# The Baldwin Effect and the Potentialities for Thoughtful Darwinism around 1900

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(from *The Riddle of Organismal Agency: New Historical and Philosophical Reflections*, eds. J. Baedke, A. Fábregas Tejeda, G. Prieto, and G. Radick, London: Routledge, in press)

## 6.1 1900 and All That

For anyone concerned with heredity and evolution, 1900 marks, first and foremost, the year of the "rediscovery of Mendel." Independently of each other, three European botanists engaged in experimental and quantitative crossbreeding research—Hugo de Vries in the Netherlands, Carl Correns in Germany, and Erich von Tschermak in Austria—published papers which converged strikingly not only on each other's work but on that of a long-dead and previously little-known Augustinian monk from Moravia, Gregor Mendel (see, e.g., Olby, 1990, pp. 528-530). As enthusiasm for Mendel's original paper began to spread, first under the banner of "Mendelism," then under "genetics," so too did the remarkable story of its rediscovery. Soon that story took its place with similar ones from the history of science—Newton and Leibniz converging on the calculus, Darwin and Wallace converging on natural selection—as an illustration of a curious general truth: when a scientific discovery's time has come, it becomes irresistible, inevitable. In the Mendelian case, had there not been three rediscoverers in 1900, there would have been six in 1901: so, at any rate, judged the American anthropologist Alfred Kroeber, looking back from 1917 (Kroeber, 1917, p. 199). The standing of the Mendelian rediscovery went on to climb still higher over the next decades, as defenders of Darwin's theory of natural selection succeeded in showing that the Mendelian gene concept was what natural selection had needed all along. From the perspective of this new "Modern Synthesis," 1900 was a pivotal year, when the revival in the fortunes of Darwinism, then at a nadir, first became a possibility.

Less well remembered is another triple convergence, no less relevant to heredity and evolution, and taking place just a few years earlier—yet about as different as could be from the Mendelian triple as a clue to the energies animating the era's biological debates. In 1896, the American psychologist James Mark Baldwin, the American palaeontologist Henry Fairfield Osborn, and the English comparative psychologist Conwy Lloyd Morgan independently proposed a form of natural selection that could result in acquired characters becoming hereditary. Called "organic selection" by Baldwin, and a number of other names since then, it was enduringly renamed "the Baldwin effect" in a 1953 essay in *Evolution*, the house journal of the Modern Synthesis, by its major paleontological contributor, George Gaylord Simpson. In Simpson's view, the Baldwin effect is best thought of 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." (Simpson, 1953, p. 112)

Simpson devoted most of his essay to evaluating the status of the Baldwin effect in *circa* 1950 biology, including those precincts of it—notably in France—where debate about the evolutionary significance of purposive activity by individual organisms remained lively. But near the start he reflected on what it revealed about *circa* 1900 biology:

> That three workers independently thought of the Baldwin effect at the same time demonstrates that the idea was in the air, that it was the 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. (Simpson, 1953, p. 110; emphasis added)

Elsewhere (Radick, 2023, pp. 301-302, 365, 381) I have recommended Simpson's juxtaposing of the Baldwinian and Mendelian triples as a corrective to a picture of *circa* 1900 biology that many of us inherited along with elementary Mendelism—a picture that tends to make the Mendelian turn in biology look like a foregone conclusion.[1] Yes, for some biological workers, curious to know what could be gleaned via crossing and counting about the transmission

[1] To quote from the Biology 101 textbook that I used: "It was not until the year 1900 that biology finally caught up with Gregor Mendel" (Campbell, 1993, p. 280).

patterns of all-or-nothing unit characters, the Mendelian ideas of dominance, recessiveness, the three-to-one ratio, and so on were in the air. But for other workers, attuned to questions about how developing organisms and their descendants adapt to—and sometimes act on—environments, and how variation and selection bring about evolutionarily consequential change, what was in the air was the Baldwin effect. Here I want to expand the frame around the Baldwinian triple to exhibit something of the creative resourcefulness of Darwinian discussion in the 1890s and 1900s. As we shall see, it was a thoughtful discussion twice over: in its recognition of complexity, and attention to the drawing of distinctions and articulating of options; and in its openness to what Conwy Lloyd Morgan called "mental factors in evolution." I begin with Morgan's survey under that title for a 1909 volume commemorating a hundred years since Charles Darwin's birth and fifty years since the publication of the *Origin*. Next I consider in a little more detail three topics that Morgan touched upon: female choice in sexual selection; the Baldwin effect ("organic selection" for Morgan); and the English comparative anatomist Edwin Ray Lankester's proposal about what he called "educability." Finally I turn to look at the thoughtful Darwinism of an instructive figure for all interested in that era in developmental plasticity, adaptive evolution, and inheritance, the English zoologist and biometrician Walter Frank Raphael Weldon. In conclusion I offer some brief remarks on how differently the period between the rediscovery of Mendel and the Modern Synthesis looks once we give the Baldwinian triple its due.

