From Machine-Theory to Entelechy: Two Studies in Developmental Teleology

FREDERICK B. CHURCHILL
Department of History and Philosophy of Science
Indiana University, Bloomington

The 1880's and 1890's were exciting decades for a young embryologist. At the outset, Wilhelm Roux announced his program of Developmental Mechanics (*Entwickelungsmechanik*),[1] designed to seduce investigation away from endless comparative descriptions of embryos into an experimental analysis of developmental events. Eduard Pflüger, Gustav Born, and Oscar Hertwig, to name a few, championed the same experimental approach in embryology at nearly the same time. By the 1890's the ranks of experimenters had swelled to include Hans Driesch, Curt Herbst, T. H. Morgan, and many others. It was a time when certain techniques developed in plant physiology and cytology converged onto embryology to broach questions about the activities within the cleaving egg —questions, more specifically, about the role of the nucleus in heredity and development, about the formative influences exerted by some cells upon other cells or by external stimuli, and about the regenerative capacities of experimentally altered embryos. Amphibians and echinoderms were the chief martyrs in these quests, but roundworms, gastropods, even protozoa, served embryology too. There were almost as many explanations of development and heredity as experimental animals, and often the choice of the latter determined the tenets of the former. Yves Delage, at the turn of the century, described over thirty general theories of heredity, most of them contemporary and many of them arising directly from experimental embryology.[2]

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[1] Roux first used the term *Entwickelungsmechanik* in the introduction to a series of papers in experimental embryology. "'Einleitung' zu den 'Beiträgen zur Entwickelungsmechanik des Embryo'," *Z. Biol., 21* (1885), 411–428.

[2] Delage, Yves, *L'Hérédite et les grands problèmes de la biologie*

One of the most highly speculative yet provocative theories of the time came from the pen of August Weismann. Since I will refer to it on a number of occasions it is worth describing it briefly. Known as the germ-plasm theory of 1892,[3] it was an all-embracing theory which attempted to explain evolution, development, and heredity completely within mechanistic terms. Weismann postulated the existence of a germ-plasm which was located within the nucleus and was subdivided into a hierarchy of self-replicating units, each level of which served to explain a different set of phenomena. The pertinent feature of the germ-plasm theory, as far as this paper is concerned, was Weismann's belief that embryonic development consisted largely of qualitative nuclear divisions which segregated the developmental or chromatin material into increasingly divergent and differentiated parcels. The system functioned like clockwork, it was beautifully logical and clearly stated, yet it was all too often the *bête noire* against which other embryologists designed their experiments and deployed their own explanations of development and inheritance.

Against this background of experimental embryology and Weismann's germ-plasm theory, I wish to discuss Hans Driesch and teleology in biology. As a student, Driesch had for two semesters heard Weismann lecture in Freiburg i/Br.;[4] he had then studied under Ernest Haeckel and in 1889 had earned his doctorate on a subject which reflected the morphological interests of the master. For the next decade Driesch and his close friend, Curt Herbst, played the roles of footloose travelers and free-lance biologists. Interspersed between long trips were stops at the marine stations at Trieste and Naples, where Herbst analyzed chemical stimulants on development and Driesch turned his hand toward experimental embryology.

In his first and best-known experiments Driesch succeeded in 1891 in separating the first two blastomeres of sea urchin eggs and showed that each half developed into a whole pluteus.[5] This work contradicted earlier experiments performed by Roux on frog blastomeres and directly challenged Weis-

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générale, 2nd ed. (Paris: Schleicher Frères & Cie., 1903). Particularly useful is the synoptic chart on p. 437.

[3] I have discussed the origins of the germ-plasm theory in "August Weismann and a Break from Tradition," *J. Hist. Biol., 1* (1968), 91–112.

[4] Hans Driesch, *Lebenserinnerungen, Aufzeichnungen eines Forschers und Denkers in entscheidender Zeit* (Basel: Ernst Reinhardt, 1951), 53-54.

[5] Hans Driesch, "Entwicklungsmechanische Studien. I. Der Werth der beiden ersten Furchungszellen in der Echinodermenentwicklung. Experimentelle Erzeugung von Theil- und Doppelbildungen." *Z. wiss. Zool.,* 53 (1891–92), 160–178.

mann's germ-plasm theory when it appeared full-blown the following year. Later experiments performed on different stages of development, as well as regeneration experiments on *Tubularia,* confirmed his earlier results, and being no exception to the prevailing mood, Driesch too brought forth elaborate explanations of development based on limited evidence. Two of these explanations will be examined in detail: the first, published in 1894, was later referred to as Driesch's "machine theory of life;" the second, published in 1899, became his declaration of vitalism.

In turning to Driesch's *Analytische Theorie* of 1894,[6] one finds an elaborate and at points sophisticated explanation of embryogenesis. The text itself was nearly two hundred pages, and Driesch tells us it was written in Zurich during his summer retreat to the Alps.[7] The introduction of the essay presented a critical summary of what he called the "Roux-Weismann theory," a theory which Driesch viewed as "a pyramid stood on its point: below, the hypothetical basic notion, above, finally as a heavy base on top—my simple experimental results." The hypothetical notion at the inverted apex was that of qualitative nuclear division, and as Driesch up-righted the pyramid he intended to replace this basic assumption with a broad base of demonstrable cellular reactions. The analytical theory presented "the typical processes of ontogeny as being triggered by the typical protoplasmic differences inside the germ." [8] Driesch devoted the first section of his monograph to the details of these processes, and it is worth following his argument closely to see the sort of explanation he fashioned.

