
WEISMANN'S THREE CRITIQUES TO THE INHERITANCE OF THE ACQUIRED CHARACTERS

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ABSTRACT. This paper is a critical discussion of the mode of Weismann's reasoning in his critique of soft inheritance. The paper shows that far from presenting a parsimonious and straightforward line of reasoning in arguing against the inheritance of acquired characters and in favor of the almightiness of Natural Selection, Weismann's argument in such connection is threefold as it includes both an empirical case against the IAC and a conceptual attack to that sort of heredity. It is further argued that even at the conceptual level alone two distinct lines of arguing against the viability of the IAC as an evolutionary factor can be distinguished. I will sustain that all in all, none of the arguments proposed by Weismann is conclusive in showing that the IAC is principally impossible, but also that Weismann rightly noticed this when assessing the effectiveness of his critiques. The paper advances a further point: even if the Evolutionary Synthesis seems to be currently expanding in ways not entirely contemplated by Weismann and the Neo-Darwinists, these directions do not convey a vindication of the *Lamarckian theory of inheritance* and thus don't fly in the face of Weismann's empirical argument. Even if they did, that wouldn't prove Weismann wrong conceptually.

KEY WORDS. Weismann, Darwin, Natural Selection, Inheritance of acquire characters, Evolutionary Synthesis, theories of inheritance, Lamarckism, Neo-Lamarckism, Ockham's razor, scientific evidence.

1. INTRODUCTION

It is sometimes helpful to start off by saying the obvious. In this paper I will take the *inheritance of acquired characters* (IAC) to represent the idea that phenotypic traits acquired during the life span of organisms are then transmitted on to the next generations of individuals, thus causally shaping the direction of evolution. Understood in this way, the IAC has been historically conceived of as an important causal factor in such accounts of evolution as those presented by people ranging from Jean-Baptiste La-

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marck to Erasmus Darwin. The notion has also resonated in the work of figures like Robert Chambers, Herbert Spencer, Ernst Haeckel or William McDougall to mention but a few. It is perhaps more note-worthy to add Charles Darwin to this list. Indeed, both with regards to the theory of the inheritance adopted in *The Variation of Animals and Plants under Domestication* (1868) and in his influential account of the transformation of habits into instincts in *The Expression of Emotions in Man and Animals* (1872), Darwin presents slightly different versions of the same basic framework that Lamarck had aptly phrased at the beginning of the nineteenth century.

The standard narrative in the realm of the history of biology (Mayr 1982) has it that August Weismann's research work proved instrumental in the later dismissal of such an evolutionary mechanism. This understanding, which shall not be challenged here (but see Churchill, 2015 for a more nuanced historical approach), goes on to sustain that Weismann's importance within the history of evolutionary theory consists of the fact that he demonstrated that the IAC does not hold experimentally and proposed the doctrine of the separation between the *soma and the germ-line* instead. In turn, this paved the way for the principle of Natural Selection (NS) to become the all-important causal factor in our current understanding of evolution. Under the form of the central dogma of molecular biology, *Weismann barrier* has worked as if were as an important assumption in the constitution of the Modern Synthesis. It is one that in closing the door to any additional causal principle affecting the course of evolutionary changes of populations other than NS itself (with the remarkable, albeit much debated case of drift) throws the IAC to *the trashcan of history (of science)*. In this respect, it would be entirely safe to declare that the main contribution of Weismann to the development of biological theory is a negative one; for it consists of the purification of the framework we use to think of evolution as a process. Clearly enough, the insistence on that negative character does not downplay its pertinence in the slightest, so long as the history of science ought to be grateful not just for the discovery of how Mother Nature plays her tricks but also (arguably even more so) for the exclusion of the ways she doesn't.

So far so good. As stated, this is a clearly defined story, which its basics tenets will not go questioned here. There is however a caveat to keep in mind: in thinking about the IAC hypothesis, August Weismann did not merely attack the viability of the mechanism empirically; he also went on to criticize it conceptually. As the paper will show, even granting that both attacks do in fact converge, these are two different angles to tackle the issue from, which in turn, need to be kept separate with scrupulosity. Avoiding confusion will be the entire name of the game in this connection.

