

INTRODUCTION

What is development and interdisciplinarity?

The aim of this section is to provide a setting for the rest of the book. This is achieved in two ways. Firstly, by historical overviews and evaluations of the debates about the nature of development, which culminate in contemporary interpretations of ontogenetic development. Secondly, by providing the rudiments of an interdisciplinary framework for studying child development and pinpointing the challenges arising from such a framework.

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The concept of development: historical perspectives

CELIA MOORE

Introduction

The concept of development is rooted in the biology of the individual life cycle. It encompasses the subsidiary ideas of growth, differentiation from homogeneous to heterogeneous matter, and morphogenesis (the assumption of ordered form, an idea included as part of differentiation for most of history). Development also comprises the concept of reproduction, in which the origin of an individual from parents is related both to the resemblance of offspring and parents (heredity) and to the observation that species breed true to type. The history of developmental psychology has been fed by many streams, but developmental biology was the wellspring for its origin during the closing decades of the 19th century.

The ancient legacy

Aristotle (384–322 BP) presented the first detailed conception of development, along with a vivid natural history of embryology in diverse life forms, in *On the Generation of Animals*. He replaced the atomistic preformationism of earlier thinkers with an epigenetic conception in which the embryo differentiates progressively from a homogeneous origin, with parts such as heart, lungs, and limbs and their spatial arrangement only gradually taking shape. Both epigenesis (Fig. 1) and preformationism were destined to endure as the two grand synthesizing images that have competed in the minds of developmentalists throughout history.

The three central features of Aristotelian epigenesis derived from his material, efficient, and final causes. These included a distinction between the material cause from which the embryo is produced and nutrients to support the growth and maintenance of the embryo; an explanation of differentiation as the action of a non-material generative principle in the semen of males (the efficient cause) on the formative material from females

(menstrual blood of humans, the white of a bird egg, etc.); and an explanation of the particular form taken by an organism and its parts in terms of final causes (purpose or plan). The central epigenetic idea was that there was a male principle that acts on generative material secreted by females, setting developmental processes in motion that progressively actualize potentials inherent in the material. Although his theory of generation mixed metaphysics with science, including as it did both vitalistic and teleological elements, Aristotle nevertheless defined the major developmental questions and led the way for empirically minded successors to continue the inquiry some two millennia later.

Concepts from 17th- and 18th-century embryology

The modern history of developmental science can be started with the 17th-century scientists who resumed the work of the ancients (Needham, 1959). Of these, William Harvey (1578–1657), most celebrated for his discovery of the circulation of blood, stands as an important transitional figure in the history of developmental thought. His work on generation, as it was then still called, took Aristotle's epigenesis as a starting point. Harvey believed that all life begins from an egg. One of the major developmental issues of Harvey's time centered on the nature of embryonic nutrition and the distinction between nutrients and formative matter in the egg. Harvey demonstrated that the distinction was meaningless: nutrients were assimilated by the embryo as it took form. He reconceived epigenesis as the entwined, synchronous processes of growth (increase in mass) and differentiation. This contrasts with Aristotle's equation of epigenesis simply with differentiation of a finite mass of formative material. It also contrasts with the preformationism of Harvey's contemporaries.

Preformation was developed in part out of dissatisfaction with the vitalistic leanings of epigenesis

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and in part out of the enthusiasm that attends a major technological advance. The newly invented microscope was revealing a previously invisible world and opening the possibility of even smaller worlds awaiting technical improvements in lenses. It prepared a way around the problem of differentiation by making it plausible to deny its necessity. Turning the microscope on eggs revealed a high degree of organization in the tiniest of embryos, giving rise to the ovists; turning it on semen revealed a swarm of active animalcules (spermatozoa), giving rise to the spermists. If such organization was present so early, why not from the very beginning? Although most preformationists were ovists who thought that life was preformed in eggs, the enduring icon of preformation is Nicholas Hartsoecker's 18th-century drawing of what such a human animalcule would look like if only it could be seen clearly. This was not, however, the clearer vision that was to come with improved microscopy. Anatomists such as Caspar Friedrich Wolff (1733–94) saw such things as tubular structures growing out of the folding of two-dimensional sheets, and not from the swelling of miniature tubular structures. The 18th-century debates ended with embryos that were epigenetic in Harvey's sense: simultaneously growing and taking shape. These debates, however, left the problem of heredity unsolved.

As use of the term 'generation' suggests, the concept of development through the 18th century included reproduction along with growth and differentiation. The most salient feature of reproduction in this context is what we would now call heredity. Offspring are of the same type as parents: chickens invariably come from chicken eggs, and ducks from duck eggs. These and similar regularities in nature were taken to reflect the over-arching plan behind the whole of existence. The preformationist concept of *embôitement* (encasement), which was promoted by Wolff's adversary Albrecht von Haller (1708–1777), was an attempt to eliminate the problem of heredity. In this conception, progressively smaller embryos were stacked inside one another such that all generations were present from one original creation. This was a plausible idea at the time because of the generally shared presumption of a short history of life on earth.