Drawing upon the familiar sea urchin as the paradigm, Driesch illustrated how his analysis proceeded. The formation of the mesenchyme cells at the vegetative pole of the blastula was the first organ-forming process in development. "Why did it occur?" [9] Because such a question was too broad and, in fact, would not be answered by analytic means, Driesch rephrased it. "What was mesenchyme formation?" If this were viewed as a process of cell multiplication at the vegetative pole of the blastula, his causal analysis forced him to the next question of why this particular place. Some cause of mesenchyme formation must be present and spatially directed.

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[6] Hans Driesch, *Analytische Theorie der Organischen Entwicklung* (Leipzig: Wilhelm Engelmann, 1894).

[7] Driesch, *Lebenserinnerungen,* p. 86.

[8] Driesch, *Analytische Theorie,* pp. 11–12.

[9] *Ibid.,* 30–31.

"For every variation which appears," Driesch explained, "we inquire a priori about a cause." [10] What then were the causes, or better yet, the elementary cellular processes upon which Driesch could call?

Cytological studies of the preceding two decades had suggested a rich variety of processes which Driesch singled out as exerting a formative influence. These included cell division and growth, the phenomenon of cell migration, and special cell secretions. Moreover, he recognized that internal physical events had a formative role. Such were the pressures of cell growth and the pulls and pushes of germ-layers which Wilhelm His, August Rauber, and Roux had recently described; to these Driesch added capillary action and osmosis.[11] Most basic, however, of all the elementary cellular events were the little understood chemical processes which ranged from changes in salt concentrations to specific reactions in the protoplasm. Driesch concluded that all ontogenetic processes were either chemical in nature or chemically induced, and this assumption made it possible for the investigator to understand development:

> If the elementary morphogenetic processes make up in their totality the whole of the events of ontogeny then we can say the result on ontogeny comes about through chemical stages.
>
> This sentence thus means, that the effect of every elementary ontogenetic mechanism [Auslösung] is a chemical one which has physical and therefore morphological results (growth, etc.).
>
> Nothing stands in our way of presenting the majority of such chemical effects as fully graspable and comprehensible; that is we can become clearly acquainted with that newly made substance which initiates the new morphological event as such although we may never say why this alone now arises.[12]

In intimating that there was a limit to human knowledge about the organism, Driesch also indicated that this was at some point beyond the basic chemical processes. Finally, he argued that the nucleus played the dominant role in directing such chemical changes, although he took a firm stand against Roux's and Weismann's contentions that differentiation was a matter of qualitative nuclear division.[13] Driesch described none of these cellular events in detail, but it is well to remember that in his

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[10] *Ibid.*, 32.

[11] *Ibid.*, 35–39, 40–42.

[12] *Ibid.*, 43–44.

[13] *Ibid.*, 45–48.

Analytische Theorie he offered a guide to a solution and not the solution itself.

Besides the above cellular processes Driesch utilized a specific mode of physiological activity which became an essential part of his understanding of development. He collectively described these reactions under the general category of *Auslösungen* or "releases," yet since "biological releases" were commonly invoked during these years it is hard to say how Driesch became inspired to think in such terms. His constant companion, Curt Herbst, in an endeavor to show how they could be useful in understanding ontogeny, was involved at that very moment in cataloguing all the known stimuli and responses.[14] Herbst's information was largely derived from the works of plant physiologists, such as Julius Sachs and Wilhelm Pfeffer, and his intent was to apply the methods and some of the conclusions formulated about tropisms to cell differentiation. Toward the end of his long monograph Herbst distinguished between *Auslösungreize* (releasing stimuli), and *Strukturelle Reize* (structural stimuli). It is clear that Herbst took as his model for the *Auslösungreize* the mechanical opening of a valve in a machine—hence the notion of a surge of new activity.[15] Driesch, too, used the same mechanical model and referred in a general way to Pfeffer and Eduard Strasburger,[16] although he undoubtedly also discussed the matter many times with Herbst. The important feature of applying the methods and terminology of tropism studies to differentiation rested in their extreme mechanistic implication, and it is not uninteresting that Sach's prize pupil, Jacques Loeb, at that very time was also employing the same tools to analyze animal form.[17]

The releases were viewed by Driesch as chemical events which in turn released secondary chemical changes of far greater magnitude than the release or trigger itself. The released reactions could in themselves play the role of trigger for a third generation of chemical reactions, and so ontogeny, becoming an ever-expanding constellation of stimuli and re-

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[14] Curt Herbst, "Ueber die Bedeutung die Reizphysiologie für die kausale Auffassung von Vorgängen in der tierischen Ontogenese," *Biol. Centralblatt, 14* (1894), 657–666, 689–697, 727–744, 753–771, 800–810; *15* (1895), 721–745, 753–772, 792–805, 817–831, 849–855.

[15] *Ibid., 15* (1895), 818–822.

[16] Driesch, *Analytische Theorie,* pp. 178–179.

[17] See particularly "On Some Facts and Principles of Physiological Morphology [1893]," reprinted in Jacques Loeb, *The Mechanistic Conception of Life,* (Cambridge, Mass.: Harvard University Press, 1964), pp. 78–104, as well as the Introduction to the same volume by Donald Fleming.

sponses, continued to progress. Driesch envisioned that such triggering reactions occurred within cells, between neighboring cells, between germ-layers, or even between organs. He furthermore designated all such triggering interactions as instances of induction, and although his discussion was again limited to a theoretical level, he cited Roux, Herbst, and Loeb as having discussed actual examples.[18]

Perhaps the most intriguing of the fundamental processes which Driesch described arose out of his attempts to explain the temporal sequence of stimuli and responses. Cell division itself offered a temporal scale for the ordering of events; so the inductions which followed one another in regular order were associated directly with the passing generations of embryonic cells and organs. In pursuing the problem further, Driesch made one of his most innovative suggestions.[19] Development itself, he proposed, implied a process of differential stimulation. This meant portion *x* of a hitherto uniform layer or organ acquired histological characteristics (viz. a chemical state) which distinguished it from the remainder of that layer, let us call it portion *y*. What interested Driesch was the fact that when portion *x* developed its new characteristics, its capacity to follow the pattern of development which portion *y* then took became suppressed. His evidence was drawn from halving experiments which he had performed on late blastulae of sea urchins. Where the vegetative half of the severed blastula closed over its wound and carried on the process of mesenchyme formation and gastrulation, the animal pole seemed incapable of developing any further than sealing the cut surface. It remained a blastula, and as far as Driesch could discover its ectoderm was incapable of invaginating and becoming endoderm; it had become determined as far as these two primitive germ-layers were concerned.

