

On the Heuristic Value of Hans Driesch's Vitalism



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Abstract In the first half of the twentieth century the harshest critics of Hans Driesch's vitalistic theory depicted it as an animistic view driven by metaphysical moods, while others merely saw it as a barren hypothesis. In the last decades the heuristic value of vitalistic principles was nevertheless suggested. In this chapter I examine the epistemic role of Driesch's critical vitalism in the progress of embryology. I first show that it did not contribute to falsify mechanical explanations of development such as Wilhelm Roux's mosaic theory and Driesch's own embryonic induction model. However, Driesch's argumentation for vitalism led to the final formulation of the most challenging developmental *explanandum* of the twentieth century: the harmonious-equipotential system (HES). I point out how major *explanans* like Charles M. Child's metabolic gradients, Hans Spemann's induction fields and Lewis Wolpert's positional information were conceived as promising answers to Driesch's problem.

Keywords Hans Driesch · Harmonious-equipotential system · Entelechy · Experimental embryology · Epigenesis · Gradient · Field · Wilhelm Roux · Positional information

1 Introduction

In the December 1913 issue of *Nature* the British morphologist Ernest MacBride (1913: 400, 401) made critical remarks against Hans Driesch's main proof of vitalism; if the value of a biological theory "is its fruitfulness in connecting facts and in leading to the discovery of new facts" then the concept of *entelechy* – which represents a nonspatial organizing agent that drives the organism towards the realization

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of its purpose – is “barren”. Rudolph Carnap later rejected Driesch’s vitalism for similar reasons. While the laws of science provide “*explanations* for observed facts” and “a means for *predicting* new facts not yet observed”, Driesch’s entelechy “does not give us new laws” and “did not lead to the discovery of more general biological laws” (Carnap’s emphasis 1966: 16; Chen 2018). Philipp Frank (1932/1998: 85, 125), another logical positivist, even severely considered that vitalism comes from the surrender of scientific *rationale* driven by “metaphysical moods”. If “the problem of the *method* of biology remains unaffected by the controversies between vitalism and mechanism” (Driesch’s emphasis 1913), is the idea that living bodies are guided by nonphysical agents strictly metaphysical? It may not be after all a coincidence that Driesch became a philosophy professor in 1909 and gradually abandoned his empirical research.

However, metaphysical principles have historically guided the elaboration of fruitful hypotheses and have been key elements of successful research programmes (Lakatos 1976). As a “meta-theoretical commitment” (Normandin and Wolfe 2013: 5), vitalism may indeed have *epistemic virtues* such as a distrust of simple explanatory models and their expansive generalization (Hein 1972: 165). Dupré and O’Malley (2013: 312) have suggested that vitalism in general acts as a “heuristic that stimulates productive inquiries into the nature of living and non-living things”. Does Driesch’s vitalistic view had a significant heuristic value for the progress of biology? To answer this question, we must first distinguish negative from positive function of a potential vitalistic heuristic. Negative heuristic of vitalism must clearly contribute in revealing the falsehood or at least the insufficiency of existing or virtual mechanical models, i.e. their flaws and their basic inadequacy with known living phenomena. On the other hand, using vital principles as *explanans* does not alone constitute a positive heuristic. Vitalism must rather guide the elaboration of biological concepts, theories, hypotheses or methods that somehow are added to the toolkit of successful research programmes. These derived epistemic products must therefore be involved in fruitful *explanans* that may lead to the discovery of new facts.

In order to examine this hypothetical heuristic, I proceed in this chapter as follows; first I investigate the potential role of Driesch’s vitalistic turn in the falsification of the Roux-Weismann thesis and Driesch’s own embryonic induction model. In the next section I shall: (1) evaluate the epistemic function of Driesch’s ultimate *explanandum*, the *harmonic-equipotential system* (HES), in the context of Charles M. Child’s gradient theory, Hans Spemann’s investigations on organizers and Lewis Wolpert’s positional information theory and (2) determine the role of Driesch’s vitalism in its formulation.

2 Driesch’s Empirical Falsification of Mechanical Models

As an embryologist, Driesch deeply undermined ontogeny most successful mechanical explanation of the 1880s: the so-called “Roux-Weismann thesis” (Hertwig 1896) that a mosaic of self-differentiating parts is led by the unequal distribution of

performed chromatic factors during cell division. He also highlighted the insufficiency of the induction model that he had elaborated as an alternative to Roux's mosaicism. In both cases the *explanans* was highly challenged by experiments that occurred before Driesch's vitalistic turn in 1899. Here I then show that Driesch's vitalism did not act as a negative heuristic on existing explanatory models.

2.1 *Entwicklungsmechanik and the Roux–Weismann Thesis*

We must first look back at the early history of *Entwicklungsmechanik*, Driesch's research program as an embryologist. Development, claims Wilhelm Roux (1885: 414), the originator of the program, is “the production of visible manifoldness [*Mannigfaltigkeit*]” and the origin of this manifoldness remains ontogeny greatest mystery: Is development new formation “in the strongest sense, the real increase of an effective manifoldness” (*Epigenesis*) or “the mere expression of latent and pre-existing differences” (*Evolution*)¹ (414)? This is the problem this new program for embryology mainly tried to solve.

Roux (1883) suspected that most of this morphological and functional manifoldness was already latent in the newly discovered chromosomes – which were soon related to heredity and called *idioplasm*² by the Neo-Darwinian August Weismann and others. Typical development would then involve the transfer of complexity from the chromatic organization to the becoming somatic organization by means of indirect cell division. But first the *modus operandi* of differentiation had to be specified. The formation of the whole embryo or of one of its parts is *self-differentiating* if it depends only on its own inner factors, while its differentiation is *correlative* if it also depends on external determinations. Self-differentiating development led by the nucleus would mean the actualization of pre-existing manifoldness in the germ – while correlative differentiation may have “epigenetic” effects, the production of new manifoldness.