Qualitative change was established as a central fact of development by the end of the 18th century. However, it is possible to read too much into that victory for epigenesis. Firstly, developmental thought during this formative period was focused on the embryo, which is an early stage of life. By pushing back the time of differentiation far enough, the difference between a preformed and an emergent embryo becomes negligible (Needham, 1959). This is particularly true for developmental psychology, which is concerned with post-embryonic life. Secondly, the conceptions of heredity that came to dominate in the 19th and 20th centuries

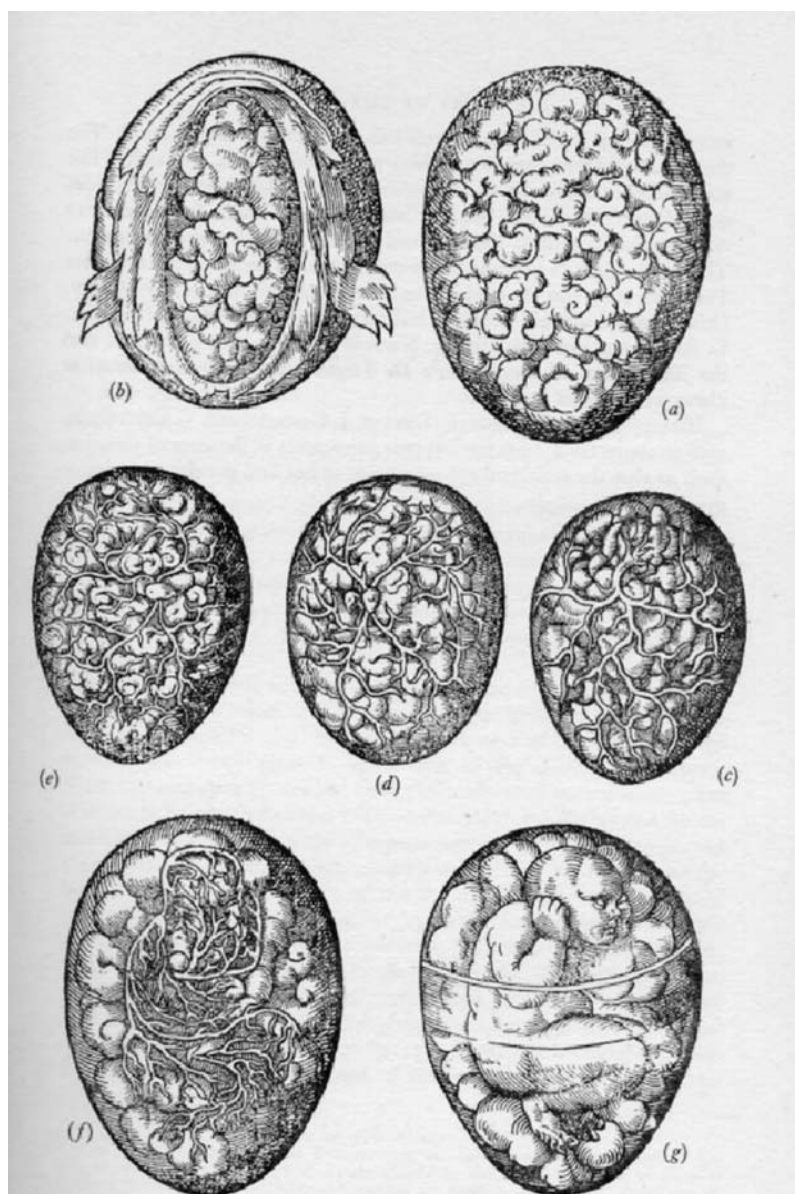


Figure 1. A 16th-century conceptual illustration of what Aristotle's epigenesis might look like if observed. Drawing from Jacob Rueff, as reproduced in J. Needham, 1959. *A History of Embryology*. New York: Abelard-Schuman.

have more in common with the preformationist concept of preexistence than with the epigenetic concept of emergence. Of all the concepts comprised by the ancient idea of generation, heredity was the one that has dominated biology during most of the history of child development.