## 6.2 A Centennial Celebration

Near the start of "Mental Factors in Evolution," Morgan quoted Darwin counterfactually imagining that our world had been one where "no organic being excepting man had possessed any mental power," or where "his powers had been of a wholly different nature from those of the lower animals." In such a world, Darwin had guessed, "we should never have been able to convince ourselves that our high faculties had been gradually developed" (Darwin, 1871, vol. 1, pp. 34–35; Morgan, 1909, p. 425). In writing as extensively as he had on what Morgan called "mental evolution," Darwin had thus taken full advantage of the opportunities that the actual world presented for pressing home his general case for "organic evolution." What was more, he had brought to the task what Morgan judged to be a winning combination of considerable skill as an observer, a straightforwardly naturalistic view of the mind as a product of nervous physiology, and confidence that the puzzle of the origin of consciousness was no more his worry than the puzzle of the origin of life. "Mental Factors in Evolution" was Morgan's appreciation and updating of his brilliant predecessor's treatments of mind and behaviour in four key works: the *Origin of Species* (1859, though Morgan cited the sixth edition of 1872); the *Expression of the Emotions in Man and Animals* (1872, in the posthumous 1890 second edition); the sexual-selection chapters—really a book within a book—of the *Descent of Man, and Selection in Relation to Sex* (1871, citing the second edition of 1874); and the evolution-of-mind-and-morals chapters of the *Descent*.

For Morgan, the most important updating was to do with the role that Darwin had assigned to Lamarckian inheritance in the shaping of animal instincts and emotional expressions. In the chapter on instinct in the *Origin*, for example, Darwin had represented complex instincts as primarily due to natural selection, yet allowed for Lamarckian supplementation as individual organisms coping with new environments formed new adaptive habits which, over time, became hereditary (Darwin, 1859, p. 209). Morgan's own experimental work in comparative psychology had been devoted to the disentangling of instinctive actions from learned ones (see, e.g., Boakes 1984, pp. 32–44), and he wrote admiringly of Darwin's emphasis on the distinction. But, after the experimental and theoretical assault on Lamarckian inheritance of the German zoologist August Weismann in the late 1880s, the idea of the learned becoming hereditary was no longer widely accepted, and Morgan instead drew attention to a couple of more recent proposals that, in strictly Darwinian fashion, honoured the more general insight about the biological significance of the interaction of learning and inheritance. One was Lankester's notion that, in Morgan's phrase, "'educability,' not less than instinct, is hereditary" (Morgan, 1909, p. 427). The other was organic selection, in which adaptive modifications in behaviour and even structure acquired during an individual's lifetime are not, as they were for Lamarckians, "the parents of inherited variations" in the same direction, but merely their "foster-parents or nurses," on the view that the acquired modifications, in helping to adapt the organism to its environment, contribute to the survival of whatever coinciding variations the organism chanced to be born with (Morgan, 1909, pp. 428–429). As for Darwin's work in the comprehensively Lamarckian *Expression*, Morgan suggested that Darwinian reform lay in taking seriously how emotions and expressions alike can invigorate action in ways that promote survival and so be subject to natural selection (Morgan, 1909, p. 435).

Emotions and their expression are nowhere more extreme than during courtship – for Darwin, the realm of sexual selection, in the forms of male combat and female choice (Darwin, 1871, vol. 1, p. 232). From the start, the prominence that Darwin gave to the latter had been controversial, not least with Wallace. As Wallace saw it, males attempting to outcompete each other, with victory going to the ones that chanced to be born with a competitive edge, and the passing on of their advantageous variations to their offspring as the prize, was just natural selection. But females exercising choice in line with their sense of beauty was something else, with, in Wallace's disapproving words (quoted by Morgan), "none of that character of constancy and of inevitable result that attaches to natural selection, including male rivalry" (Wallace, 1889, p. 283; Morgan, 1909, pp. 436-37). Morgan did his best to suggest that in the details Darwin and Wallace were not really all that far apart, and that in any case their disagreement should not distract attention from the undoubted importance of pairing situations in driving mental evolution. In the male, the stimulus of seeing, smelling, or otherwise sensing a female unleashes instinctive, often highly baroque sequences of emotionally charged display: the legacy of eons of selection among ancestors whose mental and behavioural repertoires were thus advanced beyond the point where natural struggle alone could have taken them. And in the female, what mattered in a complementary way, psychologically and evolutionarily, was the perceptual discrimination as well as emotional energy that she brought to the business of accepting only the "most vigorous, defiant and mettlesome male" as a partner (Morgan, 1909, p. 438).