Also, perhaps to make things a little bit more complicated than the standard narrative suggests, there's considerable debate (Müller and Pigliucci,

2010) in current evolutionary theory about the need for the Modern Synthesis to be *expanded* in directions, which, some (Avital and Jablonka, 2000, Gissis, and Jablonka, 2011, Szyf, 2014, Noble, 2015)would say, represent a vindication of the very idea of Lamarckism. It must be consider that the discussion partly pertains to the ways in which the Weismann barrier is to be rethought in the light of recent developments in the areas of evo-devo, phenotypic plasticity, niche-construction or epigenetics, to name but a few milieus.

This paper primarily focuses on the conceptual side to Weismann's reasoning on the IAC. I consider his argument with the aim of showing that far from being so simple and straightforward as it is sometimes pictured, its structure encompasses two lines of thought, each presenting different assumptions and implications. I will finally argue that contrary to what is suggested at times, the new developments in evolutionary biology, much as they center on the admittedly very *Lamarckian leit motiv* of the effects of behavior on evolution (Ongay, 2012) do not contradict Weismann's debunking of the pitfalls of Lamarckism when his argument is understood properly.

2. THE EMPIRICAL CASE AGAINST THE IAC

It is well known that in advancing the notion of NS as a causal factor shaping the transformation of organisms, Darwin adopted a somewhat pluralistic standpoint. One that is best captured in the famous line of the *On the Origins*, where he recognizes to be "convinced that Natural Selection has been the main but not the exclusive mean of modification" (1859, p. 69). One clear way to understand this statement would be to assume that it makes reference to the IAC mechanism playing a causal role in evolution. In fact, Darwin did not just allow for the IAC to take place; *he also used it as an explanatory factor* in his theory of pangenesis (Darwin, 1868).

Weismann, on the other hand, didn't agree with Darwin on this matter. The very title of his 1893 work, *Die Allmacht der Naturzüchtung* (1893) is indicative about a conception of evolution in which the principle of NS gets understood as an exclusive causal agency. Even if this conception is not the one that Darwin originally envisioned, it is important to notice that the architects of the Modern Synthesis would embrace it fully, thus deploying a view of evolution which has been often (and rather critically) conceived as *panselectionist* (Gould and Lewontin, 1979).

What has happened in between, or so the story goes, is that Weismann has made clear that the IAC hypothesis is not factually viable a mechanism accounting for the transformation of populations. There is an empirical as well as a conceptual side to his critique to the inheritance of acquired traits. One of the pieces where the empirical case is made more cogently

is *The Supposed Transmission of Mutilations* (1888). In this notable work, August Weismann demonstrates experimentally that mutilations inflicted on the phenotype of individuals seem not to be transmitted to the morphology of the offspring of those organisms. It needs to be emphasized that the results also suggest that mutilations don't recur in various generations to come. Weismann (1888) affirms that these results led him to the conviction that, despite what Darwin may have thought, the acquired traits are not transmitted from generation to generation: "I for one frankly admit that I was in this respect under the influence of Darwin for a long time, and that only by approaching the subject from an entirely different direction was I led to doubt the transmission of acquired characters. I gradually gained a more decided conviction that such transmission has no existence in fact" (p. 422).

Philosophers often recall an epistemological point originally made by Pierre Duhem (1906) and given currency to by W.V.O. Quine (1953). Contrary to what some over-simplistic versions of falsifiability seem to suggest at times (but see Popper, 1959 for a contrast) no experimental results taken in isolation may ever suffice to falsify a hypothesis. The reason to this is that scientific hypothesis are standardly tested in an holistic fashion in relation to a set of auxiliary assumptions without the presence of which, the hypothesis in question would not produce empirical predictions. When an experiment *in crucis* brings about evidence against the bundle of hypotheses put to test, there is no principled way to ascertain which part of the network has gone astray. Interestingly enough, Weismann is not epistemologically naïve in this regard, as he acknowledges explicitly that his results alone don't suffice to conclude that the transmission of mutilation is impossible in principle. It is easy to see why such a prudent attitude towards what the experiments help sustain is wise: *perhaps more generations are needed for the mutilations to recur again*. Here's how Weismann formulates this roughly *quinean point*: "(...) no conclusive theoretical objections can be brought forward against the supposition that the hereditary transmission of mutilations requires (e.g) 1,000 generations before it can become possible" (1888, p. 433).

