THE BALDWIN EFFECT

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Historical Introduction

Characters individually acquired by members of a group of organisms may eventually, under the influence of selection, be reenforced or replaced by similar hereditary characters. That is the essence of the evolutionary phenomenon here called "the Baldwin effect."

The possibility of such an effect was noted independently and almost simultaneously by J. M. Baldwin [1] (1896), Lloyd Morgan (1896), and H. F. Osborn (1896). Lloyd Morgan (*e.g.*, 1900) and Osborn (*e.g.*, 1897a and b) made occasional later references to the effect (or factor, principle, or hypothesis, as you will). Baldwin (especially 1902) followed it up in greater detail. E. B. Poulton early joined the discussion, as did several others in the period 1896–1905, approximately.

That three workers independently thought of the Baldwin effect at the same time demonstrates that the idea was in the air, that it was an inevitable outgrowth of the intellectual atmosphere of the time. That time was at the height of the neo-Darwinian *versus* neo-Lamarckian controversy and shortly before the rediscovery of Mendelism gave a radically different turn to biological thought. There was a sharp issue, still familiar to all of us. Organism and environment obviously interact and obviously are closely fitted, that is, adapted to each other. Yet, as was already clear in the 1890's, it is improbable (to say the least) that the effects of the interaction can become heritable directly and in the same form. The Baldwin effect ostensibly provides a reconciliation between neo-Darwinism and neo-Lamarckism. To the extent that it may really occur, it provides a mechanism that is capable of making acquired characters hereditary—or of seeming to do so. Baldwin, Lloyd Morgan, and Osborn all explicitly postulated the Baldwin effect as a way out of the neo-Darwinian–neo-Lamarckian dilemma.

Mendelism and later genetic theory so conclusively ruled out the extreme neo-Lamarckian position that reconciliation came to seem unnecessary. After general acceptance of Mendelism and before clear statement of the modern synthesis of evolutionary theory, the Baldwin effect was seldom discussed in detail, although it continued to be mentioned under various names in reviews of evolutionary theory (*e.g.*, Delage and Goldsmith, 1912; Lull, 1917; Herbert, 1919). Huxley (1942) brought the "unduly neglected" Baldwin effect into the synthetic theory as a subsidiary factor. It is so recognized by most followers of the synthetic theory (*e.g.*, Mayr, 1951), although it is seldom assigned a major role in evolution.

In the meantime the notorious conflict about theories of genetics and of evolution was developing in the U.S.S.R. Until 1948 the most active and able Soviet biologists were contributing substantially to the synthesis of genetics and what was elsewhere usually called neo-Darwinism. There was, however, increasing ideological opposition to Mendelism and to theories of evolution that include random or indeter-

[1] James Mark Baldwin was born in Columbia, South Carolina, in 1861 and was educated at Princeton and under Wundt in Germany. He taught at several universities, including Princeton in 1893–1903 (the period of work on the Baldwin effect) and the Johns Hopkins, 1903–1908. After 1908 he spent some time in Mexico and finally settled in France, where he died in 1934. He was a pioneer in experimental psychology and an indefatigable writer and editor. His interest in evolution was part of a widespread effort to develop an evolutionary psychology. (See Boring, 1950; Langfeld, 1944.) Lloyd Morgan and Osborn are more familiar to evolutionists.

minate processes, as neo-Darwinism was accused of doing. The result was a conflict which because of its political apriorism must be called pseudo-scientific but which in form closely paralleled the genuinely scientific disagreement of the neo-Darwinians and neo-Lamarckians in the 1890's. In the U.S.S.R. the conflict was between Mendelism (associated with neo-Darwinism through the synthetic theory) and Michurinism (essentially the same as neo-Lamarckism). The similar situation had a similar result: Soviet students independently thought of the Baldwin effect. First was apparently Lukin around 1936,[2] and others followed up and strongly emphasized this trend of thought, notably Kirpichnikov (*e.g.,* 1947), Gause (*e.g.,* 1947), and Schmalhausen (*e.g.,* 1949).

As everyone knows, Michurinism was triumphant in the U.S.S.R., and Mendelism and neo-Darwinism were, in effect, outlawed in 1948. It is significant that particularly virulent attack was made on Schmalhausen's work, which embodied the Baldwin effect. The Baldwin effect could, as its earlier proponents had suggested, be considered as a compromise between the opposing schools, and compromise was ideologically even less acceptable than Mendelism.