Even in courtship, however, there is learning from experience as well as instinctive action. For Morgan, the *Descent* overall had laid the foundations for burgeoning psychological studies into the complex interactions between the hereditary and the acquired. From play in animals to progress in human civilization, the teasing apart of the contributions of instinct, emotion, and intelligence, and the understanding of each of these elements as a product of natural selection, was the work of investigators building on Darwin's precedents in comparative psychology, developmental psychology (then called "genetic psychology") and other sciences. There was growing awareness, for example, that with natural selection having long ago ceased to operate among civilized peoples, the instinctive bases of the social behaviour underpinning morality was, in Morgan's words, "somewhat out of date" (Morgan, 1909, p. 445). In closing he returned to educability, as a key notion for evaluating both our current evolutionary position and Darwin's achievement in elucidating it:

> The history of human progress has been mainly the history of man's higher educability, the products of which he has projected on to his environment. This educability remains on the average what it was a dozen generations ago; but the thought-woven tapestry of his surroundings is refashioned and improved by each succeeding generation. Few men have in greater measure enriched the thought-environment with which it is the aim of education to bring educable human beings into vital contact, than has Charles Darwin. His special field of work was the wide province of biology; but he did much to help us to realise that mental factors have

> contributed to organic evolution and that in man, the highest product of Evolution, they have reached a position of unquestioned supremacy (Morgan, 1909, p. 445).

## 6.3 A (Deflationist) Defense of Choice-Making in Females

I want from here to concentrate on the years 1894 to 1906 in order to examine more closely four expressions of the period's thoughtful Darwinism touched upon in Morgan's essay: the defence of female choice; the discovery of organic selection; the Darwinizing of educability; and what, in his discussion of sexual selection, he described as a near future when "Mendelism and mutation […] have been more fully correlated with the basal principles of selection" (Morgan, 1909, p. 437). Although all are relevant to the biological understanding of organismal agency, female choice bears on it so directly that we should pause to note both how much emphasis Darwin gave to female choice in the *Descent* and, in consequence, how much debate that emphasis provoked, within the scientific community and well beyond it. Could the subtle shadings in the patterns on the wing feathers of male Argus pheasants really have come into being incrementally for no other reason than that female Argus pheasants found such ornamentation beautiful and chose their mates accordingly? Darwin revelled in the idea, but his critics balked (Darwin, 1871, vol. 2, pp. 400–401; Cronin, 1991, pp. 165–181; Richards, 2017, pp. 466–516; Milam, 2010, pp. 9–28). As one reviewer of the *Descent* wrote: "We must attribute to the hen Argus Pheasant the aesthetic powers of a Raphael in order to account for the decorations of her mate" (quoted in Richards, 2017, p. 466). By the 1890s, there was even a political edge; in her 1894 book *The Evolution of Woman*, the American suffragist Eliza Burt Gamble argued that the lesson for the human world was surely that women needed to be economically emancipated, for only then would they be free to choose the fittest men and so keep the evolution of the species on track—a message that resonated with other socialist and feminist writers (Erskine, 1995, pp. 112–113; Hamlin, 2014, pp. 128–65).

That year saw the publication of Morgan's *An Introduction to Comparative Psychology*, where he first put in canonical form the deflationist methodological rule that came to be known as "Morgan's canon." In essence, it commands the comparative psychologist not to attribute to animal minds more than is needed psychologically in order to explain observed behaviour. If you see a dog opening a gate, do not assume that the dog understands the principle of the latch and then reasoned its way to the action. Before you are entitled to that reason-attributing interpretation, you need to rule out the possibility that what you saw was the result of something psychologically humbler—that the dog was just imitating another dog, say, or learned to open the gate through a prior history of blind trial-and-error. In an earlier statement of his canon, Morgan had justified it on the view that since language and reason go together, and non-human animals seem to lack language, they probably lack reason too. Strikingly, in his *Introduction*, he offered an entirely different, more elaborate, more Darwinian rationale.[2] Consider, he suggested, three hypothetical relationships between a dog's mind and your mind. It could be that the dog's mind is like your mind except that it is missing one or more higher psychological "levels" that you enjoy, like reason. It could be that the dog's mind has all of the levels your mind has, but to a lesser degree. Or it could be that the dog's mind is fitted to the struggle for existence as the dog's wild ancestors knew it—with the result that the dog's mind could well be very different indeed from your mind. In Morgan's view, the third possibility had to command assent from the evolutionist. But it was also the most demanding to put into practice, since the least anthropomorphic (Morgan, 1894, pp. 53–59).

