Baldwin and His Many Effects

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1 Introduction: The Very Idea of the Baldwin Effect

In recent years, a number of evolutionary theorists have spoken well of a turn-of-the-twentieth-century idea that since the nineteen fifties has gone by the name of "the Baldwin effect" (Hinton and Nowlan 1987; Dennett 1995; Deacon 1997). The general thrust of the idea is to urge that, under some conditions, learned behaviors can affect the direction and rate of evolutionary change by natural selection. In such cases, cultural inheritance of a learned behavior across an indefinite number of generations creates a "breathing space" (Godfrey-Smith, chap. 3, this volume) in which inherited factors favorable to the adaptive behavior in question that either already exist, happen to crop up, or can be stimulated by the change in question—there is some dispute about this—will move along the channel already cut by culture, thereby converting learned behaviors into genetic adaptations or, alternatively, supporting learned behaviors by related genetic adaptations. In either case, natural selection will have ratified evolutionary vectors that learning began.

It was George Gaylord Simpson who in a 1953 article gave the Baldwin effect the name it has borne ever since (Simpson 1953). He named it after James Mark Baldwin, an American child psychologist who claimed to have introduced the idea in articles appearing in a paper given in late 1895 and in publications in the *American Naturalist* and *Science* in 1896 (Baldwin 1896a,b). The Baldwin effect might just as easily, however, have been called the "Lloyd Morgan effect." For the British animal ethologist Conwy Lloyd Morgan, who addressed academic audiences in the United States during winter of 1895–1896, proposed the same idea in a paper delivered

to a February 1896 session of the New York Academy of Science at which Baldwin also spoke (Lloyd Morgan 1896b; see Richards 1987: 398–399). For that matter, the hypothesis might also have been called "the Osborn effect," after the American paleontologist H. F. Osborn, who, also in 1896, published a paper that he titled "A Mode of Evolution Requiring Neither Natural Selection Nor the Inheritance of Acquired Characteristics" (Osborn 1896).

The subsequent fortunes of the Baldwin effect have varied considerably. Julian Huxley was a Baldwin booster in *Evolution: The Modern Synthesis* (Huxley 1942: 114). Simpson, by contrast, was something of a Baldwin skeptic. In his 1953 articles, he admitted that the idea is theoretically coherent, that is, not inconsistent with the fundamental principles of the Modern Evolutionary Synthesis. But Simpson doubted whether the alleged effect is empirically instantiated very often, and, if it is, whether this can be definitively shown. By the early sixties, a deeper skepticism had set in. In *Animal Species and Evolution*, Ernst Mayr recommended "discarding this concept altogether" as either a trivially true example of normal natural selection at work or a flatly false regression to Lamarckism (Mayr 1963: 611). Theodosius Dobzhansky soon followed suit (Dobzhansky 1970: 211).

Against this hardening mid-century hostility, it is striking that a rather diverse lot of contemporary evolutionary theorists, most of whom regard themselves as supporters of the Modern Synthesis, have of late become "Baldwin boosters." One reason is not hard to find. In contrast to the original Baldwin boosters, who were interested in saving some aspects of Lamarckism in the wake of the post-Weismannian turn to hard inheritance, but who differed from one another about what and how much to save, today's Baldwin boosters are typically evolutionary psychologists who are searching for scenarios in which a population can get itself by behavioral trial and error onto a "hard-to-find" part of the fitness landscape in which human brain, language, and mind can rapidly co-evolve. They are searching for what Daniel Dennett, a Baldwin booster, calls an "evolutionary crane," an instrument to do some heavy lifting fast. What Dennett calls "a Good Trick"—potato washing initiated by an individual, perhaps, which is subsequently spread by imitation among a population of monkeys—can serve as such an evolutionary crane so long as gene frequencies also change in a way that supports the behavior (Dennett 1991, 1995).

