Synthesis and separation in the history of 'nature' and 'nurture.'

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Abstract:

For much of the 20th century scientific psychology treated the relative contributions of nature and nurture to the development of phenotypes as the result of two quite separate sources of influence. One, nature, was linked to biological perspectives, often manifest as "instinct", while the other, nurture, was taken to reflect psychological influences. We argue that this separation was contingent on historical circumstance. Prior to about 1920, several perspectives in biology and psychology promoted the synthesis of nature and nurture. But between 1930 and 1980 that synthetic consensus was lost in America as numerous influences converged to promote a view that identified psychological and biological aspects of mind and behavior as inherently separate. Around 1960, during the hegemony of behaviorism, Daniel Lehrman, Gilbert Gottlieb, and other pioneers of developmental psychobiology developed probabilistic epigenesis to reject predeterminist notions of instinct and restore a synthesis. We describe the earlier and later periods of synthesis and discuss several influences that led to the separation of nature and nurture in the middle of the 20th century.

Keywords: history | instinct | inheritance of acquired characteristics | probabalistic epigenesist | nature and nurture | psychology | psychobiology

Article:

When, in 1874, Sir Francis Galton endorsed the separation of nature and nurture and prominently enshrined the phase, he called it a ''convenient jingle of words'' (Fancher, 1996, p. 233). Galton's distinction used birth as its criterion: nature was what one brings into the world at birth, while nurture represented influences that act after birth. In fact, Galton's separation was speculative and biologically simplistic; his ''convenient jingle'' masked enormous complexity, the dynamics of which had only begun to be appreciated in his time. Galton's use of the phrase preceded all modern theories of heredity, and in the early 20th century the approach it spawned, the biostatistical approach later associated with Karl Pearson, was strongly at odds even with the early Mendelism. Whiggish accounts of the history of the nature–nurture problem render the period between Galton and the rise of the neo-Darwinian synthesis in the mid 20th century as a matter of working out the scientific details of a fundamentally sound distinction. But this was not the case. Even during his lifetime, Galton's distinction received much criticism. In the half-century between 1874 and 1930, the sciences of biology and psychology saw several pioneers of developmental science struggle to integrate nature and nurture to determine how heredity, the emergence of form, environmental context, and the acquisition of phenotypic specialization were united in the course of individual development (e.g., Harwood, 1993; Maienschein, 1987; Weber & Depew, 2003). Cooke (1998) even suggests that before 1915, biologists rejected the term ''euthenics,'' proposed as an environmental counterweight to Galton's ''eugenics,'' precisely because the environment was assumed to be so well integrated into heredity that there was no need for a separate term to refer to environmental influences.

It was not until after 1920 that the separation of nature and nurture became a significant part of the interface between psychology and biology in America. An early period of synthesis, prominent in both German-speaking and American developmental science, was lost in America between 1920 and 1940, as a separation emerged that echoed Galton, but was unrepresentative of much of the developmental science that had dominated approaches to nature and nurture in the early twentieth century (see Keller, 2003, Part II). By mid-century, the separation solidified with the growth of the neo-Darwinian concept of instinct and the hegemony of behaviorism. But that separation was forcefully challenged in the 1960s by the paradigm of probabilistic epigenesis. Though much more widely accepted now (e.g., Jablonka & Lamb, 2005; Oyama, 1985, 2000; Oyama, Griffiths, & Gray, 2001) this re-synthesis was advocated in developmental psychobiology under the pioneering influence of Gilbert Gottlieb and Daniel Lehrman beginning in the 1950s and 1960s, a time when most life scientists accepted a sharp distinction between instinct (strictly determined by the genes) and learning (a pure result of experience). Recognizing that a synthesis had been lost before being reestablished in developmental psychobiology helps to identify and focus influences, both social and scientific, that have contributed to fluctuations in scientific assumptions about the relation between nature and nurture (e.g., Mu¨ller-Wille & Rheinberger, e2007; Paul, 1998).

Although Darwinian evolutionary theory had an important and much-heralded unifying influence on the biological sciences, the division between biological and psychological influences in the study of behavior and mind was to some extent a result of Darwinism. It is true that Darwin provided the context within which biological and psychological change could be subsumed under the same rubric—in The Descent of Man (1871) and The Expression of the Emotions (1872), he advanced arguments to show that the mechanisms he had proposed to explain bodily change could also be used to account for evolutionary change in mental capabilities, and this argument was later taken up even more pointedly by Romanes (1883) and Morgan (1895), among others. Like Darwin, Romanes and Morgan did not insist on a strict distinction between learned (i.e., psychological) and instinctive (i.e., biological) components of behavior. Both men envisioned a continuum of behaviors between purely learned behavior and the ''perfect instincts'' (Romanes' phrase), which appear fully-formed on the first occasion of their performance and owe nothing to experience. Indeed, Morgan (1895) proposed that some instinctive behavior (so-called ‘‘secondary instincts’’) might owe its existence to the gradual transformation of learned into innate behavior, through a process he called organic selection. The psychologist Baldwin (1896) and the paleontologist Oborne (1896) made very similar suggestions at about the same time (see below).

