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The Rebirth of the Morphogenetic Field as an Explanatory Tool in Biology

Abstract *I discuss two uses of the concept of the morphogenetic field, a tool of the 19th century biology motivated by particular ontological views of the time, which has been re-emerging and increasingly relevant in explaining microbiological phenomena. I also consider the relation of these uses to the Central Dogma of modern biology as well as Modern Synthesis of Darwinism and genetics. An induced morphogenetic field is determined by a physical (e.g., gravitational) field, or it acquires a physical (e.g., visco-elastic) field's characteristics. Such a morphogenetic field presents only a weak challenge to the Central Dogma of Modern Synthesis by indirectly, albeit severely, constraining variability at the molecular level. I discuss explanations that introduce structural inheritance in ciliate protozoa, as well as the experimental evidence on which these arguments are based. The global cellular morphogenetic field is a unit of such inheritance. I discuss relevant cases of structural inheritance in ciliates that bring about internal cellular as well as functional changes and point out that DNA is absent in the cortex and that RNA controls neither intermediary nor the global level of the field. I go on to argue that utilizing knowledge of known physical fields may advance explanations and understanding of the morphogenetic field in ciliates as the unit of both development and inheritance.*

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1. Introduction

> [T]o an evolutionist, the interesting question about …cytoplasmatic localization is not whether such localization is essential for proper development, but whether, if the localizations are changed, the result will be an adult which produces eggs with similarly altered localizations.
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> In general, the answer to such questions is no. There are a few well-established exceptions, of which phenomenon of 'cortical inheritance' in ciliates is perhaps the most important. Neo-Darwinists should not be allowed to forget these cases, because they constitute the only significant experimental threat to our views. (Maynard Smith 1983, 39)

Judging by recent studies of the so-called structural inheritance in ciliates and related phenomena of cytoplasmatic inheritance, one might conclude that Neo-Darwinists have reason to be worried.[1] And these

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cases might be only one instance, albeit the most important one, of the more pervasive resurgence of the concept of morphogenetic field.

Although the origins of the morphogenetic field concept are linked to rather obscure *Naturphilosophie* and the Romantic understanding of life and science, it was a potent tool in the 19th century study of morphogenesis. While it was initially sidelined in an age of biology predicated on Darwinism married to genetics and the microbiological study of hereditary units (i.e., the so-called Modern Synthesis), the morphogenetic field has been increasingly playing an indispensable role in explaining development, morphogenesis and inheritance. Indeed, some biologists argue that the emerging concept of morphogenetic field represents a serious challenge to and a comprehensive alternative for the so-called Central Dogma of modern biology (Bray 2001, Chapter 4; Gilbert, Opitz and Raff, 1996, 368; Hjelm 1986; Goodwin 1984).

The core of the Central Dogma is that the genes (DNA) are the exclusive hereditary units, and that virtually unlimited variations at the molecular level – the result of mutations and recombination – produce traits that become the subject of natural selection, thereby allowing a wide range of potential and actual evolutionary changes (Dawkins 1982, 1995; Maynard Smith 1983). Thus, according to the (refined) Weisemanian Neo-Darwinist germ-centrism, DNA controls the details of protein synthesis and activity in morphogenetic and developmental processes (Nanney 1984; Maynard Smith 1983; Dawkins 1982).

Following the above-quoted warning from Maynard Smith that the adherents to the Central Dogma should not overlook the cases of cytoplasmatic inheritance, I will discuss the extent of the present challenge to the tenets of Modern Synthesis that stems from the studies based on the morphogenetic field while explaining the nature of the concept.