Development beyond the embryo

Embryology thrived during the early 19th century as a comparative, descriptive science of anatomical development. Its dominance in biology fitted well with the general intellectual climate of the time. The concept of

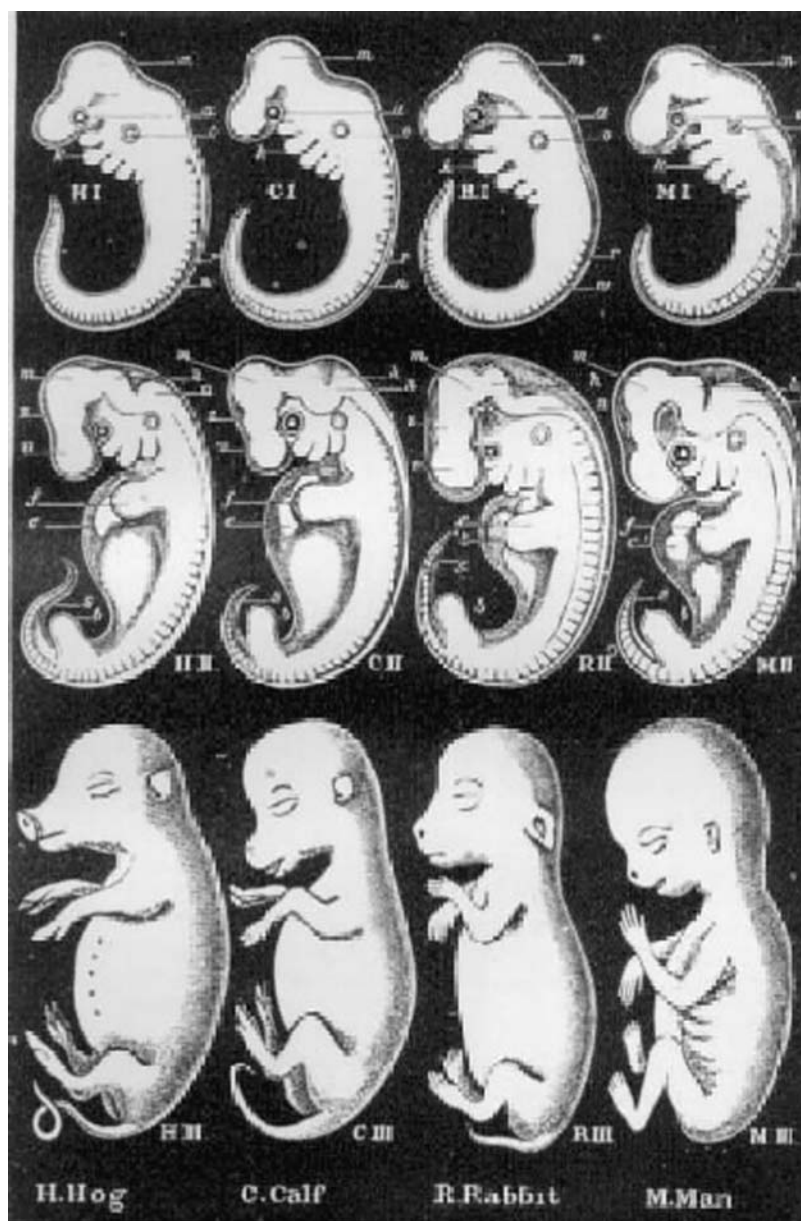


Figure 2. A 19th-century illustration of the relation between ontogeny and phylogeny. From E. Haeckel, 1897. *The Evolution of Man*. New York: D. Appleton and Co. Haeckel's illustrations are presented as empirical, but exaggerate the similarity across species. From S. J. Gould, 1977. *Ontogeny and Phylogeny*. Cambridge, MA: Harvard University Press.

progress was in the air, shaping new ideas in cultural anthropology, sociology, and philosophy as well as those in the natural sciences. This led in natural science to a reconception of the grand plan of nature, that great chain of being, from a static structure to a work in progress and, eventually, to the theory of evolution as the foundation of the life sciences.

Karl Ernst von Baer (1792–1876) synthesized the growing field of anatomical embryology in a set of generalizations that extended the concept of epigenesis beyond the embryo, through the adult stage of a life

cycle. This connected embryology with comparative anatomy and taxonomy, allowing von Baer also to extend the concept of development to include diversity of life forms. From this broad array of data, von Baer observed that shared traits in a group of embryos appear earlier than special traits; that more general structural relations in traits appear before the more specific; that embryos of different forms in the same group gradually separate from one another without passing through states of other differentiated forms; and that embryos of higher forms never resemble adults of lower forms, only their embryos. These observations and ideas left a deep mark on Charles Darwin's mid-century theory of evolution. They were seen to support the idea of evolution as descent with modification from ancestral forms.

In the first textbook of the field, Herbert Spencer (1820–1903) presented psychology as a division of biology, new in its subject matter of the conscious mind, but otherwise using methods and concepts general to the life sciences. Spencer had an abstract concept of development as progress, which he applied across many disciplines. He saw progress as related to the epigenetic tradition of Aristotle, Harvey, Wolff, and von Baer in embryology. This viewpoint was adopted by the influential James Mark Baldwin (1861–1934), who brought the organic tradition of the embryologists into 20th-century developmental psychology. Concepts of assimilation, growth, and differentiation that were first articulated for nutrients and anatomy were re-worked to accommodate experience and the mind. These ideas, in concert with the powerful influence of Darwinian evolutionary theory and the subsequent rise of functionalism, shaped the emergence of developmental psychology and its history well into the 20th century (Kessen, 1983).