Although Morgan and Romanes espoused a view of behavioral evolution in which numerous intermediates were expected to exist between learned and innate behavior, the mechanism(s) they proposed to account for it were uncomfortably close to the view, generally attributed to Lamarck, that the effects of individual experience can affect the germinal material and so be inherited by the offspring of the affected individual. Darwin (1868) had endorsed such a view in his theory of pangenesis and until the 1880s, nature and nurture were united largely by the concept of the inheritance of acquired characteristics. Because it presumed that environmental influences could, under some conditions, alter heredity, the concept represented a fluid and flexible union of nature and nurture, one in which over time instinct and habit could merge seamlessly into one another. But the idea was vigorously opposed by those who styled themselves neo-Darwinians [or as Romanes (1897) called them, ‘‘ultra-Darwinians’’]. The neo-Darwinians maintained that natural selection, acting on preexisting germinal variation, is the only mechanism of evolutionary change, and dismissed alternatives as unacceptable.

Perhaps the harshest critic of the apparently Lamarckian elements of Darwinian theory, and a strong advocate of the neo-Darwinian alternative, was the embryologist August Weismann. Weismann (1893) proposed an influential theory according to which the germinal material, responsible for transmitting inherited traits from one generation to the next, was sequestered during development and insulated from effects produced by the environment of the developing organism. Traditional accounts of Weismann often present his view as giving the environment no role in heredity. Winther (2001), however, distinguishes Weismann’s original views from the Weismannism that grew as more and more cellular discoveries formed the core of genetics. Weismannism usually asserts that Weismann saw heredity as an entirely internal process. But the mature Weismann acknowledged the role of the environment as a possible source of new germplasm variants that could drive evolution. He also shared the developmental frame of mind common to many 19thcentury biologists. Churchill (1999) notes that during his early career Weismann did a great deal of developmental research, and the impact of his embryological work can be seen even in his conception of the hierarchically ordered germ-plasm as a ‘‘living, developing whole (p. 761)’’ that could continuously grow and change. But as it changed, Weismann’s germ-plasm was still the privileged cause of developed attributes. Weismann consistently maintained the ‘‘morphological sequestration’’ of germ and soma, in effect rejecting the inheritance of acquired characteristics (Winther, 2001). While they were not entirely immune to the environment, the hereditary units of the germ-plasm, Weismann’s so-called ‘‘determinants,’’ were sequestered morphologically from the body. New hereditary variants—new determinants—could be produced by environmental change, but adaptive adjustments in the body could not be transferred to the germ-plasm. Nor could environmental change alter hereditary traits. InWeismann's view the hereditary units were themselves the focus of selection in evolution. The environment could alter the variants of germ-plasm on which selection acted, but it was left to Weismann's germ-plasmic ''determinants'' to cause trait characteristics. Weismann's theory, therefore, drew a strict distinction between those phenotypic outcomes that arise from the germinal material and variants in the germinal material that might be produced by environmental effects. The distinction was later used to reinforce the separation of instinct (produced by the germ) and learning (resulting from experience), as the theory had a powerful influence on the way that both biologists and psychologists thought about the development and evolution of behavior (Johnston, 1995). Galton in fact used it to fortify his own nature–nurture distinction. By the 1930s and 1940s, Weismannism became the basis of the neo-Darwinian evolutionary synthesis that integrated Darwin's mechanism of natural selection with the mathematical extension of Mendelian genetics to populations.

But Weismannism did not carry the day until well into the 20th century. The hypothesis initiated a debate that continued for the four decades around the turn of the 20th century, as biologists and psychologists assessed the merits of Weismann's hypothesis. The rediscovery of Mendel in 1900, and Theodor Boveri's deduction of Mendel's laws from the observation of chromosomal division in meiosis, rapidly made genes central to the causal character of ''nature.'' Indeed, Weismann's hypothesis had attempted to move beyond speculative physiology and the outdated notions of gamete formation prominent in the mid 19th century. But as Churchill (1978, p. 453) notes, Weismann's assumption of sequestration was a ''logical barrier between the hereditary material'' and an environmentally sensitive organism; it was not an empirical necessity. Much empirical evidence was at issue, and even after the turn of the 20th century, Weismann's proposal and its Mendelian interpretations were not always taken to imply the separation of nature and nurture. Rather, even as knowledge of genes and gene transmission grew between 1910 and 1930, many scientists attempted to integrate nature and nurture and to relate their synthesis to evolution. Recast in many forms, the inheritance of acquired characteristics remained part of the debate. Peter Bowler states that the concept of the inheritance of acquired characteristics was abandoned ''not because it lacked proof, but because Mendelian genetics was so much easier to elaborate into a conceptual foundation for the study of heredity'' (1983, p. 60).

The concept is not a unitary one, and by 1900 it had changed greatly from the original idea proposed by Lamarck.1 By 1910, debates about the inheritance of acquired characteristics were often framed in terms of the difference between somatic induction and parallel induction. In brief, this distinction focused on the difference between environmental factors that could directly influence body and germ-plasm in parallel (parallel induction) and those which could only influence the germ-plasm following a prior alteration in the body (somatic induction). In the latter, the environment first altered the soma in a way that influenced function. Then, through the prior change in soma, the body mediated a change in the germ-plasm (e.g., Przibram, 1911–1912). Weismann viewed nutritional and temperature influences as examples of the former; but he consistently rejected the latter, denying the environment a constructive role acting indirectly on the body to influence heredity.