With the Darwinian credentials of his anti-anthropomorphic "canon of interpretation" in place, Morgan proceeded to recast comparative psychology by its light through the rest of the book, coming at the end to the problem of comparing animal and human minds, not least in their powers of aesthetic judgment. Characteristically, Morgan now introduced a distinction along canonical lines, between holding a standard in the mind, and judging that one thing comes closer to the standard than another, and merely preferring one sense-experience over another. For Morgan, since choosiness among female birds during courtship could be satisfactorily explained as an instance of the latter, it should be:

> Many biologists […] believe that birds select their mates from among numerous suitors because of their song or because of their bright plumage. Suppose a bird has two males before it, both of which are endeavouring by display of plumage, and by love-antics to win her choice. She selects the brighter, and more graceful performer. Does not this, it may be asked, imply that she has a standard of excellence, and selects that mate which she perceives as the nearer of the two to such standard? But admitting, for the purpose in hand, the correctness of the biological interpretation, that there is an exercise of choice on the part of the hen-bird, it does not necessarily follow that […] she compares the two competing males to an ideal standard, or even the one with the other. It is quite enough to suppose that A evokes a stronger emotion and a stronger appetence than B, and that she is therefore drawn to A rather than to B. There is no necessary […] framing of an ideal of excellence. And if the facts, supposing them to be biologically well founded, can be explained on the hypothesis of sense-experience, the greater appetence prevailing, we are bound by our canon of interpretation not to assume the higher faculty [of judgment against a standard]. (Morgan, 1894, p. 366)

When, in his centennial essay, Morgan recommended this psychologically abstemious view of the mind of the choosy female, he suggested that Darwin himself in certain passages of the

[2] For a reconstruction of the events that led to this shift in rationales, see Radick (2000).

*Descent* came close enough to it that it "seems to have Darwin's own sanction" (Morgan, 1894, pp. 438–439).

## 6.4 Learning, Inheritance, Evolution, and the Baldwin Effect

To have agency is to exercise choice, which requires some consciousness of options, some power to select between them, and some ability to learn from experience. In Morgan's next book, *Habit and Instinct* (1896), he continued to emphasize how psychologically modest a thing choosiness could be, but also how dependent it was on inherited capacities, and how fundamental it was to intelligence and all that it made possible. He illustrated with an example from his own experimental studies of newborn chicks. Offered a mix of two sorts of caterpillar to eat, a chick learns the hard way, via instinctive pecking, that one sort is tasty and the other not. When offered the same mix again, it selects only the tasty sort, shrinking away from the nasty sort. Plainly the learning was associative; and though exactly what had happened in the chicks' brain when the associations formed was, Morgan reckoned, a task for future science to elucidate, the broad outlines were clear: the stimulus experienced in the chick's consciousness as unpleasant had resulted, via some sort of cortical disturbance, in the inhibiting of the movements that that would bring about repetition of the stimulus, while the stimulus experienced as pleasant had resulted, by similar means, in the enhancement of the stimulus-repeating movements. No less clear, Morgan stressed, was that the capacity of the chick's brain to form these associations, and ultimately the habits that grew from them, was as much a part of its hereditary, evolutionarily bequeathed endowment as the instinct to peck. It was thanks to that endowment that at the chick's first encounter with the different larvae, indiscriminate pecking was automatic, but at the second encounter, the sight of the nasty sort summoned up a memory of their unpleasant taste and the chick avoided them. In Morgan's view, such choice-making, guided by experience-informed consciousness in a brain hereditarily and so evolutionarily organized to enable the requisite associations, was the basis on which all of mental evolution was founded (Morgan, 1896, pp. 147–152).

This impressive thoughtfulness about thoughtfulness, as arising where adaptive habits meet adaptive instincts and so where learning meets inheritance and evolution, was the backdrop for Morgan's proposal of his version of organic selection. He set it out in the book's penultimate chapter, entitled "Modification and Variation," and using "modification" to refer to a bodily difference acquired in the course of an animal's experience, and "variation" to refer to a bodily difference "of germinal origin" (Morgan, 1896, p. 309). The chapter begins with a review of the Weismannian case for doubt about the Lamarckian inheritance of modifications, and Weismann's own recent attempt, in his Romanes lecture at Oxford in 1894, to suggest how the post-Lamarckian Darwinian, theorizing only with variations, might re-interpret what the Lamarckian holdouts regarded as their best cases. Could the Darwinian convincingly explain how, say, the variations which made deer antlers adaptively heavier happened to coincide with exactly the variations needed in skull, neck, musculature, and so on to support the heavier antlers? In response, Weismann sketched out the possibility that the bodies of individual deer born with slightly heavier antlers grew to accommodate that heaviness, and that this developmental accommodation, recurring in descendant after descendant, sufficed to support the heavier antlers until eventually the supporting anatomy acquired its own variational basis—after which, a deer with even heavier antlers was born, and the whole process repeated, and repeated, with modification assisting variation every step of the way upward (Weismann, 1894; Morgan, 1896, pp. 312–315).