In 1885 Roux expected complete self-differentiation of the organism performed by partial self-differentiation of its components, and in order to test his hypothesis, he carried out in 1888 what became his most famous experiment: the production of half- and quarter-embryos after having punctured frog blastomeres of 2-cell and 4-cell stages with a hot needle. Spared 2-cell stage blastomeres became

¹It has been shown since Karl von Baer that development consists in the metamorphosis of simpler forms into more complicated combination of parts, what Driesch (1908: I 25) calls epigenesis “in the descriptive sense”. Roux's renewal of the old question of preformation (or “evolution”) and epigenesis (Roger 1997; Duchesneau 2012) in the context of *Entwicklungsmechanik* conditioned the elaboration of “New preformationist” and “New epigenetist” theories of development (Maienschein 2005; Bolduc 2021).

²This concept originally comes from Karl von Nägeli's theory of heredity. Nägeli distinguished a highly organized molecular structure which he called “the idioplasm” from the cell nutritive plasma – the “trophoplasm”.

semi-gastrula and semi-neurula while still being attached to the operated blastomere in disintegration. In Roux's eyes, the development of the healthy part could not depend on the remaining uncelled plasma because fixing and staining processes later confirmed that the targeted chromosomes were destroyed by the heat. Because self-differentiation seems simpler and less costly than correlation, Roux (1888/1895: 454, 455) concluded that *typical* development (without experimental disruption) of the frog embryo was also, at least until neurulation, a *mosaic* of at least four independently developing parts. He also assumed that these results would eventually be generalized to every embryonic cell and was convinced at this stage that cell division often involves what August Weismann (1893: 34) later called *heterokinesis* – the unequal distribution of the inherited idioplasm to somatic cells. Although empirical evidences showed that the distribution of the chromatic material to daughter cells is always quantitatively equal, Weismann postulated a not yet visible decreasing complexity of the somatic nuclear organization at each differentiating cell division. The formation of the somatic body would then rely on a stem tree of cells (Dröscher 2014) in which each branching division would be heterokinetic; the somatic idioplasm of each cell then only contains the *Anlagen* (morphogenic qualities) that its descendants need according to their preestablished fate. This was the best mechanical explanation for the inferred self-differentiation of blastomeres.

2.2 *The Discovery of Part Formation*

As soon as 1890 Driesch was convinced that *Entwicklungsmechanik* was the central discipline of biology but did not endorse Roux's mosaic theory despite the most recent empirical results in its favor.³

Though Roux concluded from his experiments on frogs that development is the “metamorphosis of manifoldness” rather than its new formation (Driesch 1892a: 161), these had to be corroborated with similar experiments on other species. As Oscar and Richard Hertwig had already shown that vigorous shaking of unfertilized sea urchin eggs in water resulted in the separation of parts from each other (Maienschein 1994: 51), Driesch used this method to separate the first two blastomeres of cleaving sea urchin eggs. At the stage of sixteen cells he first witnessed half-embryos as expected, but the next morning he surprisingly found typical swimming larvae of half size (Driesch 1892a: 168). For Driesch this remarkable result showed that 2-cell stage sea urchin blastomere does not receive from the fertilized egg only half of the *Anlagen*. It is rather *totipotent* because “a normally formed whole larva can come from it; a part formation [*Theilbildung*], not a half-formation” (172).

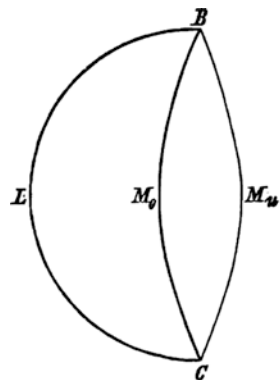
³The French teratologist Laurent Chabry (1887) obtained even more conclusive results than Roux by puncturing blastomeres of ascidian eggs. For example, the formation of a “demi-individual” from a two-cell stage blastomere without “post-generation” of the missing part clearly supported the mosaic theory (Fischer 1991: 38).

Roux (1893/1895) nevertheless interpreted this result in line with mosaicism: before these half-blastulas started reacting to their missing halves with *post-generation* process, their initial formation clearly showed the self-differentiation of the first blastomeres. In fact, Roux himself had noticed in 1888 late regeneration of punctured, seemingly dead halves of frog embryos. He understood post-generation as functional adaptation to the disruption of typical conditions and thought it must be distinguished from “direct” development (Roux 1888/1895: 520): (1) by its *modus operandi*, correlative differentiation; (2) by the material involved – a *reserve idioplasm* that is located in the nucleus of each cell. In the case of his famous frog experiment, Roux assumed (without any empirical evidence) that this back-up nuclear material travelled from the developing half to the destroyed half during gastrulation before proceeding with nuclearization and cellulation of inert protoplasmic substance. Weismann (1893) then suggested a mechanical model for regeneration that was based on multiple “accessory” idioplasms; for example, because the same worm cells give rise to the tail-end or to the head-end of the worm according to whether they are situated on the anterior or posterior surface of the amputation plane (126), he assumed that each worm cell had two accessory idioplasms (one for each end). According to this model each possible morphogenetic fate therefore relies on a separate idioplasm.

However, there is a crucial difference between these types of “post-generation” and sea urchin part formation: in the former the development of the healthy part is not affected by the regenerating part, while the latter involves the complete cellular *re-differentiation* of the isolated halves. Driesch did not witness the part formation itself but inferred that the opening of the half-blastula was closed by bringing together and merging the adjacent sides (M_o and M_u) (Fig. 1): the material which normally belongs to the median region would in this case form the right side, but at least no change of the embryo *polarity* would be required. It would involve nevertheless a global redistribution of the cell morphogenetic fates.