2. Induced Morphogenetic Fields

Experimentally based studies of morphogenetic and developmental processes suggest that the morphogenetic field might be indispensable in explaining developmental, embryogenetic and morpohogenetic processes, as the explanations of such processes introduce the level beyond

the molecular one as provider of genetic information. In arguing this point, Goodwin (1984, 219) appeals to "the empirical evidence that gene products do not generate form." Some even assert that the rebirth of the morphogenetic field is "starting to make good on Roux's prophecy" that "phylogenetic developmental mechanics would determine how changes in embryonic development cause evolutionary change." (Gilbert, Opitz, and Raff 1996, 368)

Thus, in the case of *Drosophila* embryos (Goodwin 1984, 227; Goldschmidt 1935) gene activity should be treated simply as stimuli which are not more refined than external random stimuli; these stimuli trigger a response by means of an intrinsic morphogenetic mechanism. Thus, the genes do not influence embryogenesis in a manner analogous to the computer program that determines each stage. If the embryos are exposed for brief periods to external non-specific stimuli (ether, elevated temperature, X-rays, etc.), the morphology of the adult will be altered in *specific ways* and genetic mutations will alter it in the same ways (Stent 1982; Goldschmidt 1935). The fact that random influences and genetic mutations both produce the same specific alterations supposedly indicates the limited response repertoire of a highly structured internal morphogenetic mechanism. The stability of this mechanism is the basis of the (stability of) morphogenetic processes, thereby sidelining genetic dominance beyond the stage of protein formation.

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The previous case is a particularly illustrative example of the so-called homeotic mutations (Gilbert, Opitz and Raff 1996, 363-4; Goodwin 1984, 226). In general, such mutations result in various changes of the structure of appendages. Such mutations in *Drosophila* can, for example, result in the growth of a leg on a segment of a body to which a different appendage (antenna) normally belongs. Moreover, certain gene sequences, namely the homeotic genes responsible for the formation of the appendages structure (and which mutate in homeotic mutations), *do not differ across species* (Gilbert, Opitz and Raff 1996). For instance, the order of homeotic genes in chromosomes turns out to be identical in vertebrates and the fly (McGinnis and Krumlauf 1992; Krumlauf 1993; Bachiller et. al. 1994). Also, in some cases, *the individual homeotic gene expression is identical in different species* (e.g., in humans and Drosophila) (McGinnis et al. 1990; Malicki et al. 1992).

Although homology is a complex issue that is related to the mechanism of natural selection and the concept of biological function in various

ways (Griffiths 2007), the existence of homeotic genes and their expression demonstrates the striking similarities of embryonic development across phyla. The question is – what exactly can we conclude from this?

Taking the Central Dogma point of view, one could argue that embryogenesis and morphogenesis in different phyla simply encounter similar "problems" and "obstacles" and thus result in similar solutions. This explains the similarity of the genetic sequence responsible for the similar structural changes across phyla, as well as the appearance of genes as mere stimuli in the face of the stability of morphogenetic processes.

But focusing on these "problems" and "obstacles" (i.e., constraints) has non-trivial consequences for the understanding of morphogenetic phenomena from the gene-centric point of view.

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From the gene-centric point of view "these constraints are historical and contingent in nature, arising from the existing pattern of development" (Maynard Smith 1984, 43). Yet the domain of these constraints is surprisingly narrow, thus making it possible to define them as a common underlying structure across phyla. But claim that such an "alternative to [the] view [of contingent constraints] would be that there are absolute laws of form, not historically contingent, determining what kinds of organisms can and cannot exist" (Maynard Smith, ibid.) may be incorrect: instead of looking for such independent "absolute laws," one could account for the narrow set of constraints by defining the morphogenetic field *in terms of the well-known physical fields*. Such an approach raises the question of the interaction of such a morphogenetic field (i.e., the constraining mechanism) with the genes.

The morphogenetic processes are embedded in particular physical contexts, identical across phyla. More precisely, they are constrained by known physical laws. Thus, the field-like properties of the organismal formative processes (e.g., their uniformity and stability) could *be induced in the organisms* by well-known known physical fields. Thus, the gravitational field may induce the stages and even the details of the morphogenetic processes (Goodwin 1984). Alternatively (and this alternative is physically and formally more tractable), the morphogenetic field could be a field with the induced properties of the visco-elastic field, whereby the laws concerning the shaping of the organism are accounted for by the regular laws of the visco-elastic field (Brandts and Totafurno 1997; Brandts and Trainor 1990; Goodwin and Trainor 1985).