It would have been a logical next step for a developmental theory to grow out of von Baer's embryology to explain how evolution works, but efforts in this direction did not flourish (Gould, 1977). Instead, first evolution and then genetics took on the task of explaining development while embryology declined to a marginal field. Ernst Haeckel (1834–1919) popularized the parallel between embryology and evolution (Fig. 2), giving these concepts new names and proposing their relationship in the Biogenetic Law: ontogeny recapitulates phylogeny. Haeckel's recapitulation concept reverted to the old idea of the linear progression of life from monad to man, ignoring von Baer's evidence of the ramified nature of biological diversity and the emergence of diversity in embryonic stages. However retrograde, the idea was very influential for a time. Development came to be seen as pushed by evolution, with adult forms of 'lower' animals as stages in the ontogenetic progression of 'higher' species. This stage conception retained epigenesis of form during ontogeny,

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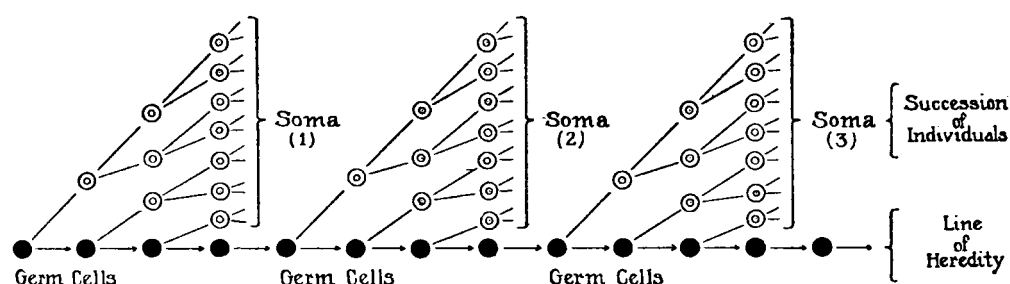


Figure 3. In Weismann's theory, heredity is sequestered in a separate line of germ cells (filled dots) that cross generations. Somatic cells (open dots) originate from inherited germ cells but cannot cross generations. From E. B. Wilson, 1925. *The Cell in Development and Heredity*, 3rd. edn. New York: MacMillan, p. 13.

but placed the cause of change in a preexistent phylogeny.

The schools of developmental psychology that arose early in the 20th century derived core conceptions from 19th-century embryology and evolutionary biology, but each took something different from these sources. The stage conceptions of development elaborated by G. Stanley Hall and Sigmund Freud built on Haeckel's flawed concept. These theorists proposed that human development recapitulated the history of human evolution and that healthy development required support of this predetermined sequence through childhood. Heinz Werner's orthogenetic principle of development as progress from a global, undifferentiated state to an articulated, hierarchically integrated state was an abstract statement meant to distinguish development from other temporal change. It was Spencerian in the breadth of its application and Aristotelian in its view of epigenesis.

William Preyer (1841–1897) was a physiological embryologist in the epigenetic tradition of von Baer who brought both concepts and methods from this field to the study of behavioral development. His 1882 book (*The Mind of the Child*), often used to date the birth of developmental psychology, demonstrated a way to transform empirical approaches from embryology for use in postnatal mental development. Preyer's concept of development, shaped by his physiological work, included an active organism contributing to its own development and the idea that achievements from early stages provide substrates for later stages. This concept had a major influence on James Mark Baldwin, who integrated Preyer's ideas with von Baer's principles and Darwin's natural selection into a developmental theory that served as a foundation for many schools of 20th-century developmental psychology, including those associated with Lev Vygotsky, Jean Piaget, Heinz Werner, Leonard Carmichael, and T. C. Schneirla.

Baldwin's concept of development focused on the relationship between the active organism and its social

milieu as the source of developmental transformation. Applied to the mind of the child, this led him to notions of circular reaction and genetic epistemology that were later to be extensively elaborated by Piaget. Vygotsky and Werner applied the ideas broadly, including cultural and phyletic evolution in their conceptions, along with ontogenetic development that served as their primary focus. Comparative developmentalists, such as Carmichael and Schneirla who used experimental methods to study behavioral development in diverse animals, remained closest to their roots in physiological embryology. They mirrored early 20th-century experimental embryology with experimental approaches to behavioral development.

