, Gottlieb, or Lewontin (see Griffiths and Gray 1994: 278), in contemporary thinking it is undoubtedly grounded in the writings of Oyama ([1985] 2000). The main goal of the DST proponents, most notably Oyama, Gray, and Griffiths, is to reframe both developmental and evolutionary biology. According to them, this reframing must take as a starting point a critique of the causal privilege that is commonly given to genes to explain heredity, development, and evolution (Oyama et al. 2001).

The DST proponents reject the claim that one could explain heredity by resorting exclusively to gene transmission and refer for that matter to phenomena of intracellular epigenetic heredity, to niche construction, and to vertical transmission of symbionts. As for development, insisting on the complexity and nonadditivity of causal interactions, they argue in favor of the causal parity thesis, according to which it is impossible to name a single factor that would supervise or determine these processes. Consequently, DST proponents criticize the notion of a “genetic program,” which implies the genes’ causal primacy; according to them, every component playing a causal role in development and reoccurring at each generation must be conceived of as inherited. The set of all processes taking part in the developmental construction constitutes a Developmental System (DS). According to the DST proponents, a DS is the main unit of evolution. Owing to this new synthesis between development and evolution, DST aims at broadening the scope of evolutionary explanations.

This thematic section is composed of three articles, which all try to evaluate DST’s claim to provide a unifying and fruitful framework for biology, and to assess its fundamental concepts and the internal coherence of this approach. Anouk Barberousse’s aim in her article is to scrutinize the elements that DST proponents present as explanatory in the new theoretical framework they put forward. She points out the role of the construction metaphor in the explanation of development and signals some of its weaknesses. Correspondingly, she shows that the relative explanatory failure of DST, as compared with its competitors, may be accounted for by the choice DST proponents have made to rely on self-organization as an *explanandum* of reproduction and development.

In her article on DST’s concept of inheritance, Francesca Merlin shows the limits of DST’s idea that any resource necessary for development is to be considered as a form of inheritance. She argues that DST does not provide any evidence of the fact that the evolutionary causal power is localized neither in any privileged factor nor in many different channels of inheritance, but is diffused in the entire DS. She finally suggests

that DST's interactionist approach, which refuses the multiple channels model of inheritance and denies any causal differentiation between developmental resources, does not provide any advantage from an experimental point of view.

Thomas Pradeu raises the question of DST's explanatory goal. He shows that there are two very different definitions of the "developmental system" in DST, so much so that one cannot consider DST as a unified theory of evolution and development. One of these definitions is about the developing organism per se, while the other is dependent upon DST's views on evolution. He thus proposes that DST is a theory about development, not of evolution and development, because it does not provide a well-articulated new perspective on evolution.

At the International Society for the History, Philosophy, and Social Studies of Biology (ISHPSSB) meeting in Exeter in July 2007, Marie-Claude Lorne organized a session about DST, entitled "DST and the Unification of Biology." Merlin, Pradeu, and Barberousse were the other speakers in that session. At the time, Lorne was a post-doctoral fellow. One year later she was appointed assistant professor at the University of Brest. She tragically committed suicide in September 2008 (see Pradeu 2009).

The session organized by Lorne was the result of a year-long collaborative work at Institut d'Histoire et de Philosophie des Sciences et des Techniques (IHPST) in Paris. We met twice a month to discuss the major DST papers. If Lorne had been alive, she would have surely finished in time and submitted the paper she was writing on DST's parity thesis, as the other three of us did. That is why we would like to dedicate this series of articles on DST to the memory of our dear and greatly missed friend Marie-Claude Lorne.

The paper that Lorne presented at the ISHPSSB meeting in Exeter was entitled *Positional Information and the Parity Thesis*. Here is a cursory reconstruction of the argument she developed in opposition to the application of the parity thesis, grounded on an analysis of the notion of information.

She first recalled the DST proponents' criticism of the idea that genes play a privileged causal role in development and evolution. In particular, DST proponents have fought against the claim that genes have a greater importance than other factors causally involved in development because they are the only carriers of information. In opposition to this idea, they have offered the "parity thesis," according to which no analysis of the notion of information has the potential to isolate genes as the privileged cause of development, because any analysis applying to genes equally applies to other, non-genetic causes of development. Second, Lorne questioned the scope and the validity of the parity thesis by means of a further analysis of the notion of information. She remarked that an important assumption of the parity thesis is that the informational discourse in biology is based on a unique conception of information. She discussed this assumption in order to defy the parity thesis. Her

aim was not to propose a new and unique concept of information in biology, but, more modestly, she wanted to show that if DNA sequences (genes) carry information in a different sense than other molecular factors like proteins do, i.e., if both cases are not instantiations of the same notion of information, then the parity thesis is false.

In her demonstration, Lorne did not start from the usual definitions of information, but from two biological mechanisms that are usually described in terms of information—protein synthesis and cellular differentiation—in order to identify which of their properties substantiate an informational discourse and which notion of information they respectively call up. She thus reversed the DST proponents' line of argument. She showed that the mechanism of protein synthesis and that of cellular differentiation are at the basis of two different concepts of information. On the one hand, the mechanism of protein synthesis substantiates the notion of genetic information, according to which informational transfer needs the existence of a template (the DNA sequence with respect to the ARN sequence) and a code (the relation between a group of three nucleotides and an amino acid). On the other hand, the mechanism of cellular differentiation substantiates the notion of positional information where the informational transfer is based on the existence of a concentration gradient and a threshold (the differentiation of a cell can be due to the fact that the concentration in proteins has reached some threshold). What Lorne showed is that DNA sequences (genes) can no more be said to carry positional information than proteins. More precisely, she claimed that if one admits that the informational discourse in biology is based on the causal relations and mechanisms it refers to, then the structural and functional differences between the mechanism of protein synthesis and that of cellular differentiation justify that they call for two different meanings of information. On this basis, she concluded that DST's parity thesis is in trouble because one of its starting assumptions is defied: the same concept of information, the genetic or the positional one, cannot be applied to both cases, i.e., to DNA sequences (genes) and to proteins. In other words, Lorne argued that the DST proponents have not shown that the primacy of genes in terms of their informational role cannot be sustained. Nevertheless, she admitted that it remained to be explained in what sense genetic information in terms of template and code could possibly ground the privileged role of genes.

We hope this series of articles will show that DST is still useful for anyone willing to investigate current key biological concepts (heredity, development, epigenetics, and information), and yet even so does not fulfill its whole agenda.

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