Yet even if the morphogenetic field determines localizations in the cytoplasm, and even if it regulates the morphogenetic and developmental processes by severely constraining the formation of the proteins (i.e., if development is defined as a particular stabilization of the field equations), the question remains: are the changes it can cause inherited (by it)? Nothing in the arguments we have discussed suggests that the positive answer is correct. Nor is it clear whether, due to its very limited variability (the distribution of the condition of the physical field – gravitational or visco-elastic – on which it depends remains unchanged over time) the morphogenetic field can assimilate any significant changes.

To claim that the DNA-program paradigm is challenged by the necessity of introducing the induced morphogenetic field (as Goodwin does) is to attack too broad a claim. The proponent of the Central Dogma can respond by saying that while the unfolding of the DNA-based program may indeed be influenced by the developmental constraints, "[t] here is ... nothing 'un-Darwinian,' " or more-precisely un-Neo-Darwinian "about the claim that there are developmental constraints" (Maynard Smith 1983, 44).

In short, it is not clear how this argument challenges the first aspect of the core of the Neo-Darwinian view since in order for the morphogenetic field to be the unit of heredity, it must be capable of containing and passing on a variation to offspring. First, the fact that it comes to dominate only the post-protein production stage is not pertinent to this function, as the structure of the protein has been already altered if mutations have occurred. Second, the externally induced morphogenetic field has limited variability. Although this characteristic is advantageous in providing the stability of the morphogenetic processes, it severs the field's capacity for assimilating significant alterations, as *it* cannot be significantly altered (the range of the "order parameter" of the field equations is very small). In order to perform the inheritance function, the field would have to be potentially sufficiently variable (almost as much so as genes). Thus, despite the morphogenetic field's developmental significance as a severely constraining factor, variations are due to genes, and more importantly, are *passed on by genes*.

The induced morphogenetic field might pose another modest and indirect, but still significant challenge to Central Dogma, however. Thus, that the variations (by mutations) at the molecular level are unconstrained might be irrelevant, as the mutations do not result in one-to-one

mapping with the actual changes of phenotype: most mutations are idle because of the highly structured and invariant morphogenetic field. The inherited particulars (DNA molecules) are efficient only in that they stabilize particular solutions of morphogenetic field equations within a very limited repertoire (Goodwin 1984, 229). The example of *Drosophila* embryos and homeogenic genes might provide more substantial evidence that the scope of potentially effective genetic variations and hence the scope of the genetic program are indirectly but severely constrained by the morphogenetic field (Gilbert, Opitz and Raff 1996, 364-5; Goodwin 1984),[2] thereby rendering the second component of the Central Dogma irrelevant or at least prompting its thorough reformulation.

Yet the morphogenetic field does not inherit the actual traits which result from the genetic variations. Strictly speaking, inherited characteristics result from the mutations-selection coupling, irrespective of how severely are mutations constrained. In fact, the view that "declaring the morphogentic field to be a major module of developmental and evolutionary change is setting it up as an alternative to the solely genetic model of evolution and development" (Gilbert, Opitz and Raff 1996, 368) should be taken with caution, if by "evolutionary change" one means the production and inheritance of variations. The inherited variations are both produced and inherited by the genes (DNA), although their success depends on the morphogenetic field as an additional albeit dominant (i.e., the most constraining) external factor. In other words, the conclusion that the induced morphogenetic field delivers on Roux's prophecy is unsubstantiated.

3. An Anomaly That Won't Go Away:
The Structural Inheritance in Ciliate Protozoa
And The Global Cellular Morphogenetic Field

If anywhere, the hereditary function of the morphogenetic field is found in *ciliate protozoa*. In this case, the morphogenetic field is very variable, and as such, it is claimed to inherit the changes that are externally inflicted on adult individuals. Jablonka (2005, 122) suggests the following (roughly appropriate) analogy: "It was as if the descendants of a person whose leg had been amputated inherited the same handicap."