Heredity and development

The fact of organic evolution and Darwin's theory of natural selection to explain how it works were widely accepted by the end of the 19th century. This made a mechanism of heredity the most important missing link in biology. Evidence for Lamarckian inheritance had been found wanting, which was disappointing in the light of the adaptability of organisms through use and disuse. The search for a genetic mechanism took a decisive turn away from the organism with the introduction by August Weismann (1834–1914) of the germ plasm concept at the close of the century (Fig. 3). The cell had been established as the basic unit of life by 1838. Egg and sperm were subsequently identified as cells, and the first step in ontogeny was reconceived as their fusion. Weismann demonstrated that the cell divisions giving rise to egg and sperm occurred in a specialized population of cells sequestered from the rest of the body. This had the effect of separating the concepts of reproduction and heredity from that of development, and making the hereditary material preexistent to development.

If the 19th century was the age of progress, the 20th century was the age of information. The metaphors used

to discuss development were drawn from the cultural well of cybernetics and computers (Keller, 1995). In keeping with this new orientation, the concept of plan was reintroduced to guide the progressive emergence of form during epigenesis. However, the 20th-century plan was written in a digital code inherited from a line of ancestors, not an idea carried on the informing breath of an agent in semen as it was for Aristotle.

The search for a hereditary mechanism led to the rediscovery of Gregor Mendel's non-blending hereditary particles, the location of these particles on chromosomes in the cell nucleus, the discovery of the DNA molecule, and the definition of a gene as a code that specifies phenotype. In 1957, Francis Crick (1916–2004) stated the central dogma of biology as the one-way flow of information from gene to product. The central dogma had taken its place alongside Darwinian evolution as one of the twin pillars of biology. The study of development thus became incidental to the major biological agenda. Indeed, molecular geneticists adopted single-celled bacteria as their organism of choice, in part because they do not undergo the irrelevant complications of metazoan development. The term 'developmental biology' came into wide use as a replacement for embryology by the middle of the 20th century to describe a field that was now largely focused on cytoplasm in cells rather than on either organisms or the hereditary molecules found in cell nuclei.

Conclusions

The success of genetics fostered a new generation of predeterminists who conceived development as differentiation under the control of plans inherited in genes. They took a biologically differentiated organism as their starting point, using mainstream genetic ideas to explain biological development. Predeterminists and environmentalists debated developmental theory in terms of the nature–nurture dichotomy. The predeterminists claimed a major informative role for nature, which they equated with inherited plans; the environmentalists claimed a major informative role for nurture acting on a *tabula rasa* organism. The ascendancy of the central dogma had the effect of putting constructivists in the Baldwinian tradition

outside mainstream biological thought for most of the 20th century. Constructivists have an organic conception of epigenesis as emergent differentiation entwined with growth, achieved through organism–environment transactions. This conception is not compatible with either preexistent plans or the nature–nurture dichotomy.

There are signs that the long reign of the central dogma is coming to an end in biology. Developmental genetics has focused attention on the activation of genes and made cytoplasmic elements at least equal in importance to an increasingly passive DNA molecule. The embryo has re-emerged as a central figure in both development and evolution. With some irony, the age of information that gave us simplifying genetic codes has now given us the science of complexity, making it not only possible but fashionable to study complex, developing organisms with new tools. It remains to be seen what lasting changes in the concept of development will follow these current trends.

Acknowledgments

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See also:

Understanding ontogenetic development: debates about the nature of the epigenetic process; Constructivist theories; Dynamical systems approaches; Conceptions and misconceptions about embryonic development; Behavioral embryology; Behavior genetics; Developmental genetics; James Mark Baldwin; Jean Piaget; Wilhelm T. Preyer; Lev S. Vygotsky; Heinz Werner

Further reading

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Understanding ontogenetic development: debates about the nature of the epigenetic process

GILBERT GOTTLIEB

Introduction

The debates concerning individual development go back 2,500 years to the time of Aristotle in the fourth century before the present era. During his investigations of the embryo and fetus in a wide variety of species, Aristotle opened up fertilized eggs at different stages of incubation and noted that new structures appeared during the course of incubation. He was the first to perceive the antithesis between *epigenesis* (novel structures emerge during the course of development) and *preformation* (development is the simple unfolding or growth of preexisting structures). All subsequent debates about the nature of the developmental process are founded to some extent on this dichotomy. I say 'to some extent' because when one surveys the history of embryological thought, as, for example, embodied in Joseph Needham's (1959) marvelous work, *A History of Embryology*, there is a second debate of utmost importance that is really at the heart of all debates about the nature of the developmental process: what causes development? What causes development to happen?

By the late 1700s and early 1800s, the debate over preformation and epigenesis was resolved in favor of epigenesis. Before proceeding to a review of the debates about the causes of epigenetic development, it is informative to go a bit deeper into the notions of preformation and epigenesis.

Preformation: ovists and animalculists

There were two main versions of preformation. Since, according to this view, the organism was preformed in miniature from the outset, it was believed by some to lie dormant in the ovary of the female until development was started by fertilization. This view was held by the ovists. To other thinkers, the preformed organism

resided in the semen of the male and development was unleashed through sexual union with the female. These were the animalculists.