Sea urchin blastomeres are indeed totipotent, admitted Roux, but only because they can rely on a reserve nuclear material that can take over “indirect” development

Fig. 1 Simplified illustration of a half-blastula hemisphere. **L** left side material; **B** and **C** poles of the median plane; M_o and M_u adjacent edges of the median region. (Reproduced from Driesch 1892a)



in case of “defect.” Roux (1893/1895: 839) still acknowledged that how this material was triggered and at what scale cell correlation was taking place was totally unknown at this point. Driesch (1894: 11) however expressed his opinion on the current state of mosaicism with a vivid image: “Roux’s theory is a pyramid stood on its point: below, the hypothetical basic notion, above auxiliary hypotheses pile up and finally as a heavy base on top – my simple experimental results”. Even Weismann (1893: 137) sensed the threat of Driesch’s crucial experiment for his whole Neo-Darwinian system, questioning the reliability of the experimental method (Churchill 2015: 418). The *ad absurdum* multiplication of accessory idioplasms that was needed to match all possible morphogenetic fates of sea urchin blastomeres was definitely *ad hoc*. Idioplasms then represented the unbearable epicycles of Weismann’s system as the new regulative phenomena seemed impossible to save.

2.3 *Driesch’s Method, Axiom and Prospective Approach*

When he published his result on part formation, Driesch (1892a: 161) thought that it “exceeded yet known physical (mechanical) phenomena” but expected that “it will probably be subordinated to the mechanistic view of the whole phenomenal world.” This position, which he called “unmetaphysical vitalism,” was in line with the mechanistic heuristic⁴ that dominated research programmes in morphological and physiological sciences at the time. In his methodological essay for *Entwicklungsmechanik*, Driesch (1891) philosophically justified the biological quest for mechanical explanation appealing to Otto Liebmann’s Neo-Kantism. If space is a pure form of perception and geometry is its science, then any natural phenomenon first ought to be geometrically – hence mathematically – represented (Waisse-Priven and Alfonso-Goldfarb 2009: 42). Natural events must secondly be expounded in physical terms. In this view, knowledge of organic forms first requires the mathematical formulation of the problem, while the latter is only solved “*when it is [...] reduced to the laws of mechanics and represented as a consequence of these laws*” (Driesch’s emphasis, 1891: 9).

In light of part formation and other fruitful experiments such as the “compression effect” (see Posteraro, Chapter [Vitalism and the Problem of Individuation: Another Look at Bergson’s Élan Vital](#), in this volume), Driesch followed to some degree this methodological order by first formulating the problem using geometrical notions such as mathematical function – i.e. the correlation between two variables

⁴This mechanistic heuristic prohibits the insertion of a teleological cause into the *explanans* of phenomena and leads to a convincing or provisional explanation of high level regularities in terms of lower level regularities which are provided by physiology, chemistry, physics and their technical applications.

($x=f[y]$) – and location in space. In this way he started elaborating a new *explanandum* – which he will later call HES – under the formulation of this axiom: “*The relative location of a blastomere in a whole will probably determine what will generally come out of it; if it is different, it will result in something else. In other words: its prospective relation [morphogenetic fate]⁵ is a function of [is correlated to] its position*” (Driesch’s emphasis 1892b: 39). The formulation of this axiom entails the rejection of Roux’s distinction between typical self-differentiation and adaptive correlation: if the fate of the blastomeres generally depends on their relative position within the embryonic whole, then the differentiation of their future cell lineage is *essentially* correlative. If the blastomeres of some species do in fact never re-differentiate and if some do it later than others, it may be due to unknown physical obstacles, such as the consistency of their egg protoplasm (Driesch 1908: I 73). The idea of unequal transmission of hereditary determinants through cell lineages was giving way to holistic determination.

This position led Driesch to rethink the problem of the origin of developmental manifoldness in a *prospective* way. Starting from a given visible manifoldness, Roux was asking *retrospectively* for its causal origin; a given form was either already implicit in the germ from the beginning (preformation) or a new formation (epigenesis). Driesch (1894: 75–78) now sees inherited manifoldness as the material conditions of morphogenetic *possibilities* – which he calls *prospective potency*. The increasing restriction of these potencies takes place during development until the morphological fate of the parts – or *prospective value* – is irrevocably defined. The question of preformation and epigenesis then takes this form: “Is the prospective potency of each embryonic part fully given by its prospective value in a certain definite case; is it, so to say, identical with it, or does the prospective potency contain more than what the prospective value of an element reveals in a certain case?” (Driesch 1908: I 77). For example, the regeneration of dissected sea urchin gastrulas shows that ectodermal and endodermal cells have reduced prospective potencies compared to the totipotent blastomeres; they also have different prospective potencies because an ectodermal cell cannot re-differentiate into an endodermal cell and vice versa. Furthermore, all (ectodermal or endodermal) cells that belong to the same germ layer have the same prospective potency – i.e. they are equipotential – because a whole dwarf layer can regenerate from its dissected parts. This new prospective view and its related concepts played a key role in determining the holistic properties and specificity of developmental systems. These systems were now asking for a convincing mechanical explanation. This second methodological step represented the embryologists’ greatest challenge.

⁵Driesch (1899: 41) later specifies that the terms *prospective relation* (*Beziehung*) and *prospective value* (*Bedeutung*) both refer to the realized morphogenetic fate.

2.4 Driesch's Induction Model and Its Empirical Falsification

Because he acknowledged that eggs are purposeful arrangements of complex physico-chemical relations, Driesch never tried to *immediately*⁶ account for part formation and other cases of re-differentiation in physical terms. In *Analytic Theory of Organic Development* (1894), he rather elaborates an explanatory model that reduces the functioning whole (the *explanandum*) to the inferred properties and activities of its parts. With his “machine theory of life” Driesch (1896) was the first to introduce the idea of cell induction as a differentiating mechanism and anticipated the embryonic field theory.