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2 Brigandt (2007) makes a similar, although more general point, concerning homology, that he draws mainly from (Müller 2003). However, this work does not provide an account of the actual mechanisms of the constraints as Goodwin's does, which makes Brigandt's argument open to Maynard Smith's objection (noted on p. 7).

The first, although not the strongest, case of the supposed structural inheritance in ciliates is the well-studied inheritance of inversions of *ciliary rows*.

One can rotate (invert) experimentally by 180-degrees the configuration of ciliary rows in *Paramecium tetraurelia* and *Tetrahymena thermopile*, as well as the configuration of marginal ciliary rows in *Stylonychia mytilus* and *Paraurostyla weissei*. The inverted rows are generated in the so-called fusion of cells-clones *with identical nuclei* with the "invasion" of ciliary rows (i.e., of a particular configuration or orientation in which they flap) from the cortex of one cell to the cortex of the other. The division of the fused cells (the conjugating cells) results in a singlet progeny with an inverted ciliary rows (inverted with respect to the orientation of cilia prior to the "invasion" from the other cell).

Ciliary-row inversions are inherited for more than 800 fissions in clones, and the nucleus and the DNA in the nucleus seem to play no role. Sonneborn (1970, 353), who pioneered these studies offered what we might call a strong interpretation of the phenomenon: the molecular cortical geography, whatever its exact structure might be, determines the initiation, migration and orientation of basal bodies (i.e., cilia), not the external (nucleotic) molecular or cellular influence, as nuclei are identical in the "invader" and the "invaded" cells. And such molecular geography is responsible for the inheritance of the configuration in the clones.

One might doubt the soundness of such an interpretation, and wonder whether the nuclei really remain identical. Based on what we know about other similar cases, it could be that the nucleus in the detached cell mutates rapidly upon detachment and is responsible for the inversions. The role of the nucleus in such a case would remain unclear (e.g., why does the result of the mutation coincide with the result of the invasion of cilia from the other cell?), but its content would remain an effective unit of inheritance.

There is an experimental answer to this objection (Frankel 1989). The genetic mutations result in either the appearance of erratic ciliary units outside the rows or the disorganization of the rows, while the ciliatory units preserve the normal position (relative to accessory structures). When the cell membrane or epiplasm is disrupted molecularly (through mutations) or otherwise, the ciliary units retain their position – unlike in the fusion experiments.

Even more striking is inheritance of the so-called doublet configuration – a functioning unit of two cells fused at the anterior and posterior ends. The doublets are produced by three different techniques: first, by the failure of separation of conjugating cells, second, by the spatial adjustments that follow arrested cell division, and finally, as a response to microsurgically created fusions. The cells produced by the second and third technique are typically stable. In the inherited homopolar doublets (i.e., doublets with no handedness) the morphology drastically changes, despite the lack of mutation (i.e., molecular-genetic information has not changed): the duplicate sets of surface structures around the common endoplasm lack internal division – we have a doubled cortical organization. Now, in the doublets conjugating with singlets, the doublet ex-conjugate gives rise to a doublet clone and the singlet to a singlet, even though the ex-conjugate clones are genetically identical.

Moreover, the nuclear conjugation[3] can be experimentally accompanied by a massive exchange of internal cytoplasm, thus ruling out the control of the process by organelles. And when the nucleus is divided unequally and imported into doublets and singlets, it grows back to its usual size. (Frankel 1989, 88-91) This could imply that the development of the nucleus and its content is controlled by the doublet organization, not *vice versa*. It is not surprising then, that Sonneborn (1963) concluded from the study of doublets that the cortex remains the only candidate for the control of development and that it is responsible for inheritance.