The attention of those who, like Dennett, are looking for mechanisms for rapid evolution was first turned to "Baldwinesque" scenarios by a series o publications that appeared in 1987. The most important of these was G. E Hinton and S. J. Nowlan's "How Learning Can Guide Evolution," which in the course of reporting on genetic algorithms that seemed to do precisely what the title of their paper suggested, not only referenced Baldwin's 1896 papers, but claimed that Baldwin had already demonstrated what their computer simulations now illustrated (Hinton and Nowlan 1987; see also Ackly and Littman 1992; and Puentedura, chap. 11, this volume). Equally significant was the fact that John Maynard Smith, doyen of contemporary British Darwinian, not yet chastened by the scorn he subsequently displayed for treating simulations of complex adaptive systems as actual biological knowledge, gave his blessing to Hinton and Nowlan's results in an article in Nature in October of the same year (Maynard Smith 1987). The year 1987 also saw the publication of Robert Richards' Darwin and the Emergence of Evolutionary Theories of Mind and Behavior, which gave a lucid account of the Baldwin effect in its original setting (Richards 1987). The concerted flurry of interest in the Baldwin effect that first manifested itself in 1987 apparently stimulated Dennett to endorse the idea in Consciousness Explained (1991) and later in his best-selling tract Darwin's Dangerous Idea (1995). Dennett implies that the orthodoxy of the Baldwin effect had never been in much doubt, and that even if it had been, "Hinton and Nowlan and Maynard Smith have shown clearly and succinctly how and why it worked," thereby rendering the Baldwin effect "no longer a controversial wrinkle in orthodox Darwinism" (Dennett, chap. 4, this volume). Terrence Deacon too has made significant use of what he takes to be Baldwinian themes in his The Symbolic Species (Deacon 1997). As we will see, however, his approach differs from Dennett's.

In this chapter, I propose to elicit some reasons why the very idea of the Baldwin effect appeared promising in its original setting, increasingly unpromising to the founders of the Modern Synthesis, and why in recent years it has seemed promising once again. I will do so by reconstructing the arguments of the original Baldwin boosters, their mid-century critics, and contemporary advocates in terms of the quite different theoretical assumptions that each party took, or takes, for granted. My claim will be that the history of the general idea that "learning guides evolution by natural selection" reveals that the Baldwin effect does not reliably refer either to a

theory-neutral empirical phenomenon, or to a single hypothesis, or to an identifiable mechanism, and that these facts explain why the Baldwin effect has been so diversely received. Because it has never been shown to be a theory-neutral phenomenon, articulations and assessments of the general idea depend on different contrasts and on different, often contradictory, theoretical backgrounds. They depend, in the first instance, on what you are arguing against—Lamarckism, for example, or slow-poke balancing selection. But they also depend on what brand of Darwinism you are presupposing. It is possible that the Darwinian frameworks of today's Baldwin boosters differ from Simpson's by about as much as Simpson's differed from Baldwin's or Lloyd Morgan's. If so, it should come as no surprise that characterizing the Baldwin effect, deducing it from principles, verifying it in fact, explaining how it works, and recommending it as important, depends primarily on a variety of shifting and contested theoretical ideas.

Let me add that I do not say this in order to join forces with Baldwin skeptics. The reasons that deter me from becoming a Baldwin booster on Baldwin's terms also deter me from becoming a Baldwin skeptic on the word of anyone who simply presupposes Simpson's or Mayr's assumptions. Admittedly, I would hate to buy into the contemporary enthusiasm for Baldwinism if it commits me to an unacceptable explanatory scheme. On the other hand, I would hate to have a good idea go unused simply because it does not fit a presupposed theoretical framework. For as many philosophers and historians of science have shown, it is as profitable under some conditions to call a conceptual scheme into question as it is to dismiss an idea for its lack of fit with received assumptions (Lakatos 1970; Laudan 1977).