Many of the preformationists, whether ovists or animalculists, tended to be of a religious persuasion. In that case they saw the whole of humankind having been originally stored in the ovaries of Eve if they were ovists or in the semen of Adam if they were animalculists. Based upon what was known about the population of the world in the 1700s, at the time of the height of the argument between the ovists and animalculists, Albrecht von Haller (1708–1777), the learned physiologist at the University of Göttingen, calculated that God, in the sixth day of his work, created and encased in the ovary of Eve 200,000 million fully formed human miniatures. Von Haller was a very committed ovist.

The sad fact about this controversy was that the very best evidence to date for epigenesis was at hand when von Haller made his pronouncement for preformation: "There is no coming into being! [*Nulla est epigenesis.*]" No part of the animal body was made previous to another, and all were created simultaneously . . . All the parts were already present in a complete state, but hidden for a while from the human eye." Given von Haller's enormous scientific stature in the 1700s, we can only assume that he had an overriding mental set about the question of ontogenesis (development of the individual), and that set caused him to misinterpret evidence in a selective way. For example, the strongest evidence for the theory of encasement, as the theory of preformation was sometimes called, derived from Charles Bonnet's observations, in 1745, of virgin plant lice, who, without the benefit of a male consort, reproduce parthenogenetically (i.e., by means of self-fertilization). Thus, one can imagine the ovist Bonnet's excitement upon observing a virgin female plant louse give birth to ninety-five females in a 21-day period and, even more strikingly, observing these offspring themselves reproduce without male

contact. Here was Eve incarnate among the plant lice!

Epigenesis: emergent nature of individual development

The empirical solution of the preformation–epigenesis controversy necessitated direct observation of the course of individual development, and not the outcome of parthenogenetic reproduction, as striking as that fact itself might be. Thus it was that one Caspar Friedrich Wolff (1733–1794), having examined the developmental anatomy and physiology of chick embryos at various times after incubation, provided the necessary direct evidence for the epigenetic or emergent aspect of individual development. According to Wolff's observations, the different organic systems of the embryo are formed and completed successively: first, the nervous system; then the skin covering of the embryo; third, the vascular system; and finally, the intestinal canal. These observations not only eventually toppled the doctrine of preformation but also provided the basis for the foundation of the science of embryology, which took off in a very important way in the next 150 years.

Fortunately, the microscopes of the late 1800s were a significant improvement over those of the late 1600s, whose low power allowed considerable reign for the imagination. Figure 1 shows the drawing of a human sperm cell by Nicholas Hartsoeker in 1694. Needless to say, Hartsoeker was a convinced animalculist prior to looking into the microscope.

Nature versus nurture: the separation of heredity and environment as independent causal agents

The triumph of epigenesis over preformation eventually ushered in the era of experimental embryology, defined as the causal-analytic study of early structural development, which unhappily coincided with the explicit separation of the effects of heredity and environment in Francis Galton's formulation of the nature-nurture dichotomy in the late 1800s.

Francis Galton's influential legacy

Francis Galton (1822–1911) was a second cousin of Charles Darwin and a great admirer of Darwin's concept of natural selection as a major force in evolution. Galton studied humans and advocated selective breeding or non-breeding among certain groups as a way of, respectively, hastening intellectual and moral evolution

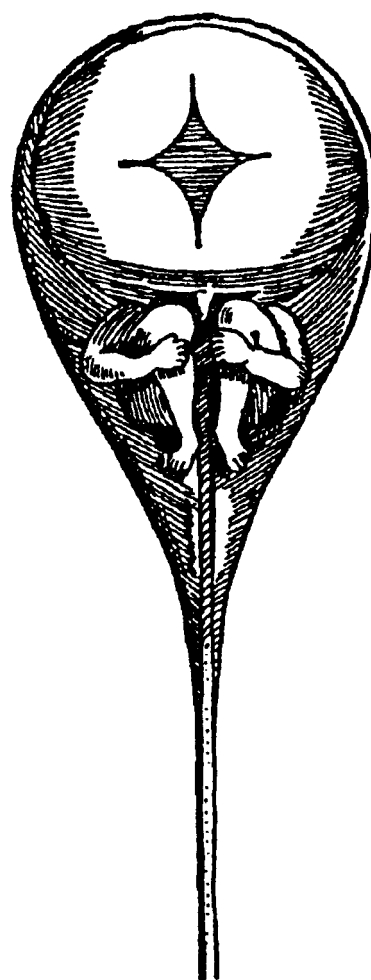


Figure 1. Drawing of the contents of a human sperm cell by the preformationist Nicholas Hartsoeker in 1694. From J. Needham (1959). *A History of Embryology*. New York: Abelard-Schuman.

and saving humankind from degeneracy. Galton coined the term *eugenics*, and its practice in human populations eventually resulted from his theories, among others. He advocated positive eugenics, which encouraged people of presumed higher moral and intellectual standing to have larger families. (Negative eugenics, which he did not explicitly advocate, resulted in sterilization laws in some countries, including the United States, so that people judged unfit would have fewer children.)