Although these cases might seem definitive evidence for that the DNA does not play a role in cortical inheritance, this understanding can be questioned at a more general level. In fact, the entire case might be deemed essentially irrelevant to what we normally regard as inheritance. First, the nucleic materials (i.e., DNA and RNA) are the basic controllers of the process that governs the changes in configuration of basal bodies: *they* synthesize the cortical proteins and enable reproduction after all. Second, the peculiarities of the "cortical inheritance" do nothing to question the basic premise of the Central Dogma: rather, the configurations of basal bodies are nothing but *peculiar examples of variations of multiplicity or orientation of structural patterns while the internal cellular structure and functions remain the same*. Although, the above cases are puzzling, once could argue that they are independent

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3   Singlet ciliates have two nuclei, macro and micro-nucleus. Doublets will have either one or two macronulei. As a matter of fact, the number of doublets with one nucleus decreases with subsequent fissions and the DNA content is 50 to 100% larger than in the macronucleus of a singlet.

from the understanding of what one would label inheritance – unless of course one were to adopt an idiosyncratic and insubstantial notion of it.

The study of inheritance in certain types of the doublets, however, clearly shows that such an assessment is on the wrong track. The inheritance of the inverted (rather than merely reversed) large-scale symmetry in the so-called type III doublets is substantial, as the heritable *mirror-image global inversion affects the internal organization of the morphogenetic system (really the entire cell) and its functionality* (Frankel 2000, 93). The cortical bodies of one of the genetically identical "semicells" in such a doublet are left-handed. This affects their functionality (and that of their cloned offspring) when separated from the doublet, as the oral membranelles that control the flow of water in feeding are inverted and sweep the food away from the oral pouch, and the subsequent DNA-based reorganizations of the internal structure, quite common in ciliates, cannot change the polarity (left-handedness) of the cell. Finally, the right-handed semi-cell will propagate the right-handedness in its offspring, while left-handedness will be propagated in the offspring of the dysfunctional cell, despite the identical nucleus.

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One could also argue that "[m]ost cases of 'cytoplasmatic' inheritance turn out to depend on non-nuclear DNA and RNA, a fact which encourages a still more gene-centered and less organism-centered view of evolution" (Maynard Smith, 39).

No traces of DNA molecules have been found in the cortex of ciliates. Still, it is possible to speculate that an explanation of these processes is available at the level of the cortex: cortical RNA might be responsible for patterning and turn out to be the unit of heredity. Indeed, the RNA molecules have been discovered in the cortex. Yet exceedingly detailed studies of its function (Delattre, Conrad and Gönczy, 2006; Pelletier et al., 2006) have shown that it cannot account for the geometry of the propagation of ciliary rows – what turns out to be, as we will see shortly, only *an intermediary level* of the structure that governs development and inheritance.[4] And it is even less likely that it will account for the indispensable of *the global morphogenetic field that controls the development and inheritance of ciliates by controlling polarity of the cell.*

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4   It seems that RNA plays only a secondary role in mediating the epigenetic "program" which directs the *disintegration* of DNA in morphogenetic processes. (Nowacki et al., 2007)

The explanation of both the development and inheritance of large-scale organization found in *Oxytricha* and *Stylonychia* doublets requires such a global cellular morphogentic field. These ciliates can undergo the stage of *the cyst* which incurs a complete loss of the internal cellular structure. After dedifferentiation at the cyst stage, a normal ciliature is developed. Yet the specific local-structural information of the cortex disappears during the cyst stage. That is why the extra marginal rows that are propagated for several vegetative cell generations completely disappear after the cyst stage. They should not do so if these local structures are preserved and responsible for the post-cyst development (Frankel 1989, 89-90). Moreover, the parts of the equatorially transacted doublet of a certain type will produce the doublets of the same type with complete ciliatures (ibid.; Frankel 2000).

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Yet despite a very limited relevance of local structure, doublets brought to cyst stage excyst as doublets (e.g., a doublet III type emerges as a doublet III type, not as a singlet, despite their identical nuclei), whose geometry (polarity) is preserved. As all these structural changes affecting the cortex are propagated in the offspring, one cannot escape the conclusion that the cortical RNA can hardly be the silver-bullet, as the local cortical structure itself is irrelevant to such changes. One is led to conclude that "something global" must be inherited.

Indeed, the global polarity in ciliates exhibits supremacy over the cytoskeletal polarity. It is responsible for the fine positioning of pairs of contractile vacuole pores, as well as the position of mitochondria microtubule bands and the anterior structures. In addition, the change of global polarity is a (multi)functional change (Frankel 2000).