Recourse has further been made to the Baldwin effect in still a third context: the conflicting philosophies of finalism (generally associated with vitalism) and materialism. As in neo-Darwinism *vs.* neo-Lamarckism and Mendelism *vs.* Michurinism, the evolutionary issue here centers on the problem of adaptation. Adaptation *seems* to be purposeful. The finalist view is that it is purposeful, in fact, but materialists generally rule out purpose as a possible factor in evolution. There are several possible materialistic explanations for seemingly purposeful adaptation. Among them is the Baldwin effect, which conceivably could, for instance, account for the genetic fixation of purposeful (or pseudo-purposeful) individual activities. The controversy between finalistic and materialistic philosophies of evolution has been especially active in France, and there Hovasse (1943) proposed what is essentially the Baldwin effect to account for adaptations considered finalistic by Cuénot (1941).[3] Hovasse (1950) later wrote a short book on the subject.

Terminology and Definition

Baldwin called the effect in question "organic selection" and defined it as follows (Baldwin, 1902):

"*Organic Selection:* The process of individual accommodation considered as keeping organisms alive, and so, by also securing the accumulation of variations, determining evolution in subsequent generations."

In Baldwin's usage an "accommodation" was non-hereditary, *i.e.,* it was an acquired character, while a "variation" was (by definition) hereditary, *i.e.,* genetic. Thus his definition, somewhat ambiguous by present-day usages, designates a sequential process in which acquired characters are replaced by genetic characters. This is clear in Baldwin's discussion of the matter, which also brings in natural selection as the mechanism of replacement. Osborn and Lloyd Morgan accepted Baldwin's term with essentially his definition, and so have several later students, notably Gause. Others have used the term but not precisely with its original meaning. For example Lutz (1948) defines organic selection as "selection of the environment by the organism," a definition radically different from that of Baldwin and those who have followed him more closely.[4] The term is in any case misleading. "Organic selection" is no more organic than any other sort of selection. Moreover, the phenomenon discussed by Baldwin is not

[2] *Fide* Gause and Schmalhausen. I have not read Lukin's publications, which are in Ukrainian and Russian.

[3] Cuénot's final (posthumously published) word on the subject (1951) was less decisively finalistic.

[4] Selection of the environment may, however, be a first step in the Baldwin effect, a possibility stressed by Thorpe (1945a).

directly or solely selection anyway. It is a complex process in which selection, strictly speaking, is only one of several factors, or it is an effect that is postulated as a result of selection.

Osborn used the term "coincident selection" alternatively as a synonym of "organic selection," the significance being that the "germinal variations" selected coincide with adaptive individual modifications. The same thought underlies Hovasse's preference for "parallel selection." Both terms are again misleading in that the process involves or results from but is not as a whole equivalent to selection, and "parallel selection" is liable to confusion with the wholly different process of parallel evolution (in two or more lineages) under the influence of natural selection. Schmalhausen and some others (mostly Russian) speak of "stabilizing selection." The term is sometimes equated with Baldwin's "organic selection," but the equation is misleading. "Stabilizing selection" applies literally and in Schmalhausen's usage to any mechanism tending to fix an adaptive type and to bring it under more rigid genetic control. The Baldwin effect is one such mechanism, but not the only one and not (even in Schmalhausen's opinion) the most important.

Those ambiguities and the difficulty of finding an apt descriptive term for so complex a process led Huxley (1942) to speak of the "Baldwin and Lloyd Morgan principle,"[5] and Hovasse (1950) calls it "Baldwin's principle." That usage seems to me the simplest way toward a term both brief and unambiguous. Whether the mechanism or process in question is really a "principle" remains debatable, and I prefer the expression "Baldwin effect."

From Baldwin to Hovasse all those who have discussed the Baldwin effect under any name make it clear that what is meant is a complex sequence of events. The effect may be analyzed as involving three distinct (but partly simultaneous) steps:

(1) Individual organisms interact with the environment in such a way as systematically to produce in them behavioral, physiological, or structural modifications that are not hereditary as such but that are advantageous for survival, *i.e.,* are adaptive for the individuals having them.

(2) There occur in the population genetic factors producing hereditary characteristics similar to the individual modifications referred to in (1), or having the same sorts of adaptive advantages.

(3) The genetic factors of (2) are favored by natural selection and tend to spread in the population over the course of generations. The net result is that adaptation originally individual and non-hereditary becomes hereditary.

That description of the Baldwin effect is also a more precise definition of the term. At this point it need not be taken for granted that the effect actually occurs or has an essential role in evolution. It may be taken as a hypothesis subject to investigation.