2 Baldwin's Baldwin Effect—and Lloyd Morgan's Too

Baldwin's argument for the Baldwin effect has the following steps:

- 1. In the course of their life-cycles, "excess," "overproduced," largely random, movements and behaviors of organisms are shaped into adaptive habits by a process of selective reinforcement under the influence of physical, neurological, and "intelligent" forces, the latter including imitation, reinforcement by pleasure and pain, and in some cases means-end reasoning. (Baldwin calls these "ontogenetic adaptations.")
- 2. Ontogenetic adaptations adapt the inherited instincts that permit them to environmental contingencies.

- 3. Ontogenetic adaptations enhance the life chances of the organisms that possess them by making them more responsive to the challenges of contemporary environments. The more ontogenetically adapted an organism, the more it can "stand the stress and storm" of environmental challenge and "rise to the occasion" (Baldwin 1896c: 445, 443).
- 4. The more ontogenetically adapted an organism, the greater the probability that it will leave offspring. ("This sort of adaptation on the part of the creature keeps the creature alive by supplementing his reflex and instinctive actions, and so prevents the operation of natural selection itself" [Baldwin 1896c: 440]).
- 5. In some species, ontogenetic adaptations are made more effective by "social heritability." ("By imitation the little animal picks up directly the example, instruction, mode of life, etc. of his private family circle and species" [Baldwin 1896c: 440].)
- 6. Socially heritable ontogenetic adaptations can be maintained indefinitely in a population until germinal elements that coincide with their influence turn them into congenital instincts.
- 7. Newly evolved congenital instincts provide a platform for further ontogenetic adaptation.

Baldwin used the phrase "organic selection" to refer to the process by which an organism "selects" spontaneous movements and behaviors so that they form ontogenetic adaptations, or what he sometimes called "individual accommodations" (Steps I and 2). In Mental Development in the Child and the Race, and in his subsequent papers, he used the notion that organisms select movements and behaviors in accord with environmental rewards and punishments in order to find a mean between Spencer's stress on the role of an impinging environment in physically conforming the organism to its environment and the neo-Lamarckians' tendency to think of instincts as "lapsed intelligence," that is, as the residual effects of conscious choice (Baldwin 1895, 1896a). The former, even when it works on "overproduced" nervous discharges, renders organisms too passive to account for the fact that they learn; the latter treats them as too active in a rational, means-end way. Baldwin called attention to the interplay between novel adaptive responses and preformed congenital instincts by his careful observation of the ways in which the young are instinctively prone to imitate parents and other adults, while at the same time parents and other adults, who form a large part of the neonate's environment, encourage some movements and behaviors and discourage others.¹

In a paper delivered to the New York Academy of Sciences in February 1896, and in articles published later in the same year (Baldwin 1896b,c), Baldwin asserted that "organic selection" is also a "new factor in evolution." The social heritability of learned behaviors that intensifies and preserves ontogenetic adaptations opens up a transgenerational "breathing space" in which, through the action of natural selection working on whole organisms, ontogenetic adaptations will eventually be fixed by germ-line shifts that reduce the contingencies to which a presumably adaptive learned behavior is exposed. This process is a "new factor in evolution" not only because it explains the formation of congenital instincts that support ontogenetic adaptations, but because it putatively constitutes the leading edge of evolutionary change more generally. In opening the way to further ontogenetic adaptations, organic selection is an engine of phylogenetic progress.

Baldwin was eager to assert that he had already discerned the phylogenetic implications of organic selection in his 1895 book in order to lay a claim of priority for this idea over Lloyd Morgan and Osborn. As both Richards and Paul Griffiths point out, however, Baldwin could do so only by overlooking statements he had explicitly made in 1895 to the effect that the organic selection of behaviors by individual organisms across a series of generations is neutral between Weismannian hard inheritance and neo-Lamarckian soft inheritance (Griffiths, chap. 10, this volume; Richards 1987: 488). Nor could he have used anything in his 1895 book as the basis for such an argument. For the only relatively clear reasons that Baldwin and his contemporaries ever gave for thinking that phylogenetic shifts will predictably move in the direction first marked out by Baldwin's ontogenetic adaptations depend on August Weismann's hard account of inheritance, which was not only inconsistent with Lamarckism, but was apparently suggested to Baldwin by Lloyd Morgan in 1896 (Richards 1987: 493).