Of course, this is not to say that the IAC is a scientifically respectable hypothesis to be given equal treatment with NS. What Weismann means to maintain here is something different: perhaps one could never rule out conclusively that the inheritance of acquired traits is *possible*, but then again there are a lot of otherwise very silly ideas that we couldn't ever dismiss in the same demandingly conclusive manner. No reason to panic over here. The strict application of the Duhem-Quine thesis notwithstanding, it is common practice for scientists to dispense with certain factors so long as the best evidence at hand strongly suggests that they just don't hold in fact.

3. THE CASE AGAINST THE IAC: WHAT'S TO BE SAID CONCEPTUALLY?

There is however a conceptual ramification to tackle also. It is an avenue Weismann explores in *On Heredity*. This is what he has to say in this piece:

It is perfectly right to defer an explanation, and to hesitate before we declare a supposed phenomenon to be impossible because we are unable to refer it to any of the known forces. No one can believe that we are acquainted with all the forces of nature. But on the other hand, we must use the greatest caution in dealing with unknown forces, and clear and indubitable facts must be brought forward to prove that the supposed phenomena have a real existence, and that their acceptance is unavoidable.

It has never been proved that acquired characters are transmitted, and it has never been demonstrated that without the aid of such transmission, the evolution of the organic world becomes unintelligible (1883, p. 80-81).

I hope that the reader agrees that there's a slightly different approach in this paragraph. It is one that in certain ways parallels William's discussion of the notion of group selection in the chapter 8 of his book *Adaptation and Natural Selection* (1966). Much like in William's case—who incidentally also invokes the principle of parsimony (p. 245)—the argument now starts off by asserting that in the absence of evidence for the IAC and *provided, too, that the hypothesis is not otherwise needed to account for the data*, we can safely dispense with it. Weismann then goes on to argue that inasmuch as NS alone does well enough in bringing about the *explananda*, the conclusion follows that the IAC is dispensable.

It is easy to see that this argument takes support from the empirical discussion of the IAC in that it assumes that there's no evidence for such a hypothesis. In that sense, the argument is *evidentialist* in character in that it concerns what scientists are justified in believing *based on the evidence at hand*. However, that is not all. Weismann is also appealing to the principle of parsimony to argue that no unknown force should ever be postulated to explain a certain set of phenomena whenever the known ones do suffice to account for those phenomena. Finally, the present line of reasoning is a *contrastive one* so long as it pertains to the assessment of the relative merits or demerits of two different accounts of evolution.

Interestingly, Weismann uses a similar way of proceeding on other occasions. For instance, in his *Phyletic Parallelism in Metamorphic Species*, an analogous point is brought about to discuss the pertinence of invoking an *élan vital* as an evolutionary factor:

To me a vital force appears inadmissible, not only because we cannot understand the phenomena by its aid, but above all because it is superfluous for their explanation. In accordance with general principles the assumption of an un-

known force can, however, only be made when it is indispensable to the comprehension of the phenomena (1882, p. 464).

One may be tempted to think that this conceptual attack succeeds precisely where the experimental approach failed; namely, in dismissing the IAC once and for all. Unfortunately, it doesn't. Part of the trouble here has to do with the fact that it is not so easy to justify why the principle of simplicity provides with good epistemic advice even when one accepts the general (but somehow vague) idea that more parsimonious theories ought to be given preference in scientific evaluation. There's a second *crux of the matter*. One that generally applies to *Evidentialism* as an apparently sound philosophical position to keep in mind when deciding what beliefs are to be held. The flaw of any evidentialist conception is appropriately captured by the old motto "*absence of evidence is not evidence of absence*" which alarms us to the obvious epistemic caveat that there might be more things in heaven and earth than are dreamt of in *Evidentialism*. In a pluralistic vein which shows very effectively what is wrong in the usual form of scientific conservatism, Kyle Stanford (2006) has argued that no matter how evidentially powerful our pet theories may appear to be, possible unconceived alternatives are always out there waiting for their chance to pop up historically. I think that Stanford's point should be taken seriously in this context, also. If the Ockham's Razor is to be employed here, it shouldn't be missed that there are two different razors as distinguished by Elliott Sober (2015). While one version of the razor advises *silence and Agnosticism about what there's no evidence for*, the other recommends *denial and Atheism* instead. Let there be no mistake, it is the razor of *silence* and not the stronger razor of *denial* that Weismann utilizes within the present context when he writes:

If we are able to prove that we may dispense with the assumption of the transmission of the acquired characters in explaining such phenomena, of course it by no means follows that we must dispense with it or, in other words, it does not follow that the transmission of acquired characters cannot take place (1888, pp. 422-424).