In sum, there are three distinct levels responsible for patterning development: the molecular level, the intermediary level (microtubule bands) and the global level (the morphogenetic field). The last level, to be discussed at the greater length in the next section, is dominant, most likely nonmechanical and heritable (Frankel 2000, 97; Frankel 1989, 92). The molecular level of control is irrelevant for a ciliary units' patterning. RNA has only a mediating function in cortically-controlled inheritance in ciliates, while DNA does not seem to contribute at all.

As for the molecular basis of the origin of global polarity, some interesting suggestions invoke the bio-chemical field (Frankel 2000, 1991), where chemical substances acquire morphogenetic functions in the context of the cell (e.g., lithium acquires a new function within the

existing spatial circumferential structure). This is quite the opposite of the induced morphogenetic field.

The attempts to formalize the global morphogenetic field in ciliates rely on the combination of the polar maps (and polar coordinate models) which trace the assembly processes, along with the positional information adjusted to the specific processes in ciliates.[5] Bateson's idea of the principle of integration (Bateson 1892) has been revived, as well. It accounts for a system whereby the anatomy of the elements depends on their location relative to the varying property of the field; in ciliates, for example, the mutual confirmation within a set of membranelles is more important than their individual structure.

Although it is clear that Modern Synthesis can be of little help as RNA plays only a minor regulative role, the nature of both the global morphogenetic field and "the message" responsible for development and inheritance is far from being understood. The ciliate morphogenetic field is more variable than either the morphogenetic field as it was traditionally conceived, or the induced morphogenetic field could be, but as Frankel (1991) notes:

> We can only guess at the medium within which the patterning instructions reside: is it a cell membrane, the epiplasmatic layer … or some gelated ectoplasm underneath that? … And as for the message, are we talking about different molecules, (proteins? Perhaps Ca++ ions?) that are mobile, or possibly of equally mobile states of modification of proteins… or something else altogether? (Frankel 1991, 524)

Thus, one needs to talk about the dynamic change-sensitive property of the system (Frankel 2000, 91), and the basal bodies must be understood as global *structural templates*, not as informational in the sense of the DNA as informational unit (Frankel 2000, 90). The DNA-based molecular approach to the unit of inheritance expects the analysis of molecular structure to reveal the message. In the case of the morphogenetic field in ciliates, the field approach promises assembling the structure (in terms of spatial relations and polarity) will reveal the message.

Although the direct connection between physical and biological fields is not likely to produce any interesting results, *analogies* between the two might be a good starting point. Such analogies would raise a number of potentially insightful questions. To start with: is the global

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5 The cell signalling initially accounted for the inter-cell communication in cascading patterning that was governed by the genetic (DNA) information. However, there is no such information in the processes in ciliates.

morphogenetic field an essentially continuous or discrete medium? If the former is true, will mechanical theories of continuous medium (involving velocity, acceleration, displacement, and stress) suffice? Or is a development of non-mechanical field theories required? Will a vector analysis be sufficient (unit geometry vectors are used in the analysis in (Frankel 1991)), or should one approach it with tensor accounts (Brandts and Totafurno 1997)? Could such a morphogenetic field be treated as essentially permanent or is it variable? It seems that the latter is the case, but more experimental studies are needed. Frankel (1989, 241) argues that the morphological field should be treated as Bateson's field (Frankel 1989, 241) while others (Gilbert, Opitz and Raft 1996, 359; Vale and Oosawa 1990) suggest that a comparison with electromagnetic field would be advantageous.

4. A New Wave Biology?

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The structural inheritance in ciliates might be the most compelling experimental argument against the Central Dogma. But before we examine this challenge more closely, it is important to emphasize that the morphogenetic field as the unit of inheritance in ciliates is not at odds with Darwinism as such. One might interpret inheritance in ciliates as inheritance of acquired characteristics (Lwoff 1990), but natural selection can act on such acquired traits. Rather, such inheritance is at odds with the germ-centrism of Modern Synthesis.

Roughly speaking, there are three attitudes towards the Central Dogma and its significance.