So-called simultaneous discoveries are, I suppose, like that. Nevertheless, it is not hard to understand why a simultaneous discovery of this sort would have occurred in the mid 1890s. Baldwin, Lloyd Morgan, and Osborn were all responding to the same exigency—the appearance in the 1880s of Weismann's empirical proof, as it was almost universally taken to be, that traits acquired by an organism in its lifetime could not be passed directly to offspring.² What made this observation compelling was its con-

nection to a causal mechanism, namely, the early developmental sequestering of germ line cells—those original "immortal replicators"—from somatic cells. This explanation had a revolutionary effect on evolutionary thought. It instantly broke the connection between Darwinism and evolutionary mechanisms other than natural selection that Darwin himself had sought to keep open. Darwinism henceforth meant "neo-Darwinism," namely, the claim that evolutionary change was to be based exclusively on natural selection and that natural selection was to be based exclusively on hard inheritance. The origins of the Baldwin effect lie in the sudden need of "Darwinians" in the widest sense, as well as neo-Lamarckians like Osborn, either to bring their leading ideas into conformity with this set of parameters or perish. Spencerian Social Darwinism, for example, hitherto a leading account of the evolutionary process, more or less perished on the spot, or at least retreated to the redoubts of popular ideology.

Osborn provides an example of the panic induced by Weismannism. The sudden ascendancy of hard inheritance and the all-sufficiency of natural selection stimulated him to find a way to protect his directional, progressivist, endogenously-driven view of the evolutionary process ("aristogenesis") without relying quite as directly as he had on the heritability of characteristics acquired by intelligence and effort (Osborn 1896). Unlike his fellow neo-Lamarckian Edward Drinker Cope, however, who attempted to refute Baldwin simply by claiming that "it is impossible to believe that Weismann's doctrine is true" and by reasserting strenuously that "Lamarckism is true" (Cope 1896: 430), Osborn thought that his version of organic selection evaded both the direct inheritance of acquired characteristics and Darwinian natural selection.

In view of Osborn's neo-Lamarckian flirtation with something like organic selection, it is of great importance to recognize that the Baldwin effect attracted Baldwin and Lloyd Morgan for quite different reasons. Like Weismann, they were proud to call themselves Darwinians not only in the wide evolutionary sense, but in the selectionist sense as well, although like everyone else they had hitherto not distinguished very clearly between hard and soft inheritance and in some cases had to be dragged kicking and screaming to the cause. Like William James, a fellow Darwinian psychologist, they now rejoiced that Weismann's "neo-Darwinism" strengthened the hand of natural selection against Darwinism's evolutionary rivals in explaining the origin of instincts (James 1890: 684). Like James too, Baldwin

and Lloyd Morgan were delighted that Weismannism afforded them a way of pillorying Herbert Spencer, who thought of something like germ-line adaptations as arising in a single generation from the direct effects of an impinging environment combined with the direct heritability of characteristics acquired in this brute way (James 1890: 686; Baldwin 1896a,b,c; Lloyd Morgan 1896a,b).³ Lloyd Morgan and Baldwin were especially delighted to be able to accuse Spencerians and neo-Lamarckians alike of being, paradoxically, extreme "naturists," since the view that acquired characteristics are immediately heritable implied a loss of phenotypic flexibility. "Such inheritance would tend so to bind up the child's nervous substance in fixed form that he [sic] would have less or possibly no plastic substance left to learn with" (Baldwin 1902: 55; see Hoffmeyer and Kull, chap. 13, this volume).