Weismannism was challenged by a great deal of research that supported the inheritance of acquired characteristics. As late as 1924, in lectures given in Baltimore, Johns Hopkins geneticist H. S. Jennings reviewed much of the empirical evidence supporting the inheritance of acquired characteristics. He focused on the research of the Austrian zoologist, Paul Kammerer (Gliboff, 2006; Logan, 2007). Noting how controversial the notion had become by that time, Jennings also reviewed the criticisms directed at Kammerer's work. He concluded that Kammerer had strong evidence for the inheritance of acquired characteristics, and critics were unjustified in dismissing the work.2 Despite the numerous advances made by T. H. Morgan's chromosomal theory of hereditary transmission, Weismannism had failed to silence research on the impact of the environment during development. Much of this work was aimed not simply at filling in the picture by which nurture, as a separate contribution, could complement a pattern established by heredity; rather it attempted to reconcile and synthesize nature and nurture.

The historical literature on this topic is now quite large, but several examples from genetics and psychology illustrate early attempts at synthesis. In the early 20th century, the specialization produced by conceptual advances and the growth of experimentation in biology had generated a sense of crisis about how to integrate physiology, development and evolution and much effort was directed at synthesis. But these attempts at synthesis were eventually silenced by a number of influences that reinserted deep wedges between nature and nurture.

SYNTHESIS IN GENETICS AND DEVELOPMENTAL PSYCHOLOGY

German-speaking biologists especially attacked Morgan's Mendelian chromosome theory, the early 20th century heir to Weismannism (Allen, 1983; Harwood, 1993). Morgan's theory concentrated on the problem of hereditary transmission, with little attention to the relationship between heredity and development or that between heredity and evolution, relationships that had been central in 19th-century views of heredity (e.g., Churchill, 1999). German-speaking geneticists developed new theories of ‘‘cytoplasmic inheritance'' to broaden what they saw as the overly specialized transmission focus of Morgan's genetics (Harwood, 1993). The concept of cytoplasmic inheritance integrated developmental physiology, phenotypic development, and evolution in ways that respected the new precision of experimental biology. It took many forms (phenogenesis, pleiotropic interactions in gene patterns, etc.), but they all shared the desire to move beyond the nucleus and examine the truly generative power of cytoplasmic factors in accounting for constancy in development. Demonstrations such as the fact that egg fragments lacking a nucleus developed normally, led to especially intensive interest in cytoplasmic inheritance in the 1920s. Harwood (1993, Chap. 4) states that by 1930, the plasmon theory, which proposed a ‘‘genetic'' structure in the cytoplasm that regulated phenotypic development in all organisms, made the recognition of both chromosomal and cytoplasmic structures of heredity central to German genetics. It also led to much discussion of the insufficiency of natural selection and the impact of the cytoplasm in integrating development and evolution. In the interwar period, therefore, German-speaking genetics had moved beyond Galton and the exclusive genotypephenotype distinction, first proposed by Johannsen (Churchill, 1974; Johannsen, 1909) to address several genetic sources of phenotypic development, including genotype and plasmotype (Plasmotypus), a term that referred to hereditary material in the cytoplasm. It was a dynamic that placed a great deal of genetic control outside the cell nucleus.3

These developments in Germany and Austria seem, by 1930, to have had little impact on the already sharp separation between nature and nurture, between genotype and phenotype, in American life science. In the 1940s, even after several scientists who had been part of the debates in Germany (and who had become refugees from Hitler) resumed their careers in the United States, focus on cytoplasmic factors had little impact in America (Harwood, 1993). Probably following the sharper separation wrought in American genetics, much of American psychology also spoke more rigidly of functions that were either hereditary or environmental. There is perhaps no more embarrassing early example than the now infamous Kallikak family pedigree analysis of founding developmental psychologist Henry Goddard. Goddard was an expert in ‘‘feeblemindedness,’’ who in 1908 imported the Binet test to America to test children with presumed mental deficiency (Zenderland, 1998). In 1912, in a wonderful fusion of the new Mendalism with American Christian morality, Goddard analyzed over 450 descendents of a pseudonymous ‘‘Martin Kallikak,’’ a man who had two lines of descent: one was the result of his marriage to a good Quaker girl from a ‘‘respectable’’ family; the other was the result of a casual encounter with a presumed feebleminded girl (a great-great-great-great grandmother of a resident of Goddard’s New Jersey school for mentally disabled children) whom ‘‘Kallikak’’ met one night in a tavern. Goddard’s pedigree analysis was a rumor-based and pseudo-Mendelian account of the numerous feebleminded descendents of the tavern girl, which Goddard labeled with dichotomous ‘‘N’’s and ‘‘F’’s to indicate whole families of normal (N) and feebleminded (F) individuals (Zenderland, 1998, see p. 172). Though Goddard later revised his view, his books (Goddard, 1913, 1914) had enormous impact in America. In the tradition of Galtonian separation and with almost no real evidence, his pedigrees were reprinted in Murchison’s Handbook of Child Psychology (1933) as evidence of the pure impact of heredity on the majority of cases of feeblemindedness, manifest both intellectually (in IQ) and morally, in alcoholism, prostitution, and crime.

But despite Goddard’s influence, American scientific psychology too, made several early attempts at an anti- Galtonian synthesis of nature and nurture, a synthesis that was lost by as early as 1920 (e.g., Weidman, 1999). In 1900 the concepts of adaptation, development, instinct, and habit were all parts of the same mix. Several figures brought evolution, instinct, mind and development together, and linked them to the changes that gave birth to scientific psychology. Arguably, the most influential of these was the founding American developmental psychologist James Mark Baldwin.