Morgan offered his proposal as an advance on Weismann's, in showing how something like the reverse process could work too, with modification driving the adaptive change, and variation taking the role of assistant. "Modification would lead; variation follow in its wake," as Morgan put it. He supposed that modification-led adaptation would come into its own at times of rapid environmental change, when the need to adapt to new circumstances would come on too fast for new variations to do the adapting work—with the prospect of an even longer delay if, as Morgan suspected, a lineage's long survival under constant conditions actually damped down tendencies to vary. Under the altered circumstances, less plastic races would go extinct, leaving behind the more plastic ones, whose individual members could develop adaptively. Thanks to this developmental plasticity, the race would survive long enough for congenital variations in the same adaptive directions to begin appearing and be selectively preserved. In Morgan's words, "persistent modification through many generations, though not transmitted to the germ, nevertheless affords the opportunity for germinal variation of like nature"—an opportunity for natural selection to build a new instinct, afforded only thanks to innate plasticity which is no less the product of natural selection. The upshot for habit and instinct was that the connection between them could be evolutionarily consequential, but it was "indirect and permissive," not "direct and transmissive" (Morgan, 1896, pp. 315–322, quotations on pp. 319, 322).

The book had started as lectures that Morgan delivered in the United States in the winter of 1895–96. He presented his ideas on modification-leading, variation-following adaptation at a meeting of the New York Academy of Science, only to find that another speaker at the same meeting, James Mark Baldwin, presented what both recognized as the same proposal (Richards, 1987, pp. 398–399). Baldwin, but not Morgan, called it "organic selection" (Baldwin, 1896). A few month later, Henry Fairfield Osborn, independently of the other two, published the same idea again, and again under the name "organic selection" (Osborn, 1896). How to account for the convergence? The short answer is roughly the one that Simpson gave: with Lamarckian inheritance on the backfoot, in an evolutionist scientific community whose members still understood the intellectual appeal of Lamarckian inheritance for certain adaptive characters (indeed, in Osborn's case, were still Lamarckians), there was creative ferment in thinking about how apparently Lamarckian adaptation could be Darwinized, and more generally in thinking afresh about how to put together learning, habit, instinct, development, environment, and natural selection. For the longer answer, we are indebted to the historian of science Robert J. Richards, whose authoritative history of the episode supplies the details that bring out features common to other "in the air" convergences. In the case of Morgan and Baldwin, for example, there seems to have been a shared inheritance at work, in their reading of a posthumous volume from the Lamarckism-accepting comparative psychologist George John Romanes, who, without fanfare, described what in retrospect can be identified as the Baldwin effect (Romanes, 1895; Richards, 1987, p. 402, and more generally pp. 398–404, pp. 480–495).[3]

## 6.5 Natural Selection and the Organ of Educability

If, in *circa* 1900 Baldwinian spirit, we grant that learning in particular, and plasticity in general, are products of natural selection, no less than instincts are, and furthermore that the direction of evolutionary travel for a lineage under severe adaptive pressure will be from habits to instincts, then what about at larger scales? First in 1899 in a French scientific volume, and then again in 1900 in the pages of *Nature*, the distinguished English comparative anatomist Edwin Ray Lankester argued that, over the Darwinian-evolutionary long run, the trajectory went the other way, with instincts tending to give way to habit or, in Lankester's attractive term, "educability" (see Lester, 1995, pp. 172–173). He began by pointing out, that on the whole, the cerebrums of extinct mammals were much smaller than the cerebrums of their living counterparts, even when their bodies were about the same size, or when the extinct mammals were larger. What was more, that generalization seemed to hold more widely—for the reptiles,

[3] Likewise, the Mendelian rediscoverers were all aware of Mendel's paper (Olby, 1990, pp. 528–529), and Wallace and Darwin were both devoted Lyellians (Radick, 2009, p. 154). And just as apparent "sameness" dissolves the closer one looks at the individual writings in the Mendelian and Darwinian convergence cases, so too with the Baldwinian one, with David Depew going so far as to suggest that the term "Baldwin effect" does not pick out a single process (Depew, 2003). The most extensive collection of primary sources relating to the Baldwinian triple is in Baldwin's 1902 *Development and Evolution* (Baldwin, 1902, Appendix A).