In arguing that organic selection is a "new factor in evolution," both Baldwin and Lloyd Morgan asserted nonetheless that there is a natural tendency for a learned trait to become phylogenetically entrenched or supported as a learned trait. Indeed, Baldwin and Lloyd Morgan thought that something even stronger must be true, namely that "the direction at each stage of a species' development *must* be in the direction ratified by intelligence" (Baldwin 1896c: 447–448, my italics). To discover why Lloyd Morgan, followed it would seem by Baldwin, came to this conclusion, we must first sketch in a bit more detail about the sort of Darwinism to which they subscribed. To do so, we must see how they understood not only organic selection, but also natural and germinal selection.

Natural Selection

Organic selection, even when it is considered as a "new factor in evolution," is contrasted with "the natural selection of whole organisms" (Baldwin 1896c: 445, n. 3). Rather than a creative force that accumulates the results of many generations of small directional changes, natural selection is for Baldwin and Lloyd Morgan a negative, rather indiscriminate, force. It illustrates well what one wag has called "the fly-swatter theory of natural selection." It sentences whole organisms that cannot compete for scarce resources to death without issue. Baldwin wrote:

If we suppose, at first, organisms capable of reacting to stimulations \dots we may suppose the stimuli to which they react to be some beneficial and some injurious. If the

beneficial ones recur more frequently to some organisms, these would live rather than others.... The former would therefore be selected.... This is the current Darwinian position. (Baldwin 1902: 163)

To reinforce the view that this was indeed the "current Darwinian position" in these years, consider the following passage from Lloyd Morgan:

Now, what is natural selection, at any rate as understood by the master—Darwin? It is a process whereby, in the struggle for existence, individuals possessed of favorable and adaptive variations survive and pass on their good seed, while individuals possessed of unfavorable variations succumb—are sooner or later eliminated, standing therefore a less chance of begetting offspring. (Lloyd Morgan 1896b: 735)⁴

Modern Darwinians will doubtless be disconcerted by Baldwin's and Lloyd Morgan's conception of natural selection, and by their ascription of this view to "the master." Natural selection as conceived by the Modern Synthesis, and in its view by Darwin as well, does not consist in swatting down whole organisms, but in pumping up slightly divergent reproductive rates. It is not, or not crucially, negative selection of whole organisms, but positive, creative selection for minutely discriminated traits carried by organisms and underwritten by genes. On the modern view, you do not have to die young if you belong to a population whose phenotypic traits are being selected against. You merely have to be part of a population with a statistically lower reproductive output than a relevant comparison population. Baldwin and Lloyd Morgan do not share this view.

Germinal Selection

Baldwin's notion of "organic selection" is also intended to mark a contrast with Weismann's notion of "germinal selection," that is, with the differential survival of germ-line variants as they struggle *in utero* for scarce maternal resources. Germinal selection, not natural selection, is for Weismann the creative force in evolution. It protects hard inheritance by working exclusively on the sequestered germ line; and it conforms to the demand that natural selection must be "all-powerful" by ensuring that nothing that an organism can do in its lifetime to affect its external environment, or be stimulated by its parents to do, can stay the unforgiving demands of natural selection. That is because the organism itself rather than the external world constitutes the environment in which germinal selection occurs.

Using these three concepts—organic, natural, and germinal selection— Baldwin and Lloyd Morgan argued that organic selection, wherever it occurs, must form the leading edge of evolution by natural selection both within species and between them. It is Lloyd Morgan, however, who is much clearer on this point, and who probably instructed Baldwin that "the incidence of natural selection" has an effect in moving evolution in the direction pointed by organic selection. Germinal selection, Lloyd Morgan noted in *Habit and Instinct*, is not necessarily correlated to the natural selection of whole organisms at the organism-environment interface (Lloyd Morgan 1896a). There can, accordingly, be a variety of possible relationships between the three kinds, or, if you will, levels, of selection. Lloyd Morgan argues that there are three, and only three, such possible relationships when the organism-environment interaction is mediated by the organic selection of ontogenetic adaptations and the incidence of negative natural selection.