Driesch introduced two terms to describe what had happened. The *prospective potency* referred to the multifarious capacity of a particular part to develop along different lines. In the case of Driesch's sea urchin blastulae, the ectoderm at the animal pole had lost its capacity to develop into endoderm; its prospective potency had become restricted. Driesch argued that as ontogeny progressed the prospective potency of all parts increasingly narrowed; so that at the ultimate stage of development the final organs possessed a prospective potency of zero. The term *prospective value* Driesch used to denote the ultimate fate of a given part. It became one of

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18. Driesch, *Analytische Theorie*, pp. 50–62.
19. *Ibid.*, 75–79.

the mooted questions in experimental embryology of the day as to the point in ontogeny when the prospective value of a given part was actually set.

Driesch, like many of his contemporaries, believed that the nucleus played the dominant role in development and heredity,[20] but it was also his contention (and this distinguished him from Roux and Weismann) that all nuclei preserved a totality of *Anlagen.* The stand put him in a curious position, for he had to explain how the nucleus could be selective about incoming stimuli, determine in its own turn the histological character of the cell, and yet preserve the totality of its original constituents—presumably in an unchanged state.[21] His solution to an apparent dilemma came in the form of a distinction between the capacity of a cell to receive a stimulus and the capacity of the nucleus to respond. The former depended upon the protoplasm surrounding the nucleus, or, as Driesch expressed it, "The protoplasm is thus the mediator (the 'perception zone') between stimulation and the nucleus (the 'action zone')." This meant that the nucleus could always contain a totality of *Anlagen* and that the progressive restriction of the prospective potency showed by the cells in development became a cytoplasmic problem:

> With this we now solve the contradiction just disclosed: in so far as it possesses a nucleus every cell of ontogeny is the bearer in fact of all *Anlagen,* however, in so far as it possesses a specific plasma body it is only capable of receiving certain causes; since the response to a cause presupposes its reception, the cell therefore can respond each time as a whole to only certain causes.[22]

For Driesch in 1894 the process of histological change entailed a twofold process on the part of the cell and a stimulus external to that cell. The nuclei acted both as stimulators and receptors, and the cytoplasm, acting as selective filters, permitted only certain stimuli to reach the nuclei at given places and at given times. By this elaborate set up of a cytoplasmic "mediator" Driesch believed he could explain the coordinated rhythm of differential development and the har-

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[20] Driesch listed the evidence for such a position as: (1) the complicated process of Karyokinesis (mitosis), (2) the dominant role of the nucleus in the events of fertilization, (3) the evidence of inheritance from the father particularly in hybridization, and (4) the results of regeneration experiments with single-celled organisms, (*ibid.,* 46).

[21] *Ibid.,* 48.

[22] *Ibid.,* 79–81. The quotation appears on p. 81.

monious restriction of perspective potencies obvious in every developing embryo.

In its process of responding Driesch envisioned the nucleus as discharging chemical "ferments" into the surrounding cytoplasm. There they initiated the histological changes which put the cytoplasm into a different state of receptivity or induced a reaction in a neighboring part. It seems clear that he envisioned a specific ferment for each identifiable histological type, embryological and adult,[23] and he argued that this supposition, in contrast to Weismann's germ-plasm theory, kept the complexity of the nucleus to a minimum. After all, there existed far fewer histological types than unit characters. The skeleton-forming mesenchyme cells were all histologically the same regardless of where in the pluteus larva they were secreting the calcareous skeleton. Driesch, however, was not explicit about the nature of these nuclear ferments; in fact, he considered them the most hypothetical feature of his whole system.[24]

It is interesting to note that Driesch discovered in Hugo de Vries' work the appropriate model for this sort of nuclear discharge; it is particularly interesting since Driesch must have been referring to de Vries' *Intracellular Pangenesis of* 1889. Here de Vries had described a particulate theory of inheritance which by chance had a strong influence on Weismann's germ-plasm theory as well.[25] That Driesch, however, found de Vries an inspiration not for a preformed nuclear arrangement but for a nuclear mélange of assorted chemicals attested to a peculiar divergence in possible renderings of de Vries' work. "The Nucleus," Driesch explained, "appears to us a mixture of stuff, we speak not of a structure of the nucleus; thus our theory in respect to form as such is in its fictitious dress also epigenetic: the starting form, the structure of the egg, is far simpler than the end form." [26] Driesch thus presented the nucleus as a mixture of ferments with no set arrangement, and as though to distinguish his ideas even further from the germ-plasm theory, he made no effort to relate cellular differentiation and mitosis.