Galton failed completely to realize that valued human traits are a result of various complicated kinds of interactions between the developing human organism and its social, nutritional, educational, and other rearing circumstances. If, as Galton found, men of distinction typically came from the upper or upper-middle social classes of 19th-century England, this condition was not only a result of selective breeding among 'higher' types of intelligent and moral people, but was also due in part to the rearing circumstances into which their progeny were born. This point of view is not always appreciated even today; that is, the inevitable correlation of social

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class with educational, nutritional, and other advantages (or disadvantages) in producing the mature organism. Negative eugenics was practiced in some European countries (e.g., Sweden, Switzerland) and in some states in the USA for much of the twentieth century.

Galton's dubious intellectual legacy was the sharp distinction between nature and nurture as separate, independent causes of development, although he said in very contemporary terms, "The interaction of nature and circumstance is very close, and it is impossible to separate them with precision" (Galton, 1907, p. 131). While it sounds as if Galton opts for the interpenetration of nature and nurture in the life of every person, in fact he means that the discrimination of the separate causal effects of nature and nurture is difficult only at the borders or frontiers of their interaction. Thus, he wrote:

Nurture acts before birth, during every stage of embryonic and pre-embryonic existence, causing the potential faculties at the time of birth to be in some degree the effect of nurture. We need not, however, be hypercritical about distinction; we know that the bulk of the respective provinces of nature and nurture are totally different, although the frontier between them may be uncertain, and we are perfectly justified in attempting to appraise their relative importance.

(Galton, 1907, p. 131)

Since we still retain, albeit unknowingly, many of Galton's beliefs about nature and nurture, it is useful to examine his assumptions more closely. He believed that nature, at birth, offered a potential for development, but that this potential (or reaction range, as it is sometimes called) was rather circumscribed and very persistent. In 1875, he wrote: "When nature and nurture compete for supremacy on equal terms . . . the former proves the stronger. It is needless to insist that neither is self-sufficient; the highest natural endowments may be starved by defective nurture, while no carelessness of nurture can overcome the evil tendencies of an intrinsically bad physique, weak brain, or brutal disposition." One of the implications of this view was, as Galton wrote in 1892: "The Negro now born in the United States has much the same natural faculties as his distant cousin who is born in Africa; the effect of his transplantation being ineffective in changing his nature." The conceptual error here is not merely that Galton is using his upper-middle class English or European values to view the potential accomplishments of another race, but it is rather that he has no factual knowledge of the width of the reaction range of African blacks – he assumes it not only to be inferior, but to be narrow and thus without the potential to change its phenotypic expression.

This kind of assumption is open to factual inquiry and measurement. It requires just the kind of natural

experiment that Galton would have marveled at, and perhaps even enjoyed, given its simple elegance, namely, the careful monitoring and measurement of presumptively in-built traits *within generations* in races that have migrated to such different habitats, sub-cultures, or cultures that their epigenetic potential would be allowed to express itself in previously untapped ways. Thus, we can draw a line of increasing adult stature as Oriental groups migrate to the United States and substantially change their diet. More importantly we can measure the increase in IQ of blacks (within as well as between generations) as they move from the rural southern United States to the urban northeast, and its further increase the longer they remain in the urban northeast (Otto Klineberg's book, *Negro Intelligence and Selective Migration*, published in 1935). The same is true for lower-class whites coming from the rural south to the urban northeast. Galton's concept of 'like begets like,' whether applied to upper-class Englishmen or poor blacks and whites, requires that their rearing circumstances and opportunities remain the same.

Galton's dubious intellectual legacy is notoriously long-lived, no matter how many times the nature-nurture controversy has been claimed to be dead and buried. An analysis of psychology textbooks reveals the heartiness of Galton's dichotomous ideas up to the late 20th century (Johnston, 1987).

Dichotomous thinking about individual development in early experimental embryology

In the late 1800s and early 1900s, the main procedure of experimental embryology, as a means of implementing a causal analysis of individual development, was to perturb normal development by deleting cells or moving cells to different places in the embryo. Almost without exception, when normal cellular arrangements were changed developmental outcomes were altered, giving very strong empirical support to the notion that cell–cell or cell–environment *interactions* are at the heart of individual development: interactions of one sort or another make development happen (i.e., make development take one path rather than another path).