Baldwin was a co-founder (in 1894) and co-owner of the Psychological Review, and president (in 1897) of the American Psychological Association. After founding several laboratories in experimental psychology, he became less convinced of the value of experimental analysis and spent much of his career developing theories on the relationship among cognition, development, and evolution. His theories of cognitive development anticipated Piaget on the concepts of accommodation and assimilation (Cahan, 1984, 2003), and he may even have shaped Piaget's thinking through his close friendship with Piaget's teacher, Pierre Janet, who often referred to Baldwin in his courses (see Richards, 1987, Chap. 10). In 1896, Baldwin proposed the concept of ''organic selection,'' later called ''the Baldwin Effect,'' as a fusion of learning and evolution (Richards, 1987; Weber & Depew, 2003). Independently proposed in the same year by Lloyd Morgan and H. F. Osborn, ''organic selection'' can refer to several phenomena (Depew, 2003; Hall, 2001). In Baldwin's use, the term referred to the ontogenetic adaptations, many learned or imitated, that enable an individual to react efficiently to the evolutionary demands of a novel or changing environment. In the process, individuals hone inherited ''instincts,'' and in this way ontogenetic adaptation can increase reproductive success and alter the intensity of natural selection. Emphasizing the importance of social processes, Baldwin assumed that learning, imitation and intelligence resulted in patterns that could become ''phylogenetically entrenched'' (Depew, 2003, p. 10) in ways that enabled nongenetic contributions to development to fine tune the process of evolution. While not truly Lamarckian, Baldwin's explanation depended on the union of and continuity among learning, conscious effort and instinct in a way that united nature and nurture. Hoffmeyer and Kull (2003, pp. 254–255) quote Baldwin, who said in 1902: ''the ordinary antithesis between 'nature and nurture,' endowment and education, is largely artificial. . . .'' Rather, as a result of the fusion of physical heredity with what he called social heredity, ''the creature actually depend[s] upon some conscious resource (imitation, instruction, etc.) to bring the Instinct into actual operation.'' Baldwin, Lloyd Morgan, and others presented organic selection and social heredity as the bases of a psychological synthesis of nature and nurture, one expressly intended to advance the primacy of selection, while giving the environment a constructive role in development and evolution.4

Even before 1920, however, some psychologists considered Galton's phrase and the separation it implied to be biological fact. By 1950, the separation of nature and nurture was promoted by neo- or ultra-Darwinist views of evolution, which ignored the role of development in phylogeny, and by a Janus-faced experimental psychology, which widely assumed that separate contributions of nature and nurture (genes and learning, but rarely both coacting), shaped phenotypic development and psychological function. By mid-century if development was considered at all, it was treated as the passive unfolding of relationships already present in heredity.

THE WEDGE BETWEEN LEARNING AND INSTINCT

The separation between learning and instinct was reinforced in psychology by the methodological approach taken to the study of animal learning around the turn of the 20th century. Thorndike (1898, 1911), perhaps the most influential of the early workers in the field of animal learning, devised techniques that, as he put it, were intended to ‘‘get the association process free from the helping hand of instinct’’ (Thorndike, 1911, p. 30). Thorndike accepted uncontroversially that animal behavior included both learned and instinctive elements, and in his own work elected to study the former. The procedures that he used in his experiments on learning were carefully designed to pose challenges that were within the general scope of the animal’s capabilities, but were sufficiently different from its natural environment that they could not be solved by whatever instinctive predispositions the animal brought to the experiment. Thorndike sought to ensure that the behavioral competence shown by his animals could be attributed only to the effects of learning, and later contributors who built on his work (such as John B. Watson and other behaviorist psychologists) inherited both Thorndike’s nonecological methodology and his separation of learning and instinct as fundamental to their analyses (Johnston, 1981).

Despite the emphasis of Thorndike and others on the analysis of learning, the concept of instinct was alive and well in American psychology at the end of the 19th century. Deeply influenced by Darwin’s writings, William James drew on the pragmatism of Charles Saunders Peirce and James Dewey to develop his functionalist view of psychology, a view in which instinct figured prominently.

On the basis of little more than speculation, James described more than 20 human instincts in his Principles of Psychology (James, 1890). Subsequent writers added enthusiastically to that list until Bernard (1924) was able to catalog over 850 major classes of instincts proposed by psychologists. Some accounts of instinct assumed a neo- Lamarckian fusion of nature and nurture, others did not. But in almost all cases, very little real evidence for the existence of an instinct was required for it to be proposed, and the unrestrained character of theorizing about instinct soon produced a backlash.

In 1919, Knight Dunlap published the opening salvo in what became known as the anti-instinct movement, a wide-ranging critique that sought to eliminate instinct as an explanatory concept in psychology. Dunlap (1919) objected specifically to the teleological use of the instinct concept (e.g., McDougall, 1908), which he criticized as vague, nonspecific, and inherently circular. However, he accepted the more mechanistic concept of instinct espoused by writers such as Romanes and Lloyd Morgan, as an explanation for some instances of behavior.