In his *Analytical Theory* Driesch brought a number of fundamental assumptions to bear on the general question of the spatial ordering and temporal sequence of embryological events: (1) the great array of elementary chemical and physi-

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23. *Ibid.,* 179–180.
24. *Ibid.,* 91.
25. Churchill, "August Weismann," p. 106.
26. Driesch, *Analytische Theorie,* p. 86.

cal phenomena, any one of which could act as a release of further events; (2) the distinction between the prospective potency and prospective value of the cell; and (3) the three-cornered balance between the nuclear reception of a stimulus, the release of specific ferments, and the continued and restrictive differentiation of cytoplasm. The process of development implied that each stage was not so much the cause of the next stage as its "receptive station." [27] Since each nucleus remained the bearer of all "Anlagen," ontogeny was not to be seen as a determined unfolding of set steps. The prospective potency simply narrowed as the development of each part proceeded toward an ultimate value. The fate of any cell was in truth a function of its position with respect to the whole, and if its position changed, as was bound to happen with sectioning experiments, the fate changed within the limits of the prospective potency at the time.

When one turns to the second major section of Driesch's text, it is immediately clear that he was dissatisfied with the highly imaginative and completely mechanistic explanation of ontogeny which he had just completed. Dissatisfied not so much because of the explicit details, but because of what he felt was a serious limitation to the entire analytical approach. This second section was entitled "The Ontogeny as Development in Light of Teleological Considerations."

Driesch stated his position at the outset:

> One has indeed expressed the opinion that every stage of ontogeny is the necessary consequence of the preceding stage and the cause of the following one; this sentence, however, is not to be accepted without further ado, for ontogeny is not a united process but is a combination of many processes which are not only in part totally separate from one another but in this independence are actually "given" processes. In other words, we understand . . . these processes only in part by understanding their causes.
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> We must therefore explain . . . ontogeny as a causal regularity striding along in a pronounced mystery; causal analysis of ontogeny leaves us only fragmentary pieces.[28]

His analysis had left Driesch a description of individual processes and a recognition of the balance between stimuli and responses; yet he felt denied an understanding of the given harmony of ontogeny which invariably fashioned a mature animal from distinct and often unrelated events. Driesch

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[27] *Ibid.*, 82–83.

[28] *Ibid.*, 128.

claimed that he remained as unenlightened about what was going on as if he had wandered onto a pier during the initial stages of the construction of a ship.[29] Parts and pieces lay in confusion about him, and he could understand their relation only when he knew their ultimate purpose. Ship and pluteus larva were the undeniable goals of given processes, and only by introducing a teleological view could he understand them.

Yet Driesch made it clear that such a teleological view was not to be construed as simply an intellectual reversal of the causal chain. Such a heuristic query about the end point of a process could be helpful, he remarked, in understanding the upheaval of a mountain range or creation of a river delta; the geologist simply worked backward in time so as to gain a better understanding of the phenomenon at hand. This heuristic use of teleology was a common practice of contemporary embryologists; C. O. Whitman, E. B. Wilson, and Frank Little used such language throughout their cell lineage studies.[30] Driesch, however, had something very different in mind. He turned to the authority of Kant in invoking a teleological interpretation of the organic world. Setting aside the question of whether he properly understood the *Critique of Teleological Judgment,* it is clear that he embraced a teleological approach as necessary for the understanding of the harmony in ontogeny which he had so belabored in the first section. The completed adult or mature larva was an explanation in itself for the structure of an egg. "Said in another way," Driesch argued:

> Because the viable whole is given as a clear recognizable end of the totality of all the processes of ontogeny, we judge on the ground of an objective necessity therefore, these processes to be *as though they were fixed according to quality and order by an intelligence.* With these words we give the really adequate expression to the critical teleological standpoint."[31]

For a full understanding of the mature functioning system,

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[29] *Ibid.,* 129.

[30] *Ibid.,* 129. See also Charles Otis Whitman, "The Embryology of Clepsine," *Quart. J. Microscop. Sci., 18* (1878), 215–315; Edmund B. Wilson, "The Cell-Lineage of Nereis. A Contribution to the Cytogeny of the Annelid Body," *J. Morphol., 6* (1892), 361–480; Frank Lillie, "The Embryology of the Unionidae, A Study in Cell-Lineage," *ibid., 10* (1895), 1–100. J. H. Woodger has made a similar observation about Wilson in *Biological Principles: A Critical Study* (London: Routledge & Kegan Paul, 1967), pp. 431–432.

[31] Driesch, *Analytische Theorie,* p. 131.

Driesch applied the same standards, and his teleological interpretation of both ontogeny and physiology seemed to imply that the architecture given to the egg at the outset was beyond analytical investigation.

At least one critic, Wilhelm Haacke, was quick to point out that one of the great achievements of the theory of organic evolution was its capacity to explain the origin of animal forms and hence particular egg structures.[32] In this connection it is not surprising that Driesch extended the same teleological argument of a goal-directed process to organic evolution. Like many of his contemporaries Driesch saw in Darwin's theory of natural selection an argument for blind chance creating complex forms. He added the further reproach that it was impossible for him to conceive how a viable and perfected species could change into a second viable species by passing through generations of imperfect forms. The ridiculousness in this stance approached the comical from the embryologist's point of view (". . . so verwandelt sich die Absurdität der 'Zufallsansicht' beinahe in Komik"), for imperfect eggs couldn't even reach maturity. The logic of the Darwinian argument seemed to Driesch as absurd as his understanding of Darwin may seem to us. But his rejection of natural selection forced him (or perhaps allowed him) to explain organic evolution in terms of a "given" functional harmony in egg and adult alike which purposefully responded to a changing environment.[33]

In concluding his teleological discussion, Driesch introduced a final term which he declared was nothing more than a substitute for the intelligence which seemed to order biological events. "Instead of saying the ontogenetic elementary-events are so arranged with respect to time, place and quality as if they were arranged by an intelligence concerned with the goal of development, we now say that the *Bildungstrieb* has arranged these events." [34] The term *Bildungstrieb* served as a useful expletive. It was the *Bildungstrieb* which created the structure of the egg, it was the *Bildungstrieb* which constructed the self-regulating physiological system, it was the *Bildungstrieb* which induced the new phylogenetic adaptations. [35] Driesch did not appear to rely on the term once he introduced it and explained its teleological import; he was, however, careless at the outset when he likened its use to the physicist's use of *Kraft*.