- (i) Germinal selection can occur in a way that opposes the direction of individual accommodations or ontogenetic adaptations. In this case, more effort will have to be poured into learning to compensate for what is going on at the germinal level. This will involve a greater expenditure of energy and a greater vulnerability to contingencies. This in turn entails a greater likelihood that the effort will fail at some point, and that individuals and populations bearing such inherited factors will be swatted down by negative natural selection. As Lloyd Morgan puts it, "Any congenital variations antagonistic in direction to [organic] modifications will tend to thwart them and render the organisms in which they occur liable to elimination" (Lloyd Morgan 1896a: 320).
- (ii) There might be a neutral relationship between germinal and organic selection, in which neither supports nor hinders the other. In this case, there will be no correlation at all between the two levels. Both will go their merry way, the former at the germ line level, the later at the level of culture. So the case is irrelevant to questions about the effect of learning on adaptive and evolutionary vectors.
- (iii) If, finally, germinal variants are fixed in the germ line in a way that coincides with the direction of learned behavior, the adaptive behavior will be reinforced by inherited factors.

Lloyd Morgan writes:

By their innate plasticity the several parts of an organism implicated by their association with the varying parts are modified in individual life in such a way that their

modifications co-operate with germinal variation in producing an adaptation of a double-origin, partly congenital, partly acquired. The organism then waits, so to speak, for a further congenital variation, when a like process of adaptation again occurs. Thus race progress is effected by a series of successive variational steps, assisted by a series of cooperating individual modifications. (Lloyd Morgan 1896a: 315)

Assuming the relevant definitions of key concepts, what Lloyd Morgan is describing is a logically valid inference to a win-win situation. The scythe of natural selection will eventually shift the populational mean in successive generations toward a situation that makes the behavior in question more widespread in the population and screens off any contrary tendencies that may originate in the sphere of germinal selection. In the long run only the germinal elements that reinforce the direction of organic selection by increasing its heritability are retained "because natural selection kills off the others" (Baldwin 1896b: 447). Baldwin's inference that "the future development at each stage of a species' development must be in the direction ratified by intelligence," where intelligence means a variety of ways of responding flexibly to environmental contingencies, including anticipation of likely consequences, is thus grounded in an argument that eliminates any other possibility. Note that on this view no violation of Weismann's injunctions against the inheritance of acquired characteristics will have been incurred. Nonetheless, the agency-accentuating effects that had hitherto been monopolized by Lamarckism, some of which Baldwin and Lloyd Morgan are concerned to preserve, would have been reaffirmed within a decidedly Darwinian framework. Note too that Baldwin and Lloyd Morgan are not arguing that a phenotype is driven into the genotype. Their idea is that germinal and organic selection coincide to evolve a congenital instinct that is stable enough to buffer the organism's efforts to respond to environmental pressures, but at the same time open enough to allow further modification by ontogenetic adaptation. What we would call a feedback loop between instincts and behaviors has been expanded to embrace a wider loop between organisms that are ontogenetically adapted and the arrow of evolution.

3 The Baldwin Effect and the Modern Synthesis

The original explanatory framework in which the Baldwin effect was formulated—a complex of concepts in which organic selection of ontogenetic

adaptations produces individual "adaptations," negative natural selection swats down whole organisms before reproduction, germinal selection plays a creative role producing heritable adaptations, and phylogeny is decidedly progressive—is wholly abandoned by the Modern Synthesis. Physiological and behavior adaptiveness, even when reinforced, is not an adaptation, but merely the instantiation of genetically underwritten inherited adaptations; natural selection affects reproductive rates of populations, and only indirectly relies on the life or death of individuals; the variant alleles that are the creative material of natural selection code for phenotypes at the organismic, not at the germinal, level (at least until the rise of gene-level selection); and, finally, evolution by natural selection is not inherently directional. These differences pose questions about whether the Baldwin effect could survive in any recognizable way in the new theoretical environment. My suggestion is: not very well.