A different and more radical version of the anti-instinct critique was that of Zing-Yang Kuo (e.g., Kuo, 1921, 1922, 1929). Kuo’s primary argument against the concept of instinct was that it precluded an understanding of the development of behavior by substituting the label ‘‘instinct’’ for an analysis of how behavior comes into being. Instinct theorists generally attributed the development of instinct to maturation, a passive unfolding of inherited potential, which Kuo considered to be no explanation at all. His position was reinforced by the embryologist Carmichael (1925), who made the same point in regard to anatomical structure, drawing on experimental results to conclude that ‘‘Heredity and environment are not antithetical, nor can they expediently be separated; for in all maturation there is learning: in all learning there is hereditary maturation’’ (Carmichael, 1925, p. 260). Kuo went on to bolster his conceptual criticisms with a long series of experimental studies of the behavior of chick embryos [beginning with Kuo (1932a); see Kuo (1967), for a review of the entire series], illustrating his contention ‘‘that the development of behavior is a gradual and continuous process, and not a sudden manifestation of instincts nor a result of trial and error learning’’ (Kuo, 1932b, p. 109).

Kuo opened the shells of developing eggs to observe the behavior of embryos, demonstrating that the precursors of postnatal behavior such as pecking, swallowing, and walking could be described in the embryo. His observations confirmed his belief that the understanding of behavior had to be based on the analysis of its developmental antecedents, not on the inadequate concepts of instinct and learning. Kuo’s was the first empirically supported statement of the necessity of transcending the separation between nature and nurture in order to understand behavior. Although he is generally remembered as having rejected the concept of instinct, what he was really rejecting was any attempt to partition behavior into separate classes (learned and instinctive) and give different accounts of each. He did not reject instinct in order to embrace learning, as did many American psychologists of the 1930s and 1940s. He rejected both instinct and learning in order to embrace a developmental synthesis that would lead to an understanding of all behavior. The position articulated by Kuo was later rearticulated and refined by Gottlieb (1970, 1976, 1997), Lehrman (1953, 1970), and Schneirla (1949, 1956) and forms the basis of the approach to development known as Developmental Systems Theory (see Johnston, 2007; Oyama et al., 2001). However, throughout the period from 1930 to the 1980s, the synthesis offered by this perspective failed to gain anything like widespread acceptance—indeed, it remained something of a minority view and its proponents found themselves constantly having to re-engage the opposition between nature and nurture.

POLITICAL, METHODOLOGICAL, AND BIOLOGICAL WEDGES BETWEEN NATURE AND NURTURE

Many factors, too many to recount here, contributed to the shifts in the dynamic of synthesis versus separation that characterizes the history of the relationship between nature and nurture. Historians have examined the impact of changing explanatory schemes, institutional differences, an emphasis on different problems, national styles in science, and political influences and cultural fears that altered the conclusions drawn from evidence (Harwood, 1993; Keller, 2003; Paul, 1998). For a number of reasons, Kuo’s efforts were recognized only after Gottlieb employed Kuo’s methods to begin his pioneering series of experiments on the effects of experience on ducklings’ recognition of their species’ maternal assembly call. Thorndike’s heritage combined with a number of other influences that promoted the mid-century separation between nature and nurture, and with it, the division of psychology and biology: they include the traditions of experimentation in developmental and animal psychology, the rise of the modern neo-Darwinian synthesis in evolution and population genetics, the concept of instinct in European ethology, and the cultural context that shaped the acceptance of eugenics in America.

The application of the experimental method to organic development was controversial in the late 19th century, but Wilhelm Roux's concept of mechanical causation in development (Entwicklungsmechanik) established the method as the basis of a new standard of evidence (see Mainschein, 1986). Fueled by the extension of the experimental method to the problems of organic development, much of this work addressed the development of form in animals. Experimental embryology produced rapid advances in developmental biology that united form and function in the marriage of evolution, development, and adaptation. In the spirit of synthesis, psychological functionalists like Baldwin paid close attention to the growing literature in experimental embryology. But Baldwin was not primarily an experimentalist. Though the experimental method flourished in American psychology in the 1890s, experimentation had a much-delayed appearance in human developmental psychology (Cairns, 1983); the widespread incorporation of the method into developmental psychology did not occur until well into the 1930s. One reason was the dominance of Edward Titchener in early American experimental psychology.

Titchener's positivist vision of experimental introspection dominated the growth of experimentation in early American psychology partly through his widely used methods handbooks, the four-volume Experimental Psychology, that were published between 1901 and 1905 (Furumoto, 1988). These were the only systematic accounts of the new method available in America at the time. Titchener's vision, however, restricted experimentation to adult humans; he sanctioned no experimental work on animals or, especially, on children. Ethical prohibitions on the potential danger of interfering with the child's mental development compounded Titchener's rejection of experimentation in children. Experimental intervention with children was considered unnecessarily disruptive and even dangerous in a system already in the midst of such change. Wilhelm Preyer, German zoologist and embryologist whose work, The Mind of the Child (1888–1889), was central to the founding of developmental psychology, voiced methodological proscriptions requiring that observations must be unobtrusive and avoid ''every artificial strain upon the child'' (Cairns, 1983, p. 44). Almost 40 years later, in the second edition of his influential Psychology, Woodworth (1921/1929) echoed a similar restriction on experimentation with children and for similar reasons. He noted that use of the developmental or historical method and not experimentation was required in studying children because ''a process, such as the child's mental development, must not be interfered with drastically'' (p. 8). He implied that it might be dangerous, and in any case, there was no need to artificially produce a change if change was already underway—if, in his words ''something interesting is about to happen'' (p. 8). The scientist need only be prepared to observe it.