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[32] Wilhelm Haacke, "Die Formenphilosophie von Hans Driesch und das Wesen des Organismus," *Biol. Centralblatt, 14* (1894), 712–718.

[33] Driesch, *Analytische Theorie,* pp. 133, 135–139.

[34] *Ibid.,* 139.

[35] *Ibid.,* 139–142.

In the last section of his *Analytical Theory* Driesch reaffirmed his intention to stay within the strictures of what he considered Kantian teleology. Both causality and teleology, he argued, were a priori concepts, but were perfectly valid and even necessary components of research. The causal analysis which he had performed in working out the processes of ontogeny had revealed the egg to be a complex chemical and physical machine. The structure of the egg, however, could only be understood in terms of the ultimate goal of development. Causal analysis revealed the harmony in the developmental processes, teleology explained the givenness of the starting structure.[36]

With his *Analytical Theory* and particularly with his introduction of the *Bildungstrieb,* Driesch appeared to his contemporaries to be steering all too close to the forbidden shoals of vitalism. Both Roux and Emil du Bois-Reymond were critical of the turn in Driesch's thought,[37] and Driesch two years later was forced to disclaim any such vitalistic intent. "What I represented therefore was absolutely not 'Vitalism', but, at least as far as living phenomena come into the question, was directly *the current view of physico-chemical dogmatism.*"[38] He went on to explain that he had simply been willing to see that one consequence of this dogmatism was its inability to account for the purposefulness of form. In its restatement the argument remained essentially the same as that of 1894. Driesch had the opportunity to emphasize the difference between the causal understanding of the individual physiological and embryological events and the teleological understanding of a given structure. Together, the "physico-chemical" and "tectonic-teleological" view of ontogeny became what Driesch called his *machine-theory of life.* The mechanisms were researchable, the architecture merely describable—and describable most satisfactorily in teleological terms.

Driesch completed the paper announcing his support of

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[36] *Ibid.,* 162–166.

[37] Wilhelm Roux, *Gesammelte Abhandlungen über Entwickelungsmechanik der Organismen,* 2 vols. (Leipzig: Wilhelm Engelmann, 1895) II, 1020; Emil du Bois-Reymond, "Uber Neo-Vitalismus [1894]" in *Reden von Emil du Bois-Reymond,* 2 vols., ed. Estelle du Bois-Reymond (Leipzig: von Veit & Comp., 1912) II, 507–508. Du Bois-Reymond is here actually criticizing an earlier paper of Driesch's which referred to "ein unfassbarer Regulator" instead of a *Bildungstrieb;* the implications are the same however.

[38] Hans Driesch, "Die Maschinentheorie des Lebens. Ein Wort zur Aufklarung," *Biol. Centralblatt, 16* (1896), 353–368. Quotation appears on p. 365.

vitalism in 1898, and it was published the following year.[39] It may seem curious at first glance that he should have submitted this declaration to Roux's *Archiv für Entwickelungsmechanik,* but Driesch always considered himself part of Roux's experimental tradition, and in his own autobiography Roux was glad to list Driesch as one of his disciples.[40] That Driesch turned away from his earlier machine-theory of life and eventually from science altogether should not conceal the fact that he had been a highly ingenious experimenter and that many of his theoretical discussions of embryological events carried on in a style very similar to Roux's own quasi-philosophical forays.

The problem of localizing embryonic events was one of the major concerns of experimental embryology in the 1890's and indeed is still one today. Both Weismann and Driesch pitched the question of "Why an event occurred at a given place?" in a manner and at a structural level which seemed far beyond the means of an anatomical or chemical solution; both of their discussions undoubtedly suffered for it. For Driesch the question about the position as well as the specificity of elementary embryological events was important in the framing of his machine-theory of 1894; it was essential to his paper of 1899 which he entitled "The Localization of Morphogenetic Processes, a Proof of Vitalistic Phenomena."

In 1894 the limits of a causal analysis for Driesch had been at the "givenness" of the entire structure of the egg; by 1899 he felt analysis was unable even in a hypothetical way to explain certain cases of localization. He was led to such a conclusion largely by pursuing the logical consequences of his machine-theory, but a number of experiments performed on the gastrula stage of the sea urchin highlighted the difficulties in a way which the blastula did not.

The most interesting of these for his argument consisted of dividing experiments which he performed in Naples during the winter of 1894-95 and which he published in Roux's *Archiv* the following summer, the year after his *Analytical Theory.*[41]

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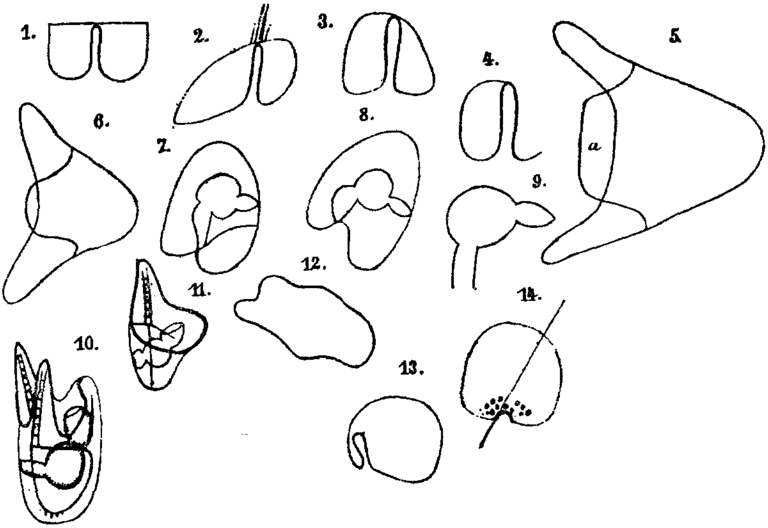
[39] Hans Driesch, "Die Lokalisation morphogenetischer Vorgänge. Ein Beweis vitalistischen Geschehens." *Arch. Entwickelungsmech.,* 8 (1899), 35–111.