Supposed Examples of the Baldwin Effect

The three processes involved in the Baldwin effect are all known to occur separately. The development of adaptive individual modifications or accommodations (sometimes called "somations") is widespread, a matter of common observation sufficiently established by the banal example of the strengthening of muscles by use. Partial or even complete correspondence between the effects of non-heritable modification and heritable mutations (broadly speaking) is also well-established in some instances. The phenocopies of Goldschmidt (1938) conclusively demonstrate this phenomenon. The existence of phenocopies, copying genetic effects without change in heredity, implies equally the existence of genocopies (Hovasse's apt term), copying non-genetic

[5] Even this length term fails to credit the simultaneous expressions of the principle, for Osborn thought of it as early as Lloyd Morgan and independently. When the coincidence was discovered, both Osborn and Lloyd Morgan deferred to Baldwin.

effects by change in heredity. That genetic effects, therefore also genocopies, can be spread through populations by natural selection requires no further substantiation at this late date.

Thus each process necessary for the Baldwin effect does factually occur. There is no reason to doubt that they could occur together, in the stated sequence, and so produce the Baldwin effect. There is even some probability that they must have produced that effect sometimes. Nevertheless two points remain decidedly questionable: whether the Baldwin effect does in fact explain particular instances of evolutionary change, and the extent to which this effect has been involved in evolution or can explain the general phenomenon of adaptation. Basis for judgment on these points is provided by brief review of some supposed examples.

Both Baldwin and Lloyd Morgan considered the Baldwin effect as a way in which, without transmission of acquired characters, habits and other learned behavior could become instincts, *i.e.,* inherited behavior. Their examples included the instinct (if such it be) of chicks to drink by throwing the head in the air, the instinct [6] in primates to grasp with the thumb opposed to the other fingers, and other examples of a similar sort. Osborn went so far as to suppose that an arboreal race of man could be developed by rearing infants in trees, where they would adaptively accommodate to the environment and where accommodation would eventually be replaced by "congenital variations." The soberer examples of Baldwin, Lloyd Morgan, and Osborn are usually open to the objection that when the characters in question are demonstrated to be hereditary there is no evidence whatever that they had occurred as accommodations before they became hereditary.

Somewhat more impressive is the example of bird song, already discussed at length by Lloyd Morgan (1896) and frequently mentioned by later authors. The characteristic song of some species of birds is learned by imitation. In other species the song is innate, hence presumably genetically determined, and in still others the situation is intermediate. It does seem possible, at least, that in some instances a learned song has become innate through the Baldwin effect. More direct evidence seems to be quite lacking, but that hypothesis has been accepted by Huxley (1942), among others.

Huxley also maintains that the Baldwin effect is usually involved in early stages of biological differentiation, that is, in the origin of races and eventually of species characterized by preferences for different hosts or food plants. Examples of such races are numerous as are also races distinguished in part by other behavioral and ecological preferences (see especially Thorpe, 1930, 1939, 1940, 1945a, b). Thorpe transferred insect larvae to new food plants, which the insects thereafter preferred, thus demonstrating that the preference may be caused by early conditioning. Other experiments, notably one by Harrison (1927), strongly suggested that natural selection of genetic variation was responsible for development of a strain with changed preferences: there was high initial mortality and only slow establishment of a population adapted to a new host plant. In that example individual modification perhaps also occurred, but the adaptation was mainly genetical. In sum the experiments by Thorpe and Harrison certainly show that adaptation to a new host may occur either by individual acquisition or by genetic selection, but they do not conclusively prove that hereditary adaptation *replaced* non-hereditary.

The most extensive experimental work on the subject is that of Gause (1947 and earlier work there cited). Asexually reproducing clones of the ciliate *Euplotes* showed individual accommodation by decrease of size when transferred from 2.5 to 5% salinity, and populations of excon-

[6] There are problems here as to whether these are instincts or reflexes, if there is a proper distinction between the two, and also as to whether the "instincts" of Baldwin and Lloyd Morgan were inherited as such and not at all learned.

jugants subjected to genetical selection under the same conditions showed a similar but more extreme response. Parallel results were obtained in adaptations of *Paramecium* to different temperatures. The results confirmed the possibility of the Baldwin effect, but I cannot agree that they demonstrated its occurrence. In fact the Baldwin effect did not occur in these experiments: they show, again, that similar adaptation may be produced either by non-hereditary modification or by genetical selection, but they do not show the latter replacing the former.