The makers of the Modern Synthesis of the 1940s and '50's varied a good deal among themselves about the answer to this question. Huxley, as I have mentioned, was something of a Baldwin booster. "The principle of Baldwin and Lloyd Morgan," he wrote in Evolution: The Modern Synthesis,

shows how Lamarckism may be simulated by the later replacement of adaptive modifications by adaptive mutations . . . In areas outside the normal habitat of the species... the extension of habitat may in the first instance be dependent on a noninherited modification of behavior, mutation and selection later stepping in to fix the change genetically. (Huxley 1942: 17, 114)

For his part—and it was a considerable part indeed—Simpson was not entirely negative. For him, the effect meant that "characters individually acquired by members of a group of organisms may eventually, under the influence of selection, be re-enforced or replaced by similar hereditary characters" (Simpson 1953: 110). So understood, Simpson thought that the Baldwin effect is "fully plausible under current theories of evolution" (Simpson 1953: 115). It can happen, however, only where several contingently related circumstances coincide. First, since adaptations are by definition based on gene frequencies, an adaptive novelty can occur in individuals within a population only if a gene or gene complex codes for a trait that has a fairly wide "norm of reaction" at the phenotypic level. In this analysis, Simpson was following the lead of the Russian Darwinian I. I. Schmalhausen, who, in struggling to defend Darwinism against state-sponsored Lysenkoism as intently as Baldwin and other Darwinian

psychologists had once struggled against Social Darwinism and neo-Lamarckism, rested his case for a Darwinian mimicry of the inheritance of acquired characteristics on the notion that genes typically have a range of phenotypic effects, and that what looks like the heritability of acquired characteristics is merely a shifted norm of reaction of genes that are already there (Simpson 1953: 115-116; Schmalhausen 1949).5 Second, a behavior or habit preserved across generations by cultural transmission can causally lead to changes in gene frequencies only if "there occur in the population genetic factors producing hereditary characteristics similar to the individual modifications . . . or having the same sorts of adaptive advantages" (Simpson 1953: 112). This is roughly Baldwin's and Lloyd Morgan's idea of a concurrence between germinal and socially inherited factors. Butand this is the crucial point—it is Baldwin's and Lloyd Morgan's idea shorn of any theoretical reasons why in the long run such a concurrence must form the leading edge of evolutionary change.

Indeed, given the theoretical framework of the Modern Synthesis there are good reasons to think that such a concurrence will seldom, if ever, occur at all. If learned behaviors are so effective in getting a useful trait passed from generation to generation at the cultural level, there will presumably be no selection pressure for the spread of genetic factors favoring that trait. Simpson claimed that in circumstances where flexible responses are required to meet the challenges of changing environments learning can be presumed to be more effective than hard-wired responses. To show this, he deployed against Baldwin the same argument that Baldwin had used against the Lamarckians. If learned behaviors do become genetically underwritten, a population will be swapping "short term and more plastic [learned behaviors] for long term, but more rigid adaptations," thus subverting the very point of the Baldwin effect (Simpson 1953: 116). On an even more skeptical note, Simpson added that it would be very difficult to tell for sure if it had happened, since the theoretical presumption must always be that existing adapted gene complexes with wide norms of reaction are merely surfacing under new selection pressures rather than that learning is antecedently causing or guiding a shift in gene frequencies. Given the variety of nature, as well as an analogy between the Baldwin effect and C. H. Waddington's "genetic assimilation" to which I will turn momentarily, Simpson was loathe to deny that the phenomenon might have occurred

at some time or another (Simpson 1953: 115). Still, he concluded that there is "singularly little concrete ground for the view that [the Baldwin effect] is a frequent and important element in adaptation" (Simpson 1953: 115).