for example—and it certainly held for humans and the anthropoid apes compared with fossil pithecoids. Assuming that natural selection lay behind the trend, what, precisely, was adaptive about larger brains? Lankester's answer was that the greater the mass of cerebral tissue, the greater the ability of the individual to respond flexibly to a given environmental situation, instead of having to rely on inflexible, one-size-fits-all instincts. The advanced position of humans could be assessed in terms of our comparative paucity of instincts. Man, according to Lankester,

> has a greater capacity for "learning" and storing his *individual* experience, so as to take the place of the more *general* inherited brain-mechanisms of lower mammals. Obviously such brain mechanisms as the individual thus develops (habits, judgments, &c.) are of greater value in the struggle for existence than are the less specially-fitted instinctive in-born mechanisms of a race, species or genus. The power of being educated—"educability" as we may term it—is what man possesses in excess as compared with the apes. I think we are justified in forming the hypothesis that it is this "educability" which is the correlative of the increased size of the cerebrum. If this hypothesis be correct—then we may conclude in all classes of Verterbrata and even in many Invertebrata—there is and has been a continual tendency to substitute "educability" for mere inherited brain-mechanisms or instincts, and that this requires increased volume of cerebral substance. […] The ancient forms with small brains though excellent "automata" had to give place, by natural selection in the struggle for existence, to the gradually increasing brains with their greater power of mental adaptation in the changing and varied conditions life; until in man a creature has been developed which, though differing but little in bodily structure from the monkey, has an amount of cerebral tissue and a capacity for education which indicates an enormous period of gradual development during which, not the general structure, but the organ of "educability" (Lankester, 1900, p. 625; emphasis in original).

Lankester went on to spell out two consequences of this view. The first was that the concentration of selection on the brain as the organ of educability, especially in humans but in any group where it happened, probably came at the expense of selection on bodily structure, thus putting even more of a survival premium on the ability to adapt to new circumstances by learning. The second was that the old Lamarckian view of instincts as "lapsed intelligence" was even more wrong than hitherto understood; for not only were the results of education un-transmissible biologically, but brain tissue could be devoted to learning only so far as it ceased to be devoted to instinct. Lankester (1900) said: "To the educable animal—the less there is of specialised mechanism transmitted by heredity, the better. The loss of instinct is what permits and necessitates the education of the receptive brain" (p. 625).[4]

[4] A note on Lankester, acquired characters, and Lamarckism. As discussed in the next section, a trademark *kvetch* of W. F. R. Weldon's was that the term "acquired character" was lousy, since every character was to some extent acquired and to some extent germinally based. In a 1912 popular science book, Weldon's second-in-command at Oxford, the Darwinian comparative anatomist E. S. Goodrich, included a passage that sounds just like Weldon on this point (Goodrich, 1913, pp. 32–8, quotation on p. 37). So good is the passage that it appears *verbatim* in an

Baldwin appreciated the resonances with this own views, as he noted in his 1902 book defending and elaborating organic selection, *Develoment and Evolution* (Baldwin, 1902, p. 35). In Morgan's 1909 essay, he heaped praise on Lankester's linking of behavioural plasticity, natural selection, and cerebral anatomy, declaring him to have thus laid "the biological foundations for a further development of genetic psychology" (Morgan, 1909, p. 441). Later in the essay Morgan indicated something of how that development was already underway. What was increasingly becoming clear, he wrote, was that there are two orders of educable intelligence, a lower perceptual order and a higher conceptual order. The former is, in fact, connected with instinct. But the latter, involving not just the greater cerebral mass that occupied Lankester but greater surface area through convolutions, is much as Lankester described. "It is through educability of this order," wrote Morgan, "that the human child is brought intellectually and affectively into touch with the ideal constructions by means of which man has endeavoured, with more or less success, to reach an interpretation of nature, and to guide the course of the further evolution of his race—ideal constructions which form part of man's environment" (Morgan, 1909, p. 443).[5]

## 6.6 Natural Selection and the Dependence of Development on Environments

Elementary Mendelism invites no curiosity about how the hereditary and the environmental interact, let alone about how that interaction might develop as an organism develops. In a basic Mendelian cross, the environment is background, either fully under control (in which case you get those lovely patterns) or not fully under control (in which case— grrr—you need to fix it, in both senses, in order to get those lovely patterns), while development is a time-consuming, potentially pattern-wrecking impediment between you and the all-or-nothing unit characters you want to count. If, in asking what was up in biology *circa* 1900, we have only the Mendelian triple to think with, then it is hard not to suppose that the convergence of De Vries, Correns,