Gause's experiments brought out other interesting points. In a medium of 1% salinity *Euplotes* was viable but showed no individual modifications. In the same medium genetical selection among ex-conjugants resulted in increase in size. In 7% salinity pure, non-conjugating clones failed to accommodate and eventually died out, but selection produced strains genetically adapted to high salinity. In these experiments adaptation occurred, but only by genetical mechanisms. The Baldwin effect was definitely ruled out as even a possibility. The results bear on Hovasse's opinion that the Baldwin effect is a usual or necessary part of adaptation.

Hovasse (1950) goes so far as to say that "the application of this principle [the Baldwin effect] can lead to a general explanation of adaptation." The path to this extreme is acceptance at face value of all the criticisms of natural selection advanced on one hand by the neo-Lamarckians and on the other by the finalists. Each of those schools claims a general explanation of adaptation, and Hovasse accepts the generality but substitutes the Baldwin effect as mechanism. That is certainly going much too far. It seems to me to require no argument now that most of the neo-Lamarckian examples supposed to show inheritance of acquired characteristics are fully explained by ordinary natural selection without invoking the Baldwin effect or any other additional principle. Yet in a few cases, the prize exhibits of the neo-Lamarckians, the Baldwin effect does provide a plausible explanation not alternative to that of natural selection but showing how natural selection can have produced the observed result.

An example of this sort is the classic one of callosities still sometimes claimed as conclusive evidence for inheritance of acquired characters (*e.g.,* Wood Jones, 1943). Many vertebrates form calluses where the skin is habitually rubbed. The calluses are protective and may therefore be considered adaptive. They may be caused entirely by individual modification and are usually intensified, at least, by such accommodation. It has, however, long been observed that in some instances the calluses begin to appear in the embryo; for example, plantar calluses in man (Darwin, 1871), sternal calluses in the rhea (Cuénot, 1951), or elbow calluses in the wart hog (Leche, 1902). The Baldwin effect could explain this phenomenon. Such examples are perhaps most suggestive of a real role for the Baldwin effect in evolution, but they do seem too trivial to establish that role as universal or even particularly important.

Among the adaptive phenomena similarly considered crucial evidence by the finalists what Cuénot (1941) called "coaptations" are perhaps the most striking. In "coaptations d'accrochage" two parts of an organism arise separately in the embryo and subsequently fit together and have a single function. An example is the femoral groove of the mantis, into which the tibia is folded. (Numerous other examples are given by Cuénot, 1941; Corset, 1931; Hovasse, 1951.) To Cuénot coaptations were irrefutable proof of finalism. Hovasse agrees that they are inexplicable by mutation and natural selection and maintains that only "parallel selection," that is, the Baldwin effect, can explain them without recourse to finalism. The Baldwin effect may, indeed, be involved, but few will agree that it is the only possible non-finalistic explanation, and there is a glaring weakness in the argument. Again there is no good evidence that the coaptations (to the extent that they are hereditary; they are not invariably or wholly so) did really begin as accommodations.

Hovasse goes still further. He attempts to meet all criticisms of natural selection by substitution of the Baldwin effect and so ends by making the Baldwin effect virtually all-powerful in adaptation. To give one more example, he cites the butterfly *Kallima*, which so closely mimics a leaf, and accepts the criticism that natural selection cannot have developed that mimicry because its advantage is all-or-none, not favored by selection until it is already established. Hovasse's own interpretation is that the ancestors of *Kallima* were changeable in color and pattern, that they actively copied leaves, and that this variable accommodation was finally fixed genetically by the Baldwin effect. This and some similar arguments seem to me so wildly improbable or, at best, so completely lacking in evidence that they merely weaken the whole case for the over-all importance of the Baldwin effect.

Status of the Baldwin Effect in Evolutionary Theory

The Baldwin effect is fully plausible under current theories of evolution. Yet a review of supposed examples and of pertinent experiments reveals no instance in which it indubitably occurred, no observations explicable only in this way, and few that seem better explained in this way than in some other. It probably has occurred, but there is singularly little concrete ground for the view that it is a frequent and important element in adaptation.

From 1896 up to now, everyone who has discussed it at any length has taken the position that the Baldwin effect is something distinct from natural selection acting on genetical variation and that its real importance is in meeting or explaining away the criticisms leveled at natural selection by, especially, the neo-Lamarckians, the Michurinists, and the finalists. The Baldwin effect is both possible and probable, but assignment to it of that role in evolutionary theory seems to me fallacious.