Despite the precise ordering of mitotic and meiotic figures, Driesch considered that correlative differentiation cannot rely on the internal determination of a complex nuclear structure but rather on the increasing complexity of a three-cornered inductive network between (1) centers of formative stimuli that are specifically localized within the embryo, (2) the protoplasm of each cell and (3) its nucleus (Churchill 1969; Caianiello 2019). He postulated that all nuclei are heterogeneous mixtures of ferments that contain all necessary *Anlagen* for development. However, as catalytic-like materials these ferments do not directly induce cell differentiation but only give “direction” (*Leitung*) (Driesch 1894: 88) to the morphogenetic processes that take place in the protoplasm. The latter is then far from being passively formed by the organized expression of nuclear qualities, but rather acts as a “mediator between the inductive cause and the nucleus” (81). In other words, it represents both a dynamic filter and a trigger that switches from a stimulus-specific responsive state to another depending on its current composition. Only under precise chemical conditions can certain stimuli from the extracellular environment modify these same conditions which can feed back on the nucleus by releasing specific nuclear ferments into the protoplasm; these would in turn reconfigure the protoplasm responsive state (90) allowing the reception of other external stimuli or a new differential release of nuclear ferments and so on.

This pattern explains how cells that differentiate into different tissues can have equipotential nuclei: the fate of each cell depends on the differential selection of extracellular stimuli and on the nuclear ferments that modified the protoplasm throughout the course of development. The protoplasm then becomes the core of a differentiation loop that connects the cell to the whole embryo. Driesch's theory also replaces the highly contested heterokinesis as the best explanation for the progressive restriction of prospective potency; under determinate changes the protoplasm would become gradually and irreversibly unresponsive to specific formative stimuli and types of ferments. And most importantly, it illustrates how the production of new qualitative manifoldness is possible:

⁶Causal analysis is still considered by Driesch (1908: I 119) as an *indirect* reduction to the laws of physics, because “the full analysis of morphogenesis into a series of single formative occurrences” may one day be completed by “the analysis into the elemental facts studied by the sciences of inorganic nature”.

Development starts with a few ordered manifoldnesses, the ones that are given in the structure of the egg; but the manifoldnesses create, by interactions, new manifoldnesses, and these are able, by acting back upon the original ones, to create new differences and so on. For each effect there is immediately a new cause and the possibility of a new specific response, namely a new specific reactivity. We infer a complex form from a simple one given in the egg [...] consequently our theory is epigenetic *with respect to the origin of form as such* (Driesch's emphasis 1894: 86).

Driesch (1914: 197) will later believe that this kind of mechanical epigenesis violates the aprioristic ontological principle⁷ that “the degree of manifoldness of a natural system can never increase of itself”. This is why in the presumed absence of an equivalent pre-existing structural manifoldness, Driesch (1908: II 197) will appeal to “entelechy as an intensive manifoldness”; by purposefully suspending determinate physico-chemical reactions in the course of development, this vital agent achieves, like “the ‘demons’ of Maxwell” (198), what mere physical systems could never achieve by themselves.

In 1894 Driesch was still trying to mechanically account for the fact that the prospective value of a cell that belongs to an equipotential system is a function of its position. The first issue was how cells were localized. As experiments had shown that the egg polarity and the median plane set the direction of further cleavage, Driesch (1894: 14) inferred that they constitute a geometrical *coordinate system* (Driesch 1899: 49) that initially localizes cells within the embryo. As the latter grows, mechanical stimuli would come from cells under physical tension (*Zuginduktion*) (Driesch 1894: 83) and the emission of chemical stimuli would occur most likely from determinate points (such as poles) within the boundary region of the whole. Driesch assumed that, depending on its position and current reactivity, each cell receives various inductive stimuli *differentially*. Yet because each germ layer or tissue is typically delineated, the protoplasmic response cannot be gradual; cells would then only embark on the path of (ectodermal, epidermal, etc.) differentiation when the amount of received stimuli of a certain type exceeds a definite threshold.

But the greatest issue remained: when a part of the original whole is missing, how the new whole becomes the center of development (Driesch 1899: 20)? How do cells *harmoniously* re-differentiate, i.e. how do they “work together” (Driesch 1914: 209) to develop organs in proportion with the size of the new whole? As we previously saw (Sect. 2.2), the most likely scenario for sea urchin part formation is that while closing over, half-blastulas do not lose their polar axis; yet Driesch considers that their cells nonetheless lose their needed alignment with the poles. Because his analytic theory alone cannot explain how disoriented cells are still able to develop normally, he then postulated that the cell repolarization started after the disturbing event and was physically mediated by the magnet-like effect of the electrical charge of each individual blastomere (Driesch 1894: 22).

However, new experiments including Driesch's own dissection of a sea urchin gastrula in 1895 highlighted the insufficiency of this model as the weight of new

⁷Though akin to the second law of thermodynamics, this general principle is not limited to energetic “intensities” but rather encompasses “diversity of distribution” (spatial arrangements).

anomalies became unbearable. Driesch sliced a complete gastrula at the equator so that each half-gastrula contained the half of both ectoderm and endoderm (Driesch 1899: 9, 10); not only were the missing parts of both halves quickly restored but also the gut of each sub-product later showed a smaller but typical shape (the strict proportion between the fore-, mid- and hind-parts of the gut was strictly maintained). How this harmonious re-differentiation can happen even without one of the polar regions, which were viewed as essential parts of the coordinating system? Together with the hydra and the starfish embryo (20–24), the sea urchin embryo is a type of HES (45) that is somehow able to achieve what Driesch calls “secondary regulatory phenomena” (47), namely the prior reinstatement of a new coordinating system according to the new dimensions of the whole. And if we follow Driesch’s induction model, the healed gastrula would then have to chemically reset all the protoplasmic filters and trigger the release of inductive stimuli from newly located emission points (Churchill 1969: 182). As a result, Driesch (1899: 37) not only concluded that there was an obvious “gap” in his analytical theory, but more significantly, that it was impossible to localize the causal processes that result in these regulatory responses. So instead of trying in vain to improve a model that was based on the “false dogma” of the machine theory of life (9), he abandoned it altogether. In 1899 he then spoke of “peculiar elementary lawfulness” (70) and “vitalistic causality” (71) but his vitalistic philosophy did not find its relatively complete form before the *Gifford Lectures* in 1907.