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obituary notice of Goodrich by an English Darwinian comparative anatomist of the next generation, Gavin de Beer. However, De Beer celebrated the passage as a brilliant development of insights that Goodrich had picked up not from Weldon but from an earlier mentor, Lankester (De Beer, 1947, p. 484). Why did De Beer think that? My guess is that, reading Goodrich's obituary notice for Lankester, De Beer misinterpreted Goodrich's praise for 1894 *Nature* letters from Lankester on Lamarckism and acquired characters (Goodrich, 1931, p. 379) in the light of the Weldonian passage in Goodrich's book. Be that as it may, anyone who goes back to Lankester's *Nature* letters will find that he came nowhere near to finding fault with the distinction between inherited and acquired characters (Lankester, 1894a & 1894b, affirming the argument of Lankester, 1890, affirmed again in Lankester, 1906, pp. 29–30). Alas De Beer went on to compound his misattribution in the august *Dictionary of Scientific Biography*, where he credited the view that every character is both inherited and acquired, and so the distinction between them meaningless, to Lankester himself (De Beer, 1973, p. 27).

[5] "Educability" went on to surface here and there in the twentieth century (Poulton, 1937, p. 402; Dobzhansky & Montagu, 1947).

and Tschermak reflects a very general orientation, and to see Mendelism itself as an inevitability, so perfect was its apparent fit with its times. To be sure, there *were* workers—notably William Bateson, the English zoologist and lead Mendelian—who came through the debates over Lamarckism convinced that the whole question of gradual adaptation to environments, whether Lamarckian or Darwinian, should be shunned in favour of a concentration on the shuffling of unit characters and the shifting of forms between internally stable states. But other workers came through those debates more engaged than ever by the question, and more adventuresome in the Darwinian thinking they brought to answering it, as the Baldwinian triple reminds us. Among their number was Bateson's most formidable opponent in the controversy over Mendelism, W. F. R. Weldon.

In the spring of 1902, shortly after publishing his controversy-sparking critique of Mendel's original paper on crossbred peas, Weldon published a second critique in the same journal (*Biometrika*, founded not long before by Weldon with his mathematical-biological allies Francis Galton and Karl Pearson) of a new book by De Vries on his anti-selectionist "mutation theory." As Baldwin wrote later that year in *Development and Evolution*, De Vries' theory, "which holds that species originate in abrupt or 'sport' variation, called 'mutation,' strikes at the very foundations of the Darwinian conception." Baldwin commended Weldon's "able, negative criticism" (Baldwin, 1902, p. 33), as well as an embryological experiment that Weldon reported in the article. He had made a hole in a hen's egg and then artificially replaced the water that ordinarily evaporates from the egg as the chick develops. The effect, he discovered, was to disrupt or even suppress entirely the normal development of the fluid-filled sac (amnion) around the embryo (Weldon, 1902, pp. 367–368). For Baldwin, what the experiment illustrated was how an eggshell normally functions to protect an environment-within-an-environment, so that an embryonic chick's immediate surroundings approximate to the environment which its free-living ancestors (which the embryo resembles) were adapted to thrive in (Baldwin, 1902, p. 193). For Weldon, the point was a complementary but rather different one. In Weldon's view, the tests that De Vries had conducted and then declared selection to have failed were bad tests, because De Vries had not considered the possibility that when he imposed new conditions on some wheat plants, the changes that ensued were not due to the selective elimination of the less fit individuals, as he had assumed, but instead were due to altered development in the new conditions. So when De Vries re-imposed the old conditions, and the plants took on the old characters, although he took himself to have shown that selection was not capable of producing permanent change, it was entirely possible that the plants had never undergone selection in the first place.

For Weldon, the chick experiment dramatized how easy it can be to underestimate the extent to which normal development depends on normal conditions, and more generally to underestimate—as De Vries had done—the sensitivity of development to environmental changes. The visible form of an organism always had to be understood as the result of the hereditary and the environmental. As Weldon put it:

> Now it cannot be too strongly insisted upon that every character of an animal or of a plant, as we see it, depends upon two sets of conditions; one a set of structural or other conditions inherited by the organism from its ancestors, the other a set of environmental conditions. There is probably no race of plants or of animals which cannot be directly modified, during the life of a single generation, by a suitable change in some group of environmental conditions. (Weldon, 1902, p. 367)