[40] Hans Driesch, "Wilhelm Roux als Theoretiker," *Naturwissenschaften,* 8 (1920), 446; Wilhelm Roux, "Wilhelm Roux in Halle a. S.," *Die Medizin der Gegenwart in Selbstdarstellungen,* 2 vols., ed., L. R. Grote (Leipzig: Felix Meiner, 1923), I, 173.

[41] Hans Driesch, "Zur Analysis der Potenzen embryonaler Organzellen," *Arch. Entwickelungsmech.,* 2 (1895–96), 169–203. In 1899 Driesch referred to this work as the stimulus which forced him to rethink the whole matter of localization. Driesch, "Die Lokalisation," p. 40.

When he sliced the completed gastrula near the equator so that each half contained ectoderm and endoderm, both halves sealed over the wound of incision and developed into healthy pluteus larvae of reduced size (compare Fig. 6 with Fig. 5). What fascinated Driesch was not only that both halves possessed the potential potency to continue normal development, but that there was a rapid establishment of the normal proportions of the original whole. The clearest case in point was



Figs. 1–14. *Sphaerechinus granularis* from Hans Driesch, "Zur Analysis der Potenzen embryonaler Organzellen" in *Arch. Entwickelungsmech.* 2 (1895), Plate XV.

1–4. Diagrams which show defects of the ectoderm and the endoderm caused by slicing operation on the gastrula: 1. animal portion with both germ-layers removed; 2. vegetative portion with germ-layers removed; 3. a lot of animal ectoderm removed; 4. nearly a half of the ectoderm removed.

5. Normal pluteus in outline.

6. Pluteus in outline, arising from a gastrula with a marked defect especially on the ectoderm. This figure is drawn on the same scale as Fig. 5 and stems from the same culture.

7–8. Plutei arising from gastrulae with large defects; notice the gut. Scale and culture same as Figs. 5 and 9.

9. Threefold segmented gut of a normal pluteus, same scale as Figs. 7 and 8.

10. Normal pluteus from the side in reduced scale.

11. Pluteus with a one-sided skeleton arising from a large defect.

12. Animal portion of a sliced mesenchyme-larva in outline, in order to show the curled form.

13. Gastrula with a small lateral gut arising from only a portion of the animal pole of a sliced mesenchyme-larva, which was sliced more as shown in Fig. 14.

the development of the primitive gut, which in normally developing gastrulae contained two constrictions and consequently a fore-, mid- and hind-gut (Fig. 10). These three sections maintained strict proportions to one another regardless of the size of the gut (compare Figs. 7 and 8 with Fig. 9),[42] proportions which in undisturbed embryos could be adequately explained by Driesch's 1894 conception of inductive stimuli and responses. Driesch argued that one could envision two constriction-determining stimuli, which, having been released from either pole, traveled along the longitudinal axis and elicited corresponding constrictions in the gut at the two places where the cytoplasm acted as receptive filters. Or, he suggested, if one preferred, one could suppose a single stimulus which similarly localized the mid-gut and incidentally determined the appropriate size of fore- and hind-gut.[43] To apply the same explanation to an arbitrarily halved gastrula, however, introduced the complicating problem of explaining reduction of strength of the polar stimuli and a relocation of the receptive cytoplasmic filters. "In the events here described," Driesch noted in retrospect,

> a sufficient basis does not reveal itself which would explain the correctly proportioned three-fold arrangement of the gut of the cut larvae; that correctly proportioned segmentation points far more to a type of phenomenon which is essentially not of a mechanical but of a specific vitalistic sort.[44]

Postponing for a moment what he meant by phenomena "of a specific vitalistic sort," let us trace closely Driesch's analysis of the events. The way out of the new difficulty was through the postulation of what he called a harmonious-equipotential system and through the enlargement of the role of teleology.

In introducing his concept of the harmonious-equipotential system Driesch put the emphasis on the problem of localizing certain ontogenetic events. The sea urchin blastula presented the paradigm. His early experiments had shown that every cell of the blastula had an unlimited potency and could differentiate into all possible embryonic and adult organs; with the gastrula there was some restriction, but each primitive gut cell could develop into any of the possible products of the endoderm. In short, Driesch claimed, "Jedes Element kann Jedes" (every element can become every element). So

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[42] *Ibid.*, 176–177.

[43] Driesch, "Die Lokalisation," p. 76n.