We now clearly see that Driesch’s “metaphysical” vitalism was the consequence rather than the condition of the empirical falsification of past mechanical *explanans*. When Driesch discovered the secondary regulatory phenomena he still adhered to the “machine theory of life,”⁸ but no longer saw how such a theory was possible.

3 The Challenge of HESs and the Positive Heuristic of Driesch’s Vitalism

3.1 *Critical Idealism and the Argument for Vitalism*

Before starting his research program, Roux (1881: 229) said that the developing organism was like a music box that can learn new songs everyday while building itself. Within a decade experimental embryology however revealed the astonishing regulatory power of many invertebrates and amphibians; these could then rather have been compared with music boxes that still play the same old song even when

⁸Innes (1987) and Sander (1997) suggested that all along the 1890s Driesch was one step away from openly identify himself as vitalist because he was already acknowledging the “teleological” character of development. I think the idea that Driesch was a “closet vitalist” until 1899 is misleading. Driesch (1899: 36) clearly defines his past mechanical conception of life as “static teleology”, which only refers to the purposeful arrangement of the egg starting structure. This view was also endorsed by Roux (1881: 2), who made the distinction between purposiveness and (nonmechanical) teleology.

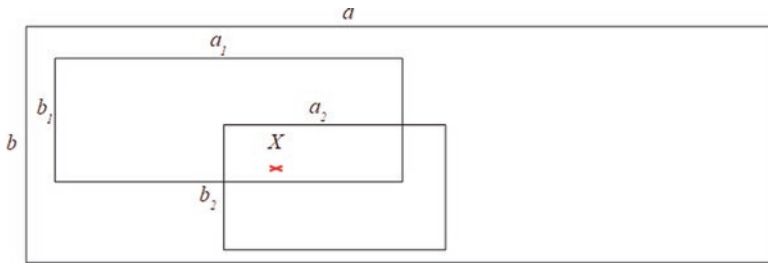


Fig. 2 One of Driesch's diagrams geometrically representing the HES formula. An element X can be part of the system $a b$ or $a_1 b_1$ or $a_2 b_2$. The prospective value of X would be different in each case. (Reproduced from Driesch 1908)

half of their parts have been removed! But after 1899 Driesch was convinced that HESs were not mere machines and he intended to prove it, not with further experiments, but with philosophical arguments.

It was then within the framework of his “Neo-”⁹ vitalism that Driesch developed the more thorough analysis of HESs. He first updated the *explanandum* to demonstrate that it was really a problem which, if approached exclusively from a mechanistic point of view, was unsolvable. He first added a variable that was missing from the 1892 axiom (Sect. 2.3): the prospective value of a cell X is not only a function of X relative position (l), but also of the absolute size (s) of the system to which X belongs (Fig. 2). The new mathematical equation was at this point $(X) = f [l, s, \dots]$ (Driesch 1908: I 124) but the “ E factor” still had to account for the necessary realization of X according to l and s in every possible case. The final formula was $(X) = f [l, s, E]$ but the exact nature of E remained to be clarified.

This is precisely where Driesch subtly leaves the *explanandum* for the *explanans*, as he explains why the E factor cannot be a self-differentiating machine:

Every volume [a b, $a_1 b_1$, $a_2 b_2$, etc.] which may perform morphogenesis completely must possess the machine in its totality. As now every element of one volume may play any possible elemental role in every other, it follows that each part of the whole harmonious system possesses any possible elemental part of the machine equally well, all parts of the system at the same time being constituents of different machines [...] you may ask yourselves if you could imagine any sort of a machine, which consists of many parts, but not even of an absolutely fixed number, all of which are equal in their faculties, but all of which in each single case, in spite of their potential equality, not only produce together a certain typical totality, but also arrange themselves typically in order to produce this totality (Driesch 1908: I 140, 153).

At this point Driesch argues that the E factor can be nothing but *entelechy* – a non-physical agent that purposefully uses the matter of the egg during development as a mean to achieve its typical form. Driesch's main proof of vitalism takes the logical form of the following *modus ponens*:

⁹Driesch differentiates his own vitalism from past “naïve” vitalism mostly by the fact that the former did not arise from the direct “contemplation of life's phenomena” (1914: 19), but rather *indirectly* by first making sure that mechanical causality was insufficient to explain these phenomena.

Premise 1: If HESs cannot be machines, then they are driven by an entelechy.

Premise 2: HESs cannot be machines.

Conclusion: HESs are driven by an entelechy.¹⁰

As we can see from the last quoted passage, Driesch also provides sub-arguments in support of the second premise: unlike HESs, no machine is contained in all its parts and no machine is fragmented without its functioning being impaired (Weber 1999). This of course applies to actual artefacts like “the phonograph” but also to “any sort of machine imaginable in physics and chemistry” (Driesch’s emphasis, 1908: II 81). Does the concept of “possible machine” is defined by any machine “that Driesch has [subjectively] in mind” (Conklin 1929: 30)?

In Driesch’s view, possible machines are virtually circumscribed by what he calls *singular or additive causality*, where the sum on the side of the cause corresponds to the sum on the side of the effect. The primary characteristic of mechanical reasoning is the localization in time and space of connected physico-chemical events, whereby the parts involved “are changed in themselves, irrespective of the others” (Driesch 1914: 199). Against Kant’s transcendental analysis, Driesch also intended to show the apriority of another type of causality – the *individualizing causality* – by which “a distribution of the things in one system of the form of a mere *sum* would be transformed into a distribution that would be in some sense a *unity* or *totality*, without any spatial mechanical predetermination of this totality” (200). By first insisting on the insufficiency of all possible mechanical account of HESs, he ensures that, in order to be known, these empirical objects need to be subsumed under the pure concept of individuality, which proves that this type of non-spatial causality – and therefore entelechy – exists in nature (207).