The first attitude I will call *evolutionary pluralism*.[6] Although they might disagree on the details, pluralists believe that substantially different mechanisms of inheritance and, thus, units of selection are at play in evolution and that genetic level is only one of them (Jablonka 2005; Müller 2003; Oyama 2000; Keller 2000, Rose 1997; Jablonka and Szathmáry 1995).

Acknowledging the diversity of the mechanisms of inheritance, the pluralist would be wary of drawing any general, let alone universal, conclusions from the case of ciliates and the role of the morphogenetic field. In their view, the structural inheritance in ciliates is not a counter example

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6 It should be distinguished from pluralistic genic selectionism as defined in Brandon and Nijhout (2007), the view that selection takes place at levels other than those of DNA, but always at the level of DNA.

to a universal account of inheritance, as there is no such account. In fact, the morphogenetic field can peacefully coexist with Mendelian molecular mechanisms (Landman 1991, 2). Moreover, at least some pluralists would acknowledge that the evidence for the pervasiveness of inheritance best accounted for in Neo-Darwinian terms is overwhelming, and that structural inheritance is merely a ripple in the Neo-Darwinian wave. Yet unlike the alternatives to the Modern Synthesis that broaden the gene-centric notion of mechanisms and units of inheritance and selection (e.g., Oyama 2000) – typically the focus of philosophers of biology (e.g. Godfrey-Smith 2000; Thompson 2007) – the case of ciliates renders the gene-centric mechanism irrelevant or introduces "reversed" genetic processes where DNA is determined by epigenetic programs and inherited as such.

Those who take the Central Dogma as an articulation of a universal mechanism of inheritance and the unit of selection (Dawkins 1995, 1982; Maynard Smith 1984) are faced with a much more demanding task. The unitarian has to accommodate any apparent exceptions that might serve as counter examples to the Central Dogma. In practical terms, other alternatives to gene-based inheritance can be accommodated, or at the very least, there are some interesting ideas as to how this could be done. Not in the case of ciliates, however. This is why the warning issued by John Mynard Smith should be taken seriously especially by unitarians: the case of the ciliates runs counter to the core tenets of the Central Dogma. Similarly, Goodwin warns that "a simple counter-example [to genocentric biology] comes from the work of Sonneborn and others in ciliate protozoa" (Goodwin 1984, 225)). This should prompt unitarians to wonder whether they should become pluralists if the anomaly persists and turns into a full-blown alternative.

The keen unitarians like John Maynard Smyth may be rare. Most proponents of the Central Dogma advocate a softer view, treating the Dogma as a fruitful research program that has repeatedly proved its superiority over other alternatives (Michod 1981).

But the case of ciliates may have serious consequences, even for those who take such a pragmatic approach.

Rather than asking whether a research program is fruitful, we should ask whether it is *advanced in a way that makes it a fruitful program*. There are, what one might call internal and external criteria of judging whether a research program is fruitful and to what extent. A program's

wide applicability is an internal criterion as it confirms the power of and advances its explanatory mechanism. Yet a program should also be judged on whether, and to what extent, it confronts hard cases as well as emerging alternatives, or if it bypasses and ignores them. This constitutes an external criterion.

As we have seen, the structural inheritance in ciliates is a (very) hard case that should worry those with pragmatic attitude to the Central Dogma as well, but is it a full-blown alternative to the Central Dogma? Is it plausible to claim that the morphogenetic field is a pervasive unit of inheritance? Could it undermine the claim of the pervasiveness and relevance, not only of universality, of the Neo-Darwinist mechanisms of inheritance?

Given the forcefulness of the case for the morphogentic field as the vehicle of inheritance in ciliates, it is not surprising that claims concerning the possibility of a Unified Morphogentic Field Theory have emerged. Such a theory could concern development and inheritance in both ciliates and *eggs*. Frankel (1982, 132) explicitly pursues this question by comparing the case of structural inheritance and development in ciliates with the classical case of the inheritance and development of the frog egg. Other studies concentrate on the properties of the morphogenetic field of the kind we find in ciliates, in other species including Drosophila (Bähler and Peter 2000).