[44] *Ibid.*, 39.

far the problem seemed little different from his 1894 description of prospective potency, but the experiments on the gastrula and his discussion of the proportions of the gut forced Driesch to go further. Not only could every element become every other, but every element remained within strict proportions to the whole: "in that every effect happens only once or a definite number of times and stands in a fast relationship to all other effects, so then I call such a living system . . . as the cleaved sea urchin's egg: a harmonious-equipotential system."[45]

Driesch warned his readers that a harmonious-equipotential system did not mean an isotropic system. The blastula of the sea urchin, after all, must possess an orientation which acted as the initial cause for the localization of mesenchyme growth and invagination. This was an important point to remember when one considered the development of two normal pluteus larvae from a divided blastula. In this case, Driesch explained, the severed halves upon closing-over reinstated the original orientation and thereupon possessed within their new systems the appropriate localizing stimulus necessary for further normal development. By contrast a Ctenophore egg, even when divided at the two-celled stage, appeared to lack the regulative ability to reinstate the initial orientation and therefore was unable to develop along normal lines.[46] Driesch seemed to be arguing that the questions of localization and prospective value in the harmonious-equipotential system were bound to the question of regulation. Referring again to his experiments on the gut, if he could assume that the original orientation of the severed gastrulae halves had been reinstated, that is, if the sealed halves were identical to the normal gastrula in every respect except size, then Driesch could sally forth with his physico-chemical machine of stimuli and responses. The size of the gut would be smaller, but the proportions of the three gut segments would remain normal. It was the harmonious-equipotential system which possessed the "regulatory capacity" to reinstate that all important initial orientation.[47]

To elucidate the distinctness of the harmonious-equipotential system Driesch reviewed the explanation of regeneration offered by his machine-theory.[48] This earlier explanation had

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[45] *Ibid.*, 74.

[46] Hans Driesch and Thomas Hunt Morgan, "Zur Analysis der ersten Entwickelungsstadien des Ctenophoreneies. I. Von der Entwickelung einzelner Ctenophorenblastomeren," *Arch. Entwickelungsmech.*, 2 (1895–96), 204–215.

[47] Driesch, "Die Lokalisation," pp. 75–77.

[48] *Ibid.*, 70–72.

sufficed in limited cases only, such as with willow trees and marine whelks. Both organisms exhibited great regenerative capacities; a willow cutting could sprout new shoots and roots when properly planted, and the whelk could regenerate an excised foot. In both cases, however, Driesch maintained that regeneration was of a determined and limited sort. The cells of the willow cutting contained a twofold prospective potency, and depending upon the stimulus, either a shoot or a root budded forth in an unorganized fashion. Each cell of the whelk's foot contained the prospective potency of the cells distal to it, so that under the stimulus of having a portion of the foot removed the remaining cells simply regenerated the missing part. Localization during the regenerative act presented no problem, for the operation itself determined the place of the new part. In neither case was there a necessary restoration of the initial orientation; although the prospective potency of all cells remained greater than their prospective value, the outcome of regeneration depended upon nothing further than cell multiplication and differentiation. In brief, these were cases of determined-equipotential systems. As an harmonious-equipotential system, the gastrula of the sea urchin was called upon to perform the far more complex task of reestablishing a new orientation and confining further development to new dimensions.

Driesch made his analysis seem more thoroughgoing, although he hardly clarified matters, by a brief excursus into the very meaning of cause and effect.[49] The upshot appears to be his conviction that all physico-chemical causes reappeared in some manner in the consequent effect; with cases of mechanical events and energy conversion this meant that effect was directly related to its cause. The "regulatory" response of the harmonious-equipotential system, however, did not carry a similar relationship. Since the response of each cell was a function of its place in the whole rather than the initial cause which brought it forth, the total response was not related to the embryologist's scalpel but seemed solely coordinated to the goal of normal development. The effect was goal-directed in a much more immediate sense than the teleological organic-machine of 1894. Although Driesch did not say so explicitly, his excursus was an indirect way of saying that his postulated three-cornered balance between stimuli, cytoplasmic filters, and nuclear ferments could not explain the "regulatory" response. To argue from the position of his machine-theory of life, Driesch would have had to suppose

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[49] *Ibid.*, 84–85.

that the arbitrary act of cutting a gastrula in half caused the appropriate chemical readjustments in all the cytoplasmic filters and at the same time elicited the release of appropriate stimuli from newly located inductive centers. This was too much for the machine-theory to bear.

Driesch argued then that this purposeful regulatory response (or that which he renamed an *Antwortsgeschehen*) in the harmonious-equipotential system was unique. To be sure, man-made machines could have regulatory mechanisms, but only in the sense that the machines substituted one "typical" course of events for another "typical" course; put into modern parlance this meant that if one program failed, the machine could switch over to another which had already been built into the system.[50] In the harmonious-equipotential system, however, there was no substitute causal chain since there was an infinite number of arbitrary ways to cut the sea urchin in two. It was the "atypical" state which led to "typical" development.

It is worth noting that these two terms, "typical" and "atypical," had a very definite meaning in late nineteenth-century embryology. In drawing up his program for *Entwickelungsmechanik* in the 1880's, Roux designated "typical" as the correlative adjective for the genetic type;[51] this meant that a "typical" response was not just a normal response but any response, normal or abnormal, which might still be part of the type or species itself. "Atypical" referred to those responses which were not of the type, and in Roux's mind this meant an externally induced and organized response. I think it highly likely that Driesch was using these terms in the same way; if so, it makes the failure of his machine-theory all the more understandable. The hereditary material, and for Driesch this implied both the nuclear ferments and the cytoplasm, could not direct an "atypical" response because the latter was not part of the system.

The regulatory response was *sui generis* because of the dilemma which arose out of Driesch's peculiar understanding of the stimulus and response systems. The centers of induction were able to control the proportionality of the new organic whole by means of controlling the extent of its own sphere of influence; on the other hand, the reacting system

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[50] *Ibid.*, 86, 89–90.