“Neo-vitalism” therefore relies on a renewed critical idealism (Bolduc [Forthcoming](#)). Because entelechy is viewed as the product of critical philosophy, Driesch does not personally see it as a metaphysical dogma, but as a legitimate scientific fact (Bognon et al. 2018). However, if we acknowledge the possibility of *a priori* knowledge as a metaphysical assumption, then Driesch’s vitalism is at least rationally grounded in metaphysics. In any case this does not make it scientifically irrelevant and its value as a positive heuristic remains to be determined.

3.2 *HES: The Developmental Explanandum of the Twentieth Century*

Although it was highly discussed among scientists in the first decades of the twentieth century, Driesch’s concept of *entelechy* never positively integrated the theoretical framework of embryological research programmes. While it was mostly yet not

¹⁰My formal reconstruction of Driesch’s argument was made in part from Driesch 1908: I 119, 187.

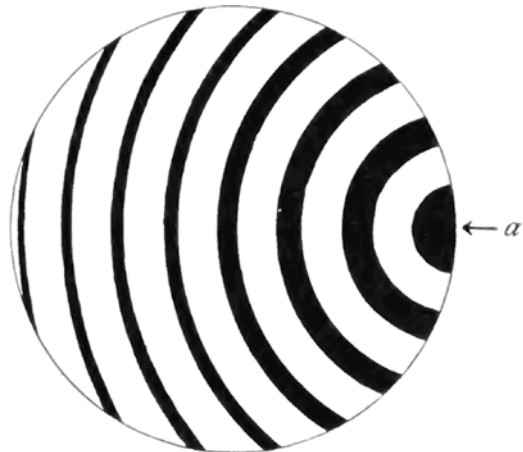
only criticized by the scientific community, its lack of heuristic value comes primarily from the impossibility of directly falsifying or corroborating Driesch's hypothesis. How could experience testify to something that is "not localisable at any point in space-time" and "being incapable of measurement, it cannot be a form of energy" (Needham 1936: 69)? Driesch himself conceded that it was "of quite limited application" as "vitalism has nothing to do with the progress of zoology as a pure science in the narrower sense of the word" (Driesch 1913).

3.2.1 Child's Metabolic Gradient Theory

At best, entelechy was used by biologists as a negative hypothesis to promote their own *explanans* for HES. Even the American zoologist Charles M. Child (1915: 24), who made relevant criticisms against the concept of HES (Sect. 3.3), thought that new vitalistic theories represented a real advance over Weismann's theory, for they "have at least the merit of recognizing and meeting squarely the real problem", namely "organic individuality" (Child 1916: 512). In Child's eyes, Driesch was right to stress on the need for a *dynamic* biological theory of the individual that "must deal primarily with processes, not structures, and with changes, not with static entities" (513). And Child explicitly meant that his metabolic gradient theory was the only plausible mechanistic alternative to Driesch's entelechy (519).

According to Child's theory, the process of organic individuation is based on stimuli coming from specific points in the protoplasmic mass (made of one or many cells) that increase the metabolic rate of the affected regions (these stimuli can be inherited or emerge *de novo* from external factors). Experiments showed that the metabolic activity resulting from points under stimulation is transmitted by axial gradients (Fig. 3) to other regions of the whole like the spreading of a wave. The intensity of a transmitted metabolic rate depends on the relative conductivity of the surrounded protoplasm and on the distance that separates a given region from the starting point (*a*); the energy of a gradient then relatively fades off as it is passed on

Fig. 3 Diagram illustrating a single axial gradient in a protoplasmic mass. *a*, the stimulation point. (Reproduced from Child 1915)



from one region to another. Many axial gradients coming from different stimulation points can simultaneously act upon the same region to a greater or lesser degree, so that the metabolic condition of the given region will result from its position in the overlapping gradients (Child 1915: 39). Most importantly, Child's major thesis is that *qualitative* differentiation comes primarily from *quantitative* differences of metabolic activity (Child 1916: 515). While irreversible differentiation is first caused by the persistence of gradients over time, changes in the stimulation pattern, mostly at the early stages of development, can transform the morphogenetic fate of the related parts. Child's gradients had a theoretical advantage over Driesch's first induction model: constellations of metabolic rates are more plastic and therefore more adaptable to new conditions than the chemical composition of cells. In sum, if a part of a lower organism that becomes isolated from the rest of the body does not lose the original gradient axes, the metabolic condition of its own parts will then proportionally tune with the size of the new whole; in the opposite case new gradients will emerge from the new external conditions. In both cases the piece can develop into a new individual (Child 1915: 46).

Because metabolic rate was in some way subject to empirical testing, Child's system had significant experimental and theoretical success during the 1930s, highlighting the role of metabolism in normal and abnormal development (Huxley and de Beer 1934/1963). Although its explanatory scope turned out to be more limited than first expected, recent studies on metabolic gradients in response to spatial stimuli in cytoplasm could still lead to a better understanding of the relationship between energetic and genetic factors in development (Blackstone 2008).

3.2.2 Hans Spemann, Organizers and Fields

Unlike Child, the German embryologist Hans Spemann openly adopted Driesch's HES concept as one of the main guiding problems of his research program (Allen 2004: 467, 468). By evolving the method of transplantation, Spemann's team was able to address the problem – first formulated by Driesch (Spemann 1938: 199) – of the prospective potency progressive restriction (epigenesis, Sect. 2.3). They, for example, exchanged a piece of presumptive neural tube from a newt young gastrula with a piece of presumptive external gills from another newt young gastrula. Each grafted piece developed not according to its origin but passively followed the development of its host (Spemann 1927: 179). These pieces were then equipotential at this stage as each one integrated perfectly into its new whole: “The development of the part is a function of its situation in the whole” (Spemann 1938: 348). Spemann also inferred that some factor was locally determining the fate of the transplanted pieces. This type of factor was famously discovered by Spemann's assistant, Hilde Mangold, when she took a piece from the upper lip of the newt blastopore and transplanted it into an indifferent region of another newt gastrula: not only did this grafted material not follow the development of its new host, but it also forced “the surrounding parts to follow its own direction” (Spemann 1927: 180), as a second embryo developed at the expense of the host material. Because it “induces a ‘field

of organization” in its surrounding, Spemann named it the “organizer”. Other organizer phenomena were quickly found in echinoderms, insects, birds and mammals.