As an alternative to neo-Lamarckism or Michurinism, the Baldwin effect supposes that accommodation (adaptive somation) is paralleled by genetic changes with similar results. Actually this is no alternative at all and still leaves the basic decision to be made. If the Baldwin effect occurs, either there is or is not a causal connection between an individual accommodation and subsequent genetic change in a population. If there is no such connection, then the truly genetic change must occur wholly by mutation, reproduction, and natural selection, and the accommodation may be irrelevant. If there is a causal connection, the neo-Lamarckian argument is as much supported as supplanted. Indeed the claim (as by Hovasse) that the Baldwin effect is usual in adaptive evolution could be taken as an argument in favor of neo-Lamarckism: frequent coincidence of somation and mutation might suggest that one causes the other. Nor is the Baldwin effect an adequate answer to the arguments of the finalists, who can as readily see directive purpose in somation as in mutation.

The synthetic theory rests on grounds that have essentially nothing to do with the Baldwin effect. Occurrence of the Baldwin effect is nevertheless consistent with that theory and (if, indeed, it does occur) is an interesting but, I would judge, relatively minor outcome of the theory. It is simply one way in which natural selection may sometimes affect populations, and clearly it is not a factor either contradictory or additional to natural selection.

Of all those who have discussed the Baldwin effect, Schmalhausen seems to me to have most nearly placed it in true perspective within modern theories of evolution. Its place, not precisely in Schmalhausen's terms, may be summarized as follows. Genetical systems do not directly and rigidly determine the characteristics of organisms but set up reaction ranges within which those characteristics develop. An "acquired character" or specifically an adaptive modification (that is, an accommodation) necessarily occurs within a genetically determined reaction range. The range may be relatively broad or extremely narrow. In any case an accommodation has genetical limits and develops only in the framework of the genetical system, but in a labile reaction range the particular form taken by a developing organism depends also on interaction with the environment. The genetical system evolves and the reaction range correspondingly changes. The range may come to cover different possibilities or it may become broader or narrower. If it becomes narrower, the possibilities for individual modification of characteristics become fewer. An accommodation that in a broader range occurs only as a specific response to a particular interaction with the environment may as the range narrows become the only developmental possibility. Then the Baldwin effect may occur: a response formerly dependent on a combination of genetical and environmental variables may become relatively or even absolutely invariable. It is not putting the matter in the right terms to say, as has usually been done, that this contrast is between "acquired" and "inherited" characters.

The ability to "acquire" a character has, in itself, a genetical basis. Selection acts (with some exceptions) on the phenotype, so that it is valid to say that selection is actually not on genetical characters but on the ability to acquire characters. This point is emphasized by an example recently discussed by Waddington (1952). The phenomenon involves, again, a broader principle of which the Baldwin effect may be considered a special case. The Baldwin effect would ensue when selection for the ability to acquire an adaptive character so narrowed the developmental range that the character would usually or invariably appear. There is, further, no evident reason why such selection might not act on genetical variation tending to push back appearance of the character into earlier developmental statges. Another aspect of the matter is that the genetical system producing such an effect may well differ in different instances. The absence, on both sides, of one-to-one correspondence of phenotype and genotype is well known. There is therefore wide possible scope for the Baldwin effect or especially for the phenomena of specialization and adaptation of which that effect is one aspect. All this does not seem to me to support the view of 'Espinasse (1952), who in discussion of Waddington's results concludes from the absence of such correspondence that the characters and adaptive changes of populations cannot usefully be interpreted in genetical terms. It only enriches and makes more widely explanatory such interpretation.

There is, finally, as Schmalhausen also pointed out, a certain balance between lability and stability of developmental ranges and norms in evolution. Wide ranges, with labile development, permit individual adjustment to the immediate environment and to short-term vicissitudes. Narrower ranges promote more highly specific and long-continued adaptation, usually advantageous under relatively constant conditions. Narrowing of the reaction range thus exchanges short-term and more plastic for long-term and more rigid adaptation. It is one of the aspects of specialization, and an important special case of evolutionary stabilization. Such a sequence need not precisely correspond with the Baldwin effect, but it includes that effect among the possibilities.

Seen in a modern context, the Baldwin effect helps to focus attention on a host of problems, especially in developmental (or physiological) genetics, well worthy of further study. It does not, however, seem to require any modification of the opinion that the *directive force* in adaptation, by the Baldwin effect or in any other particular way, is natural selection.

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