Despite Titchener, experimentation grew more rapidly in the field of animal psychology, which was more directly linked to advances in experimental biology and physiology (Pauly, 1987). The lag in the use of experiments with children was, therefore, for a time compensated for by the growth of animal psychology. In the early days of experimental introspection, animal and developmental psychology were commonly grouped together and both were distinguished from experimental (introspective) psychology. Developmental theorists like Baldwin paid close attention to the animal literature on learning, development and instinct, and animal research provided an important foundation for clarifying the relationship between learning and instinct. But it did so as behaviorism was beginning to emerge in American psychology; and though it was imbued with learning, behaviorism gave little attention to development. Thorndike's exclusive emphasis on nurture introduced a tradition of separation that was reinforced by John Watson and powerfully promoted at mid-century by the influential Hullian tradition (e.g., Weidman, 1999). Behaviorism separated animal and developmental psychology; and it did so with an overemphasis on nurture, which flourished at the time when the neo-Darwinian ‘‘modern synthesis’’ in evolution emerged in biology. The result was the mutual reinsertion of a wedge between nature and nurture. Despite early attempts at synthesis in both biology and psychology, Galtonian separation became much more prominent just as experimentation gained momentum in the science of human development.5

Gender seems also to have been a factor in the delay of experimentation in developmental psychology early in the century. In 1910, scientific psychology had a large representation of women scientists compared to other disciplines. But Titchener actively excluded participation by women in the inner circles of experimental psychology. In 1914, Christine Ladd Franklin complained to Titchener that the Society of Experimental Psychology excluded her (and all women), despite that fact that in that year it met at her University (Columbia) and discussed the problem (color vision) to which she had devoted her career (Furumoto, 1988; Rossiter, 1982). Experimentation was a masculine method at the time; and perhaps because it involved control, it reflected the classic active-passive stereotype of masculine versus feminine. Women were thought to have an affinity for children; this and their role in education gave them an important role in developmental psychology, but not, officially, in experimentation. In the preface to the first edition of his Handbook of Child Psychology, Carl Murchison confirmed both the female bias in child psychology and the male flavor of experimentation. Complaining that research in developmental psychology did not receive as much funding as was common in experimental psychology, he noted critically that many experimental psychologists still looked at child psychology as ‘‘a proper field of research for women and for men whose experimental masculinity is not of the maximum’’ (1933, p. ix, our italics). By 1933, Murchison still had to assert that child psychology should be conceived ‘‘as problems experimentally investigated’’ (1933, p. x.), something that his handbook aimed to do. But experimentation may have lagged behind in human developmental psychology because stereotypes inhibited the use of a ‘‘male’’ method in a field for which women were thought to be especially skilled.

Behaviorism's exclusive emphasis on nurture also conspired in time with great social concerns for the hereditary health of America. Madison Grant's terrifying The Passing of the Great Race appeared in the same year (1916) that Lewis Terman reported low IQs in Latinos and African

Americans, and only 1 year after John Watson had completed his term as APA president. Psychologists and citizens alike feared that the American hereditary stock was being threatened both by ‘‘miscegenation’’ and by waves of immigration by psychologically undesirable ‘‘races’’ arriving from places like Mexico, Italy and Russia. Nature and nurture became prominent political problems, and, as the debate between IQ hereditarian Karl Lashley and learning theorist Clark Hull indicates, this produced nature–nurture extremes that divided prominent psychologists and pitted strict hereditarian notions against infinitely flexible connections among stimuli and responses (Weidman, 1999). Political debates about immigration restriction led to the administration of IQ tests at Ellis Island that were intended to enforce federal laws mandating the deportation of the feebleminded. Goddard himself used the Binet test at Ellis Island to assess the relatively high levels of mental retardation thought to be present in Southern as opposed to Northern Europeans (Zenderland, 1998). It is important to note that some biologists who comfortably assumed that some things were acquired and some were inherited (among them T. H. Morgan and Edwin Conklin), were nonetheless cautious about the application of heredity to complex human psychology (see Cooke, 2002; Morgan, 1934). But many social scientists and society as a whole were not (Paul, 1998). The Immigration Act of 1924 sealed the separation of nature and nurture: when he was Vice President, future President Calvin Coolidge said in support of the law ‘‘America must be kept American. Biological laws show... that Nordics deteriorate when mixed with other races’’ (Kevles, 1985/1995, p. 97). Three years later the Supreme Court upheld the forced sterilization of mentally disabled people. The separation between nature and nurture had become an integral part of the legal and cultural fabric of America.

Changes in biology finalized the split. During the 1930s and 1940s, neo-Darwinism became established as the standard theoretical position in the modern evolutionary synthesis (Mayr, 1963). The neo-Darwinian synthesis fostered a separation between instinct and learning in a way that traditional Darwinism did not. The major accomplishment of the synthesis was to provide a compelling explanation of Darwinian natural selection in terms of Mendelian genetics. Instead of selection being among alternate phenotypes, the modern synthesis defined selection to occur among alternate genetic variants (alleles). Thus the neo-Darwinian synthesis strongly encouraged a distinction between genetically determined aspects of the phenotype (which could evolve by natural selection) and nongenetically acquired aspects (which could not). During the same period, interest in the concept of instinct faded in American psychology with the hegemony of behaviorism. Although behaviorists did not generally completely reject instinct as an explanation for behavior (Herrnstein, 1972), they considered it far less important than learning, particularly in the behavior of humans where IQ became a major hereditarian focus. However, as interest in instinct waned in American psychology, a renewed interest was developing among European biologists studying the behavior of nonhuman animals. The early ethologists, especially Nikolaas Tinbergen and Konrad Lorenz, were primarily interested in providing evolutionary explanations of behavior (see Lorenz, 1981; Tinbergen, 1951). Basing their work largely on field observations of animals in their natural habitats, they set out to answer two broad questions: how, historically, has this behavior evolved, and in what ways does it provide for the animal’s adaptation to its environment? To answer these questions, ethologists focused on instinctive behavior, a focus that made good sense from a neo-Darwinian perspective as evolutionary questions had come to presume genetically determined behavior.