The organizer was behaving, stated Spemann, “like a harmonious equipotential system of Driesch” (183). This significant association meant more than the mere subsuming of Hilde Mangold’s outstanding discovery under Driesch’s concept: Spemann here suggests that the organizer represents the key clue to the riddle of HES. It is not “intensive manifoldness”, Driesch’s “idealistic” entelechy (Spemann 1938: 347), but rather a localized structure that induces a field of organization which is, like the field of physicists, “extensive manifoldness” (302) – a pattern that operates spatially and hence materially. As transplantation experiments also showed the existence of second and third grade organizers – e.g. the *Triton* eyeball is itself induced by the mesoderm before it organizes a lens – the whole development appeared as “composed of single processes connected by organizers” (Spemann 1927: 186). Above all, the “field action” of these organizers was not a mere physical metaphor but a tool to describe and infer empirical facts (Spemann 1938: 305): in several cases the embryonic fields exceed the limits of the organ that they induce; they often overlap and when they do, one field must win the “rivalry” (311) for induction; some embryonic fields persist throughout development and during the adult stage (regeneration) even when there is no reacting material under their influence; like Child’s metabolic gradient, the power of an induction field appears to decrease from the source towards the borders; heteroplastic transplantations (grafting a piece from a donor of another species) suggest that fields release specific “genotypic potencies” (350) that were already latent in the reacting material.

Spemann admitted that biologists had “yet no real conception of what this means in the language of physiology” and that “the equipotential system capable of harmonious differentiation still remains as a real problem” before adding: “attempts to solve this problem, partly logical, partly experimental, induced several investigators to introduce into experimental embryology the conception of the ‘embryonic field’” (347, 348, 366). This statement clearly highlights the epistemic value of Driesch’s challenging *explanandum*.

3.2.3 Lewis Wolpert’s Positional Information Theory

With the discovery of gene regulation in the 1960s, a convincing explanation of HESs looked within reach. By elaborating a hypothetical cybernetic model made of different regulatory and enzymatic genes, Jacques Monod and François Jacob (1961) had already addressed the problem of how embryonic cells with the same genetic code may differentiate. But according to the British developmental biologist Lewis Wolpert (1969: 4), almost no progress had been made in the area of pattern formation since the 1920s when concepts such as regulative development, gradient and field were elaborated. Wolpert, who considers Driesch as one of his precursors (Horder 2001: 121), reinterpreted these notions within the context of his positional information theory, which he inferred directly from HESs. He formalized the latter in terms of the “French Flag problem”:

This problem is concerned with the necessary properties and communications between units arranged in a line, each with three possibilities for molecular differentiation – blue, white and red – such that system always forms a French Flag irrespective of the number of units or which parts are removed [...] This abstraction of the problem corresponds quite well with experimental observations on the early development of sea urchin embryos, and regeneration of hydroids as well as a large variety of other systems (Wolpert 1969: 5).

This simple schematic illustration of morphogenetic fate specification whereby each band of colour represents a differentiated part (e.g. germ layer) displays the same property as Driesch’s concept, namely “size invariant” regulation of typical patterns.

By referring to *The science of the organism*, Wolpert (1974: 674) pointed out that Driesch was the first to put forward the idea of position specification. In fact, Wolpert unprecedentedly inferred from the correlation between the position of a cell in the whole and its prospective value that: (1) there are *mechanisms* whose function is to specify the *positional value* of each cell – i.e. the position of each cell with respect to one or more points in the system; (2) these mechanisms are distinct from and operate prior to differentiation processes. Therefore, positional information is first “read-out” by a given cell and afterwards converted into molecular differentiation. The positional value of cells in HES is first specified by a set of reference points that form a coordinate system made of one or more bipolar¹¹ axes. In Wolpert’s landmark paper of 1969, the physiological nature of these determinations remained (and in many cases still remains) to be clarified, but the author advanced that metabolic or molecular (morphogen) gradients may be involved because threshold effect, which explains reversal of polarity and field¹² dominance, can rely on both. He also made it clear that the interpretation of positional information depends “on the developmental history of the cell and its genome” (Wolpert 1969: 16). The role of the genome in positional signalling has been notably demonstrated with the discovery of the *bicoid* gene (Wolpert 1989: 5), which codes for the Bcd protein in *Drosophila* embryo. The patterning of this gradient along the anteroposterior axis exemplifies how positional information contained in a “morphogen gradient is transformed into discrete and precise patterns of target gene expression” (Crauk and Dostatni 2005: 1888).

At some point advances like this one led Wolpert (1985: 358) to believe that the *E* factor of Driesch’s formula ($X = f[p, t, E]$) was the genetic program contained in each cell. However, in the “postgenomic” era many theorists of biology (for example Robert 2004) consider this notion just as animistic as Driesch’s entelechy. In fact, Wolpert (1989: 8) himself recognized that the original positional information theory “tried to do too much”; it is nevertheless still paradigmatic today as new versions of the French Flag model take into account the “patterning by several interacting, spatially coupled genes subject to intrinsic and extrinsic noise” (Hillenbrand et al. 2016).

¹¹“Polarity is defined as the direction in which positional information is specified or measured” (Wolpert 1969: 1).

¹²A field is constituted “when cells have their positional information specified with respect to the same set of points” (Wolpert 1969: 7).