In support he cited the work of French and German experimental embryologists whose recent research had gone a long way towards showing "that some of the most normal and universal phenomena of animal development are each directly dependent for their occurrence upon a certain group of external conditions" (Weldon, 1902, p. 367). But the conviction that, thanks to natural selection, developing forms were adapted to particular environments, and could change as those environments changed, was an old and deep one for Weldon, going back to his student days. In the 1890s research for which he was best known, demonstrating natural selection at work in modifying the shore crabs of Plymouth, he had actually done the (hard) work that he was now scolding De Vries for not having done—monitoring the growth of huge numbers of crabs in bottles to be sure that the statistical changes he was detecting in wild crabs were due to selective elimination and not developmental convergence. And when, in late summer 1902, he lectured a popular audience on "Inheritance" at the British Association for the Advancement of Science meeting in Belfast, he told them early on about the chick experiment and also experiments done by his student Ernest Warren on the waterflea *Daphnia*, whose spines got shorter and shorter as their water got more polluted, but whose offspring if born in pure water would grow a full-length spine. "Now clearly the condition of the spine […] is not exclusively acquired; and it is not exclusively inherited. It belongs to both categories" (Radick, 2023, p. 74, pp. 117–120, pp. 312–313, p. 484n32).

That idea that characters are not either acquired or hereditary, but always and complexly the product of interaction between both categories of cause, was something of a motto for Weldon (who blamed Weismann for spreading the misleading idea to the contrary). A version of it appeared in the manuscript “Theory of Inheritance” that he was working on at his death in 1906, and most actively in 1904–5. There Weldon attempted to set out his alternative to Mendelism—an alternative centred on a conception of character expression not as all-or-nothing, and dependent only on the presence or not of a dominant factor or of two recessive factors, but as variable depending on contexts, from the chromosomal-ancestral to the physico-chemical (Radick, 2023, p. 232, pp. 245–54, p. 466n39).

## 6.7 Concluding Remarks

With our field of vision of biology *circa* 1900 now expanded beyond the Mendelian triple to include the Baldwinian triple, flanked by the post-Lamarckian debate over mental evolution, the post-Morgan’s-canon debate over female choice, Lankester’s Darwinian case for educability, and Weldon’s Darwinian dissolution of the “acquired character,” we depart 1900 with a much richer sense of the options available then for being thoughtfully Darwinian, not least about thoughtfulness, including the riddle of organismal agency. In closing, let’s now look forward from 1900 and, returning to Simpson’s 1953 essay, notice two ways in which awareness of the potentialities for thoughtful Darwinism also alters our perception of what followed.

The first is to do with that “radically different turn to biological thought” as twentieth-century biology Mendelized. By 1909, as we have seen, Morgan sensed not only the turn but the new job of theoretical work it had generated for biologists as committed to the reality of selection as they were to the reality of the Mendelian gene (so named in that year). The evolutionary biology duly forged in the decades that followed recast selection as principally a matter of changing genotype frequencies, and organisms as principally bundles of gene variants. Ever since, biologists and others wanting to give organisms in their developmental, environmentally situated, choice-making complexity their evolutionary due have been critics, protesting against an orthodoxy that finds it easy to brush them aside (Radick, 2017, p. 56). They should take courage from knowing that the persistent marginalizing of their concerns is an accident of history. Had Weldon lived to complete and publish his synthesis of selection theory with chromosomal physiology, experimental embryology, Galtonian biometry, and data from Mendel-style crossing (illuminating as long one remembered its limitations), the thoughtful Darwinism of Weldon’s era – Baldwin effect included – would have framed the advances that came after (see Radick, 2023, esp. pp. 317, 365, 399–400).

My second observation is a counterpart to one I have made elsewhere in relation to the Baldwin effect's belonging to the Modern Synthesis. Recalling the prominence that Julian Huxley gave to that agency-friendly process can help us keep our discussions of organismal agency from lapsing into caricature when discussing the Modern Synthesis (Huxley, 1942; Radick, 2017, p. 56). Likewise, for all that Simpson's essay has a deserved reputation for being downbeat about the importance of the effect he named, his closing section offers a tour-de-force re-interpretation of the genetics of Synthetic Darwinism in terms of reaction norms, by way of highlighting the good that the effect could do in directing research attention that way. "Genetical systems," he begins, "do not directly and rigidly determine the characteristics of organisms but set up reaction ranges within which those characteristics develop" (Simpson, 1953, p. 111). By the lights of *circa* 1900 biology, it is much more Weldonian than Batesonian. And by the lights of 2020s history and philosophy of biology, it is closer to the genetic-determinism-rejecting Extended Evolutionary Synthesis than to conventional ideas of what the Modern Synthesis stood for. Thoughtful Darwinism, it turns out, has unrealized potentialities all over the timeline.

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