Goodwin and Webster (1982; see also Goodwin 1984) argue for the morphogenetic field as generating changes in phenotype, but their argument is weak if it relies on the concept of the induced morphogenetic field. Similar claims come from those arguing from homeotic genes (Giblert, Opitz and Raft 1996). Yet it is hard to justify general conclusions about the pervasiveness and dominant role of the morphogenetic field, given the limitations I have already pointed out.

Although unification is a noble goal if one believes in the unity of science(s) and natural phenomena, given the stage of research in the field, one should expect the emergence of a number of diverse morphogenetic field accounts. Interestingly, the state of affairs in this field resembles what was happening with respect to magnetic and electric phenomena at Faraday's time. Thus, there is a great deal of elaborate experimental testing going on, that produces substantial results which are increasingly revealing the superiority of the field approach over the dominant alternative(s), while the studied phenomena remain only

loosely related, without a unifying general formal theory of the field to connect them (despite attempts to provide such a theory by utilizing our knowledge of known physical fields).

Admittedly, it could turn out that the morphogenetic field and structural inheritance are pervasive or even basic, and that ciliates are at the forefront only because they present a suitable case for researching the morphogenetic field. The experimental research of cytoskeleton in species other than ciliate protozoa may reveal a very broad evolutionary significance of the morphogenetic field (Bray 2001, 56-60; Bähler and Peter 2000; Kreis and Vale 1999, Chalker and Yao 1996).

Regardless, the attention dedicated to the case of ciliates by those working within the ramifications of Modern Synthesis may be a good measure of the program's fruitfulness in terms of the external criterion: a lack of sufficient consideration of the cases like ciliates would render Modern Synthesis a fruitful research program only in a very limited sense. However, whether such sufficient consideration is lacking is an empirical question I cannot address here.[7]

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[7] A somewhat cynical way of directing an attempt to answer such a question would be a suggestion to find out the extent of the resources and research time allocated to the study of inheritance in ciliates and how it fares in comparison to "normal-science" projects within the Modern Synthesis paradigm. It might turn out that Maynard Smith's warning might be currently justified even more than when originally voiced, in the case of those embracing the pragmatic attitude as well.

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Slobodan Perović
Oživljavanje koncepta morfogenetskog polja u objašnjenjima u biologiji

Sažetak
Razmatram dve upotrebe koncepta morfogenetskog polja, koji je figurirao u biologiji 19. veka motivisan specifičnim ontološkim pristupima tog vremena, koji se nanovo pojavljuje i sve je relevantniji u objašnjenjima mikrobioloških fenomena. Takođe razmatram odnos ovih upotreba prema 'Centralnoj dogmi' moderne biologije, kao i prema Modernoj sinteze Darvinizma i moderne genetike. Tzv. indukovano morfogenetsko polje je rezultat određenih fizičkih sila (npr. gravitacionog polja), ili stečnih fizičkih karakteristika (npr. viskozno-elastičnog) polja. Takvo morfogenetsko polje predstavlja samo slab izazov Centralnoj dogma i Modernoj sintezi time što indirektno, iako značajno, ograničava varijabilnost na molekularnom nivou. Nakon toga se fokusiram na objašnjenja koja uvode strukturalno nasledjivanje u ciliatnim protozoama, kao i na eksperimentalnu evidenciju na kojima se zasniva ovakav pristup. Globalno ćelijsko morfogenetsko polje je jedinica takvog nasleđa. Diskutujem relevantne slučajeve strukturalnog nasleđa u ciliatima koje dovodi do unutrašnjih, kao i funkcionalnih promena i ističem da DNK nije prisutan u korteksu, niti da ima RNK kontrolu, na lokalnom ili globalnom nivou polja. Saznanja o poznatim fizičkim poljima mogu unaprediti takva objašnjenja i razumevanje morfogenetskog polja kao jedinice razvoja i nasleđivanja.

Ključne reči: Objašnjenje; biologija; morfogenetsko polje; Moderna sinteza u biologiji