3.3 *Is HES a Vitalist Concept?*

The concept of HES may be “the most distinctive and novel thing” in Driesch’s doctrine (Lovejoy 1911: 77) and clearly acted as a positive heuristic in the twentieth century embryology. However, one can still argue that, although Driesch’s neologism coincides with his vitalistic turn in 1899, it is not essentially tied with his vitalistic view and the latter did not play a significant role in its development. After all, the essential characteristics of HESs had already been identified in 1892 (Sect. 2.3), when Driesch still embraced the “machine theory of life,” like Roux and other embryologists. And according to Driesch (1899: 77, 78), the distinction between describing the *explanandum*, which results from answering, “What is actually happening here?,” and finding the *explanans* – the solution to the problem “Why does this happen?” – is clearly made when the scientific method is properly followed, as Galileo and Newton have shown. Following this reasoning, one could then affirm that the concept of HES would still have been created if Driesch had kept his original mechanistic view.

This would nevertheless be a wrong conclusion mainly because Driesch did not only view HES as an *explanandum*, but above all as his crucial *proof for vitalism*: “in the theory of the harmonious-equipotential system”, he stresses, entelechy “*must necessarily be applied*” (Driesch’s emphasis 1913). As we previously saw (Sect. 3.1), in this peculiar case he blurred the demarcation between the problem and the solution as both were parts of the same argument. The formula with the “E” factor, the diagrams, the abstract regulative power: the more the behavior of HESs seemed far from pure mechanical capacity, the more the entelechy hypothesis looked convincing.

This is why HES was from the beginning a very controversial concept. As “Driesch himself remarks that it is only ‘an approximate, as it were, figurative, method of speech,’” notices the American zoologist Herbert S. Jennings, “*no such thing as an equipotential system exists among organisms*” (Jennings’ emphasis, 1918: 586). In fact, it was Child (1908: 580) who first made a highly critical analysis of Driesch’s concept, which he called an “apparent problem” (*Scheinproblem*). Firstly, he raised that material likeness does not follow from prospective equipotentiality. Driesch’s belief that the material basis of the system is a relatively formless *means* for achieving the end of entelechy makes him deny the existence of not yet visible material differences between elementary parts coming from their past histories or external conditions: the problem then falsely appears to be “the self-production of heterogeneity from homogeneity”. Secondly, parts that are isolated from the whole are in fact never equivalent, as regional differences often remain from their previous differentiation and various internal and external changes result from their isolation. Finally, size invariance of regulative development or regeneration is only achieved *approximately* and with pieces of a certain size.

Spemann significantly pointed out what may be the paradox of HESs: although they “are perhaps never either harmonious or equipotential exactly in the sense of Driesch” (Spemann 1938: 347), they are still considered as a *real* problem. By

abstracting and extrapolating essential properties from empirical events, by giving to these properties graphical and mathematical representations and by opposing them to existing and virtual mechanical realizations, Driesch failed to convince that entelechy was the answer but had nevertheless a lasting impact on how organic development was viewed and scientifically approached.

4 Conclusion

Driesch's vitalistic thesis, whereby HESs cannot be machines and hence are driven by non-spatial and purposeful "entelechies", did not falsify explanatory models nor reveal their flaws. The Roux-Weismann thesis was rather severely questioned by the discovery of the part formation in sea urchin embryo, which was achieved by Driesch under a pure mechanistic framework. Similarly, Driesch abandoned his induction model for his vitalistic thinking because it was not up to the newly discovered secondary regulatory phenomena. Nor did the concept of entelechy directly serve as a positive heuristic; because it was not empirically measurable nor testable, it could not guide insightful experiments towards the discovery of new facts. However, Driesch's notion of HES constituted an important positive heuristic for developmental biology throughout the twentieth century: though Child interpreted it as an unfaithful representation of empirical events, his metabolic gradient theory was nonetheless presented as an answer to the problem of organic individuation as conveyed by Driesch; among other biologists, Spemann openly considered the HES as the ultimate *explanandum* of embryology and saw the field theory as a promising step towards its explanation; Wolpert based his positional information theory on the French Flag problem, which is a formalized illustration of HESs. While it is true that the elaboration of the HES concept started with the axiom of part formation in 1892 and with the prospective approach to the problem of epigenesis in 1894, Driesch designed the reference and most impactful version of this *explanandum* as an essential part of his main proof for vitalism. In 1908, holistic or "harmonious" outcomes of development were: (1) systematized and abstracted from real material restrictions; (2) represented in persuasive diagrams and by the mathematical formula with the "E" factor; (3) defined as dynamically purposeful and irreducible to mechanical means.

I believe that these results provide further insights into the process of discovery at least in developmental biology. They show that, despite having often been labeled as unscientific, substantial vitalism (Wolfe 2011) can have a real scientific value; in this case it was able to influence the way the problem of development was understood by biologists and addressed within leading research programmes. As Child suggested, the specificity of vitalistic theories may consist in recognizing the *essence* of the problem. One reason for this may be that vitalists do not carry the

burden of offering a convincing mechanical¹³ solution to it. However, this study also highlights that the boundary between the *explanandum* and its *explanans* is often permeable; by aiming attention at the holistic and “purposeful” dimension of organic development, Driesch’s concept of HES leaves in the dark the complexity of the chromatic structure and the material and functional manifoldness underlying (inter)cellular activity. But in this historical case at least, vitalistic and mechanistic thinking appear to have scientifically complemented each other, insofar as the former tended to establish what organisms can do and the latter, why or how they do it.

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¹³Here again, “mechanism” is taken in its *causal* sense. As Roux clearly stated, mechanical explanation of development mostly involves the analysis of *complex components* – which are not yet explicable in physico-chemical terms – into more elementary causal processes (Roux 1896; Needham 1936: 20, 21). Metabolic gradients, embryonic fields and patterns related to positional information are therefore complex components in Roux’s sense and are subjected to causal analysis.

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