Simpson's interest in the Baldwin effect was stimulated by Conrad H. Waddington's mention of it in connection with "genetic assimilation," which was the subject of an article by Waddington in the same issue of Evolution as Simpson's 1953 article (Waddington 1953). Waddington had reliably and replicably shown that strong shocks to fruit flies will produce phenotypes that subsequently, and often quite rapidly, become genetically heritable in later generations, even those not subjected to the initiating shock. In Waddington's view, as well as that of other respectable Darwinians of the Modern Synthesis, this happens because the shock "destabilizes a developmental system and reveals genetic variation that was previously concealed" at a much deeper level than, say, alternative alleles for darker and lighter pepper moths (Waddington 1962: 226-227). Presumably, this is what is happening in cases that one might be tempted to chalk up to the Baldwin effect. In contrast to the genetic-variation-preserving thrust of adaptation at the genetic level and the presumed plasticity at the phenotypic level that a flexible genetic inheritance favors, the Baldwin effect, as redescribed by Simpson, applies at best to unusual cases in which a population under very strong selection pressure (at the margins of its range, for example, as Huxley suggests) genetically "assimilates" a culturally transmitted phenotype by narrowing the genetic norm of reaction to a vanishing point. So described, Simpson wrote, "The Baldwin effect would ensue when selection for the ability to acquire an adaptive character so narrows the developmental range that the character would usually or invariably appear" (Simpson 1953: 116). Presumably, this will take place under conditions where loss of genetic and phenotypic flexibility is a small cost to pay under dire circumstances for basic survival. Any port will do in a storm. Leaving aside the troublingly disanalogous fact that phenotypes under genetic assimilation are not necessarily adapted, this scenario forms the basis for comparing the Baldwin effect to genetic assimilation within the framework of the Modern Synthesis. Even here, a genetic basis, albeit a newly scrambled one, precedes the expression of an adapted phenotype and so preserves the insistence of the makers of the Modern Synthesis that genetic change both precedes and causes adaptations.

This view of the conditions under which something that might be called the Baldwin effect could conceivably occur was, I want to suggest, influential in the subsequent dismissal of the putative phenomenon altogether. This negative reading is registered most clearly in Ernst Mayr's 1963 Animal Species and Evolution. In reviewing Simpson's version of the argument, Mayr pronounced the very idea of the Baldwin effect incoherent. For Mayr, the Baldwin effect falls between two stools. Baldwin's original version, he asserts, "has no validity" at all. In assuming that "organic selection" is an alternative to natural selection, Baldwin implies not a reconciliation of Darwinism and Lamarckism, but a disguised or cryptic form of Lamarckism in which phenotypic innovation is said actually to cause new genotypes rather than to favor a new arrangement or unconcealment of already existing genetic variation (Mayr 1963: 610). This was a pointed remark in light of the recent Lysenko affair. But even under Simpson's redescription, Mayr could not imagine any circumstances in which there would be an adaptive advantage to genetically fixing a previously flexible phenotype in a way that is comparable to genetic assimilation. As a universal rule, Mayr writes, "Those genes will be selected . . . which produce genotypes with an optimal modifiability of the phenotype" (Mayr 1963: 612). There is no reason to think that adaptive natural selection could play a role, then, in collapsing norms of reaction, even in cases where stress is involved. Indeed, it is just such cases that led Mayr to assert that his pet theory of allopatric speciation by means of wholesale genetic reorganization at the periphery of an isolated population is actually paradigmatic of adaptive natural selection at work.

Dobzhansky seems to have agreed (Dobzhansky 1970: 211). The premium placed by his theory of "balancing selection" on retaining vast amounts of genetic variation in natural populations was designed to highlight the presumption that adaptive natural selection favors plastic phenotypes, phenotypes with very wide norms of reaction. Both Mayr and Dobzhansky thought that selection, in favoring the evolution of phenotypic plasticity, also favors the development of cultural transmission. As the philosopher Robert Brandon puts the point, "One would expect a species subjected to [changing] conditions to become highly plastic and to develop culture" (Brandon 1996: 82). For the makers of the Modern Synthesis, culture is natural selection's greatest achievement. But the very