[51] The clearest exposition of the use of these terms can be found in Wilhelm Roux, *Die Entwickelungsmechanik, ein neuer Zweig der biologischen Wissenschaft (Vorträge und Aufsätze über Entwickelungsmechanik der Organismen*, vol. I; Leipzig: Wilhelm Engelmann, 1905) pp. 182–186.

had the capacity to rearrange all its elements to the new needs of the reconstituted whole. The necessary mutual adaptations of both sides of the system arose before a normal physico-chemical chain of events could bring about their mutual adaptations. Yet instead of trying to tinker with the mechanics of the entire system, perhaps directing more explicit questions at the nucleus and designing experiments to find its make-up, Driesch supplemented the original teleological element of his machine-theory.

Throughout his entire discussion of the harmonious-equipotential system Driesch continually referred to the evident purposefulness in the "regulatory" response. Must the physical and chemical events themselves become the intimate bearers of purpose in a way which was not intended in 1894, when Driesch considered the egg a goal-directed machine arranged as if by an intelligence?

The real reason for Driesch postulating the existence of the harmonious-equipotential system with its unique regulatory response appears to be that it was the one way for him to preserve the integrity of these physical and chemical events and at the same time allow for the complex contingencies of regeneration. "Only in this way," Driesch remarked:

> can we free the "causes," in the strong sense that we give to the word, from teleological impurities, and only in this way can we transfer, in the form of its "answerability," the teleological entity entirely into the "conditions of the system"; as such, it becomes the integrating ingredient as shown in the sense of an elementary or indivisible characteristic.[52]

Driesch thus charged the "answerability" or regulatory-capacity with the purposefulness of the system. The unfathomable element, which for the machine-theory in 1894 had legitimized teleology as a mode of scientific inquiry, by 1899 become attached to a regulative response.

It was at this point that Driesch found it useful to distinguish between "static" and "dynamic" teleology. I do not know whether these terms are original with him, but as Driesch applied them they were convenient for contrasting the teleological status of his 1894 machine-theory with the teleological processes of his harmonious-equipotential system.[53] It was

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[52] Driesch, "Die Lokalisation," p. 96.

[53] *Ibid.*, 103. Driesch elaborated upon this distinction in 1907 and 1908 when he delivered the Gifford Lectures at The University of Aberdeen. Hans Driesch, *The Science and Philosophy of the Organism*, 2 vols. (London: Adam and Charles Black, 1907–8), II, 135–136.

the dynamic teleological behavior which was unique and permitted Driesch to invoke a vitalistic theory. In 1899 he did not specify the causal contents of the *Antwortsgeschehen*, or regulatory response, for after all, the main thrust of his declaration was to show the goal-directedness of the harmonious-equipotential system. He did observe, "Only this one thing, that namely the 'vitalism' exists not perchance in the introduction of a new form of energy . . . what it 'introduces' as 'agent' is something completely and essentially of a different sort."[54] Driesch placed the *Antwortsgeschehen* beyond the constellation of physico-chemical events. The ontological status of such an agent was now experimentally secured; it appears to be only an incidental part of the story that Driesch waited till later to embellish it with the designation of *Entelechy*.

Reflecting upon the change of mind which I have just related in detail, Driesch remarked in his own biography that as early as 1895 he had begun seriously to consider a vitalistic explanation of his experimental results. In a well-known passage he remarked that such a possible solution occurred to him suddenly while taking a stroll in the woods about Zurich. Further on he was less dramatic but more explicit. "But where in the mechanistic sense," he claimed: "was there then the cause for the fact that in a given case this element renders this result and that element that result from the contents of its own completely homogeneous potencies? Formative stimuli in the sense of Herbst just weren't there."[55]

Driesch's remark was more telling than he perhaps realized. He had commented on the failure of Herbst's formative stimuli in his 1899 declaration of vitalism,[56] but he failed to recognize the extent to which his machine-theory had snared him by the promise of the simplistic chemical solution as suggested in Herbst's catalogue of trophic and taxic responses. The three-cornered interaction between centers of stimuli, nucleus, and cytoplasm was an ingenious exploitation of Herbst's study of formative stimuli, but when it failed, as it surely had to, it was Driesch's original teleological commitment which led him out of the dilemma.

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[54] Driesch, "Die Lokalisation," p. 109.

[55] Driesch, *Lebenserinnerungen*, pp. 108–111. Quotation appears on p. 109.

[56] Driesch, "Die Lokalisation," p. 57. "Auch verdanken wir ihm [Herbst] eine logische Klassifikation »formativer Reize« nach ihrem »Causalwerth« und an sie wollen wir bei unserer Frage nach dem lokalisirenden Werth derselben zunächst anknüpfen, wobei aber von vorn herein betont sein muss, dass HERBST eben seine Klassifikation nicht zu diesem unserem Zweck angestellt und die Lokalisation des morphogenen Geschehens überhaupt nicht zu einem gesonderten Problem gemacht hat."

I suspect Driesch's ultimate turn was closely linked to his conviction that the nucleus was comprised merely of a uniform mixture of chemical ferments; that is, that the chromosomes had no formatively significant organization. Such a view was not uncommon, and with at least one other adherent bore all the marks of an immediate and strongly "reductionist" point of view.[57] If the "reductionist" appellation is appropriate for the Driesch of 1894—and I think it has to be—it suggests that he denied himself the possibility of utilizing a broad range of internal cellular "formative" events. Weismann, for all his shortcomings, promoted this second approach as he discussed on a theoretical level the role of the chromosomal elements in development. It was the experimental cytologists, however, men such as Boveri,[58] who fruitfully pursued that approach *in vivo*.

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[57] Ernst Haeckel had the same attitude. See Churchill, "August Weismann," pp. 98–99.

[58] Baltzer has a nice comparison of Driesch's and Boveri's scientific approach. Fritz Baltzer, *Theodor Boveri, The Life and Work of a Great Biologist,* trans., Dorothea Rudnick, (Berkeley and Los Angeles: University of California Press, 1967) pp. 106–114.