Instinct thus became a centrally important concept for ethologists, particularly Lorenz, and it became important to distinguish, both conceptually and methodologically, between instinctive and learned behavior. Lorenz (1937) advocated the deprivation experiment as a tool for making this separation. If an animal is reared without the opportunity to interact with social companions from which it might learn, and without the opportunity to practice the behavior under examination, then one can determine whether the behavior is learned or innate by observing the animal at the point in development when it would normally occur. If, despite the deprived rearing, the behavior appears as usual, then the behavior may be diagnosed as innate; if not, then it is learned. If the behavior does appear but is abnormal in some way, then it will be possible to separate out learned and innate elements within the overall pattern, and show that only the innate elements are present (Lorenz, 1935, 1937). Only learned behavior, in this analysis, results from experience; innate behavior depends solely on maturation, a process strictly determined by the animal's inherited genetic makeup. Paradoxically, this view fit nicely with that of the neo-behaviorists in the 1950s to fully separate nature (instinct) and nurture (learning), making the former the province of biology, the latter, of psychology.

THE MODERN DEVELOPMENTAL SYNTHESIS: PROBABILISTIC EPIGENESIS

Lorenz's theory was subjected to a careful and very detailed critique by Lehrman (1953). Lehrman's critique laid an important foundation for a renewed challenge to the explanatory value of instinct and for the resynthesis of nature and nurture that was ultimately realized in Gottlieb's concept of probabilistic epigenesis. It challenged instinct on a number of grounds, among them that the deprivation experiment cannot logically be used to distinguish behavior that depends on experience from behavior that depends solely on the genes. Lehrman pointed out that even the most severely deprived conditions of rearing still provide the animal with experience, so that the effect of the deprivation experiment is to change, not to eliminate, the experience of the developing animal. It does so, of course, in a very imprecise and global manner, and Lehrman suggested that a much more productive approach would be to make limited and selective changes to the animal's experience, so as to test hypotheses about the role of various kinds of experience (rather than ‘‘experience’’ in some global sense) in development.

In making this argument, Lehrman was adopting a much broader definition of experience than that encompassed by the opportunities for observation and practice that provided the logic for the deprivation experiment, a position borrowed from his mentor, Schneirla (1949). By construing ‘‘experience’’ in these broader terms, and by pointing out the impossibility of excluding experience altogether, Lehrman completely undercut the distinction between learned and innate behavior. Like Kuo three decades earlier, Lehrman resisted the attempt by instinct theorists to identify a distinct category of behavior and explain it by labeling it innate. Attributing instinct to maturation on the basis of a deprivation experiment provides no explanation at all; the experiment shows only that the behavior does not depend on whatever experiences have been excluded, but says nothing at all about which remaining experiences may contribute to its development. For Lehrman, all behavior develops as a result of interactions between the animal and its environment, including the experience that environment provides, and the task of analysis is to explicate those interactions, not to undertake the futile attempt to divide behavior into that which is environmentally and that which is genetically caused.

Lehrman's extension of the notion of ''experience'' to embrace more than the traditional contributions of observation and practice allowed him to point out that even a completely isolated animal may produce its own experience. He used the example suggested by Kuo (1932b, p. 113), who noted that the movements of an embryonic chick's bill early in development resemble the movements of pecking and speculated that this embryonic self-stimulation might contribute to the development of pecking in newly-hatched chicks. Lorenz (1965) ridiculed this suggestion, asking what on earth the chick could be expected to learn about pecking from its own embryonic movements. This, of course, missed the point of the example, which was to illustrate that experience is a broader concept than learning, one requiring a more broadly-based analysis of development. Perhaps not surprisingly, Lehrman's rejection of the concept of instinct led some of his European critics to accuse him of claiming that all behavior results from learning (e.g., Eibl-Eibesfeldt, 1961; Hess, 1962; Lorenz, 1956; see Johnston, 2001). Their dedication to a strict and exhaustive distinction between learned and innate behavior seemingly made unavoidable the conclusion that rejecting instinct required that all behavior be attributed to learning, as the only other explanation logically available.

In a lengthy reply to Lehrman's criticisms, Lorenz (1961; translated 1965) recast the distinction between innate and learned behavior by arguing that the former depends on information encoded in the genes as a result of natural selection, whereas the latter depends on information acquired during the animal's lifetime (most notably as a result of learning). The deficiencies of this information based distinction have been extensively discussed (e.g., Griffiths, 2001; Johnston, 1987; Oyama, 1985, 2000), but it illustrates the persistence of the search for ways to maintain two separate categories of behavior.