This major conceptual advance was only incompletely realized because of the erroneous interpretation of one of the earliest experiments in the new experimental embryology. In 1888, Wilhelm Roux (1850–1924), one of the founders of experimental embryology, used a hot needle to kill one of the two existing cells after the first cleavage stage in a frog's egg and observed the development of the surviving cell. The prevalent theory of heredity at the time held that one-half of the heredity determinants would be in each cell after the first cleavage, and, indeed, as called for by the theory, a roughly half embryo resulted from Roux's experiment.

However, when Hans Driesch (1867–1941), another of the founders of experimental embryology, performed a variation of Roux's experiment by separating the two cells after cleavage by shaking them completely loose from one another, he observed an *entire* embryo develop from the single cells. Eventually, Roux accepted that the second, dying cell in his experiment interfered with the development of the healthy cell, thus giving rise to the half-embryo under his conditions.

Before he accepted that, however, Roux had begun theorizing on the basis of his half-embryo results and came up with a causal dichotomy that continues to haunt embryology to the present day: *self-differentiation* versus *dependent differentiation*. These two terms were coined by Roux as a consequence of his half-embryo experiment, which he believed erroneously to be an outcome of self-differentiation, implying an independent or non-interactive outcome, in contrast to dependent differentiation where the interactive component between cells or groups of cells was necessary to, and brought about, the specific outcome. The concept of self-differentiation is akin to the concept of the *innate* when the term is applied to an outcome of development, as in the innate (hereditary) – acquired (learned) dichotomy that is prevalent in much of psychological theorizing.

Roux, himself, gave up the self- and dependent-differentiation dichotomy as he came to accept Driesch's procedure as being a more appropriate way to study the two post-cleavage cells. Unfortunately, Roux's concepts lived on in experimental embryology in disguised form as *mosaic development* versus *regulative development*. In the latter, the embryo or its cells are seen as developing in relation to the *milieu* (environment), whereas the former is understood as a rigid and narrow outcome fostered by self-differentiation or self-determination, as if development were non-interactive. Here is the way the American embryologist W. K. Brooks (1902, pp. 490–491) expressed concern about the notion of self-differentiation:

A thoughtful and distinguished naturalist tells us that while the differentiation of the cells which arise from the egg is sometimes inherent in the egg, and sometimes induced by the conditions of development, it is more commonly mixed; but may it not be the mind of the embryologist, and not the material world, that is mixed? Science does not deal in compromises, but in discoveries. When we say the development of the egg is inherent, must we not also say what are the relations with reference to which it is inherent?

This insight that developmental causality is relational (interactive or coactive) has eluded us to the present time, as evidenced in the various causal dichotomies extant in the developmental-psychological literature of today: nature-nurture, innate-acquired, maturation-

experience, development-evolution, and so forth. We need to move beyond these dichotomies to understand individual development correctly.

Predetermined and probabilistic epigenesis

At the root of the problem of understanding individual development is the failure to truly integrate biology into developmental psychology in a way that does empirical justice to both fields. The evolutionary psychologists, for example, are still operating in terms of Galton's legacy, as witnessed by the following quotations. They start off seemingly on the right foot, as we saw in Galton's introductory remarks about nature and nurture: "The cognitive architecture, like all aspects of the phenotype from molars to memory circuits, is the joint product of genes and environment . . . EPs [evolutionary psychologists] do not assume that genes play a more important role in development than the environment does, or that 'innate factors' are more important than 'learning.' Instead, EPs reject these dichotomies as ill-conceived" (Cosmides & Tooby, 1997, p. 17). However, several pages later, when they get down to specifics, the nature-nurture dichotomy nonetheless emerges: "To learn, there must be some mechanism that causes this to occur. Since learning cannot occur in the *absence* of a mechanism that causes it, the mechanism that causes it must *itself* be unlearned – must be innate" (Cosmides & Tooby, 1997, p. 19). Since one must certainly credit these authors (as well as others who write in the same vein) with the knowledge that development is not preformative but epigenetic, in 1970, extending Needham's (1959, p. 213, note 1) earlier usage, I employed the term 'predetermined epigenesis' to capture the developmental conception of the innate that is embodied in the above quotation. (Cosmides and Tooby do not stand alone; other evolutionary theorists such as the ethologist Konrad Lorenz (1903–1986) posited an 'innate schoolmarm' to explain the development of species-specific learning abilities.) The predetermined epigenesis of development takes this form:

Predetermined Epigenesis

Unidirectional Structure – Function Development
 Genetic activity (DNA → RNA → Protein) →
 structural maturation → function, activity, or
 experience (e.g. species-specific learning abilities)

In contrast to predetermined epigenesis, I put forward the concept of probabilistic epigenesis:

Probabilistic Epigenesis

Bidirectional Structure – Function Development
 Genetic activity (DNA ↔ RNA ↔ Protein) ↔ structural
 maturation ↔ function, activity, or experience