4. IS THERE A STRONGER ARGUMENT AGAINST THE IAC?

In light of this *agnostic* use of the razor of *silence* by August Weismann, one may wonder still if there's a way to strengthen this attack so to preclude the possibility of the IAC altogether. Indeed, one argument of this sort is to be also found in Weismann's work. In *On Heredity* he affirms: "The hereditary transmission of acquired characteristics remains an unintelligible hypothesis, which is only deduced from the facts, which it attempts to explain" (1883, pp. 82-83).

Of course, given its succinctness, it is rather difficult to determine what type of an argument does this rather sketchy statement convey. Yet, one obvious way to interpret it would be to declare the IAC hypothesis empirically empty (*not merely false*) due to its logical circularity. If that were so, the hypothesis in question wouldn't count as false or for that matter true inasmuch as in the absence of any factual content at all would be devoid of truth-value. Notice that in the same way as the previous argument resembles Williams's discussion of the hypothesis of group selection in *Adaptation and Natural Selection*, the point I am considering now parallels Popper's view of NS as a tautological principle (Popper, 1972). Popper doesn't want to say that the principle of NS is wrong, what he means is something more radical instead: the very idea of NS far from representing the *vera causa* that Darwin had thought, rests on a circular and thus untestable way of reasoning, making evolutionary biology a metaphysical research program.

Needless to say that this all, if true, represents very good news for Weismann. In effect, if the IAC is rendered intelligible that would count as a very good reason for the hypothesis to be discarded scientifically. There's yet something else to consider here. Unfortunately, it is easy to see that one part of the conceptual case is incompatible with the other. While both would constitute, if sound, sensible reasons against the IAC, it is equally clear that both cannot work at the same time as it is one thing to reject the idea on evidentialist grounds and quite another to view it as an empty notion devoid of any empirical content to be tested against the *evidence*. This later approach is in effect much stronger than the earlier, but make no mistake: that is not necessarily a good thing because it might as well be *a bit too strong* if the argument turns out to *prove too much*. I hope that the reader agrees that if the IAC is *empty*, then the conclusion seems hard to escape that Weismann himself was talking about nothing when demonstrating experimentally that it doesn't hold.

Notice in passing that all in all Weismann's *long argument* on the unviability of the IAC and in defense of NS has a threefold structure. It is at some level certainly odd to see this *luxurious* complexity in display, especially for an argument at least partly based on the principle of parsimony.

5. AN EPILOGUE ON THE EXTENDED EVOLUTIONARY SYNTHESIS

Anyhow, a more positive note to finish with. Evolutionary biology is a rapidly changing area of endeavor which might currently be undergoing a particularly exciting process of expansion. However, the new developments in evo-devo and epigenetics research, cutting-edge as they undoubtedly are scientifically, contain no real vindication of Lamarckianism in the modern (*ironically: post-Lamarckian*) sense of the term as they don't

entail the genetic transmission of acquired traits by the use and disuse of organs. I grant that *Lamarckianism* is a rather vague concept as a plurality of theories can be taken as falling into that label (and not all of them would coincide with anything that Lamarck may have ever thought of). While his name has got uniquely associated with the IAC, it needs to be emphasized that Lamarck was not the first figure in advancing the notion of the soft inheritance as being an important factor in guiding the course of the evolutionary process, nor the IAC had a uniquely central role to play within his framework. Yet, I do sustain that if by Lamarckianism we isolate the notion that traits acquired during the life-span of organisms by the use of certain body-organs (the infamous *giraffe neck*) are then directly transmitted on to the next generations genetically, then this is not what the advocates of the Extended Evolutionary Synthesis want to affirm in construing models of epigenetic transgenerational heredity.

Nonetheless, even if the *Extended Synthesis* did vindicate that model of genetic inheritance, such an empirical fact would be entirely compatible with Weismann's evidentialist point so long as its use of the principle of parsimony restricts itself to the more modest *razor of silence* shying away from invoking the *razor of denial*.

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