Ironically, in his early years Gilbert Gottlieb had considerable exposure to the ethological tradition. He developed an interest in imprinting while working on his master's degree at the University of Miami. When, in 1956, he went to Duke University to pursue a doctorate focusing on imprinting, Gottlieb worked with Karl Zener and Donald Adams. Both were influenced by the European ethological tradition. Zener had worked with Wolfgang Köhler, and when Gottlieb arrived at Duke, Adams was about to go to Europe to study with Konrad Lorenz. History, like development, is probabilistic. Gottlieb had read and reported on Lehrman's 1953 paper in Adam's comparative psychology course, and a year later on the day Gottlieb was scheduled to defend his dissertation, Daniel Lehrman arrived at Duke to give a talk. Someone made Lehrman an unofficial member of Gottlieb's dissertation committee. Gottlieb remembered that Lehrman ‘‘took five minutes to read my dissertation’’ and then asked ‘‘the key question’’ on the behavioral differences between domestic and wild mallard ducks (Gottlieb, 2000). Gottlieb’s answer was, by his own admission, sheepish; but Lehrman was delighted.6 The two met again a few years later, after Gottlieb had gone to Dorothea Dix Hospital and when Lehrman came to Raleigh to give a talk at North Carolina State University. After the talk Gottlieb invited Lehrman to see his lab in the old X ward of the Hospital, which had been originally designed to house violent patients. Lehrman was impressed with the ducklings, and thereafter he regularly invited Gottlieb to talk at the Institute of Animal Behavior at Rutgers University.

After one of those visits, Lehrman asked Gottlieb if he would like to work at the Institute of Animal Behavior. Its connection with T. C. Schneirla, Lehrman’s professor, and Lehrman’s critique of Lorenz’ instinct concept had already made the Institute a major locus of challenge to the predeterminist and nondevelopmental view of the separation of nature and nurture. Concerned about how difficult it would be to reproduce the conditions of his North Carolina research farm and worried that Lehrman would not understand, Gottlieb turned down the offer. But Lehrman was understanding; according to Gottlieb, Lehrman said that this was exactly the kind of rejection for which 15 years of psychoanalysis had prepared him. The two remained close friends and colleagues until Lehrman’s sudden death in 1972, at age 53.

Through the 1990s, Gottlieb elegantly integrated his empirical analysis of the prenatal roots of behavioral development (see Lickliter, Miller, this volume) into the developmental synthesis articulated by Kuo, Schneirla, Lehrman, Gottlieb, and many others. Although he is mainly remembered for his experimental analyses of experiential contributions to development, he was also deeply interested in the role of the genes, which he (like Lehrman) understood to be essential components of the developmental system. Early in his research program, Gottlieb realized that the alterations in embryonic experience might affect genetic expression in the developing ducklings, but he was unable to arrange for an experimental test of this hypothesis (Gottlieb, 2001, pp. 45–46). Running through all of his work is a strong resistance to all attempts to privilege either genes or experience in developmental explanation. For example, despite his general admiration for Waddington (1957), he criticized Waddington’s concept of canalization for placing too much emphasis on genetic control in development (Gottlieb, 1997, p. 80–81). Gottlieb viewed his own probabilistic epigenesis, most importantly, as a synthesis that transcended any attempt to push either genes or experience to the foreground.

Until recently, that synthesis has been resisted by the deep-seated tendencies to maintain strict separations between nature and nurture, instinct and learning, innate and acquired. However, the pioneering efforts of Gottlieb and his predecessors in the 1960s paved the way for the modern developmental synthesis: a contemporary reconsideration of the dynamic and synthetic relationship between genes and environment, nature and nurture, development and evolution.

Notes

1 Many versions of so-called neo-Lamarckism existed by 1920. Some were teleological and extremely speculative (Eimer, McDougall); others were based in new discoveries in cell biology and physiology (Kammerer, Jennings); some were not truly Lamarckian at all (Goldschmidt, Baldwin) in that while they rejected strict selectionist interpretations of evolution and tried to integrate ontogeny and phylogeny, they also accepted Weismann's segregated genetic material (see Bowler, 1983; Gould, 1977/1985; Harwood, 1993; Logan, 2007; Richards, 1987; Weber & Depew, 2003).

2 H. S. Jennings, 1924, unpublished lecture notes, ‘‘Inheritance of Acquired Characteristics.’’ Herbert S. Jennings Papers, American Philosophical Society Library, Philadelphia, PA. When Kammerer committed suicide in 1926 amid accusations of scientific fraud, Jennings assumed that the work was discredited (see Gliboff, 2006). But interest continued. In 1930, geneticist T. M. Sonneborn reviewed with great interestWilliam McDougall's experiments on the inheritance of learned shock aversion in rats trained for 23 generations (see also Cooke, 2002).

3 Johannsen's distinction was a statistical one that rejected Weismann's isolation. But around 1915 Morgan and other Americans applied it to individual organisms and imposed Weismannism on the genotypephenotype distinction (Churchill, 1974). On ‘‘plasmotype,’’ see Harwood (1993, p. 69).

4 Richards (1987, p. 493) notes that Baldwin saw Weismann's environmentally produced variants as causing phylogenetic change, not reacting to it, as the Baldwin Effect proposed.

5 Personal fates also contributed. Ironically, it was Baldwin's dismissal from Johns Hopkins in 1908 in the wake of a sex scandal that led to John Watson's rapid promotion to Department Head in the influential Johns Hopkins Department of Psychology. Watson rose extremely rapidly thereafter.

6 Lehrman even signed Gottlieb's personal copy of his doctoral dissertation.

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