7 The Notions of Plasticity and Heredity among French Neo-Lamarckians (1880–1940): From Complementarity to Incompatibility

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Although it was Lamarck's homeland, France was one of the last Western countries to accept the hypothesis of a progressive transformation of living things. Indeed, it was necessary to wait until the 1880s to see transformism finally emerging as the general framework for interpreting biology. It is well known that the type of evolutionism which was developing at that time was sharply non-neo-Darwinian, and that this inclination was going to remain a peculiarity of French biological thought (Bowler 1992). Yet, however powerful it was, this neo-Lamarckian tradition was never embodied in a synthetic work that would had been a doctrinal reference. If Lamarck had his *Philosophie zoologique* (1809) and Darwin his *Origin of Species* (1859), French neo-Lamarckism was a transformism that was scattered in the contents of the publications of its main representatives. Thus the historian of science faces a curious object which, although it is powerfully rooted in a given space-time, is at the same time scattered, and not structured by a precise text or by a specific scientist. For those who wish to understand the history of this transformism, the only possibility is to try to reconstruct the work of the various evolutionists. Clarifying the internal logic of this French evolutionism becomes necessary for understanding its history. It seems to me that this logic rested almost exclusively on two notions: that of plasticity and that of heredity. The history of this transformism can therefore be understood as the ceaseless dialogue between these two notions, in a complex relationship of complementarity/incompatibility.

In this chapter, I argue that French neo-Lamarckism was initially structured by the notion of plasticity. Implicitly or explicitly, this notion was used to make the results of experimental transformism (1880–1910) understandable. Since phyletic evolution was seen as the large-scale consequence of individual changes, French neo-Lamarckian biologists had to accept soft inheritance. This kind of conception, however, caused many theoretical problems. In the third part of this chapter I focus on the problem of the articulation of these two notions, plasticity and heredity, in order to understand the explanatory impotence of this transformism during the 1920s and the 1930s.

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The Notion of Plasticity: Explaining Variation

As Burian, Gayon, and Zallen (1988) noted, “the country of Lamarck was also the country of Claude Bernard and Louis Pasteur,” a statement that highlights the fact that biological work in France was greatly influenced by experimental physiology and microbiology. This orientation was very strong during the period 1860–1910, the time of the reception of Darwin’s theory. That is why the French community was disappointed by Darwin’s book: it did not present a single (experimental) *fact* of species transformation. In order to convince French biologists, the first partisans of the transformist hypothesis had to show that it was indeed a scientific theory—that it was susceptible to experimental tests. Hence, from the beginning of the 1880s, French biologists started to envisage a project of experimental, physiologically oriented transformism.

This project developed at the same time in several branches of biology. In microbiology, many experiments performed by Pasteur and his colleagues showed that some bacteria could be transformed by varying culture conditions. These experiments, at least at the beginning, were not performed to address evolutionary issues, but to deal with practical problems (to protect livestock from the very dangerous bacterium *Bacillus anthracis*). Nevertheless, the results obtained during the 1880s seemed to show that an individual organism—a bacterium—was able to react to the environment and to adjust to it. These results were interpreted in terms of individual plasticity (see, for example, Duclaux 1898).

In teratology (the study of developmental abnormalities), Étienne Rabaud (1868–1956), who was a student of Camille Dareste (1822–1899), tried to advance the experimental research program of his master. He wanted to show that embryological development was controlled by the environment, and that phyletic evolution followed exactly the same rules as individual embryonic development (Rabaud 1914). That is why, at the end of the nineteenth century, he carried out many experiments with bird embryos. According to Rabaud, it was necessary to accept that embryonic development was not driven from the inside by heredity, but mainly from the outside by environmental changes. Thus, the organism had to be plastic.

In zoology, Frédéric Houssay (1860–1920) wanted to explain, using mechanical considerations, the present-day morphology of organisms. In particular, he was very interested in the hydrodynamic shape of fish. His idea was that the shape of most extant species of fish was the result of long-term effects of water pressure on a plastic body. Because of these stresses, ancestral organisms had been slowly transformed into present-day fish (Houssay 1912).

However, the most spectacular and clear results were obtained in botany. This research program was developed under the supervision of Gaston Bonnier (1853–1922), professor at the Sorbonne, and Julien Costantin (1857–1936), professor at the

National Museum of Natural History of Paris. They performed numerous experiments in order to establish that the morphology, anatomy, and physiology of plants were dominated by abiotic parameters such as luminosity, temperature, and humidity. Bonnier, for example, started a huge program of experimentation at the beginning of the 1880s. Cuttings of the same seedling were planted at stations in the Alps (at altitudes of 1060 to 2030 meters) and in his laboratory near Paris (Bonnier 1895). Many characteristics of the plants were rapidly affected by the new environment: their size, color, general shape, for example, were changed. The results showed clearly that by changing growing conditions, it was possible to directly (i.e., without the need for natural selection) transform living plants. As far as Costantin was concerned, the laboratory work he carried out at the same time was supposed to clarify Bonnier's results. He realized that it was possible to transform one organ into another by imposing drastic changes in growing conditions. Indeed, by cultivating a stem under a mass of thick soil, one could observe transformations which slowly made the stem look like a root (Costantin 1883). He also obtained interesting results by pushing land plants into the water during their growth, which led to the disappearance of stomata (Costantin 1886).

Whatever the trait, at every possible level and on every scale, it seemed that living organisms were capable of conforming to the requirements of their environment. All these results strengthened the idea of the transformability of life, and were widely discussed in France at the end of the nineteenth century. The data were rationalized by the notion of plasticity, that is, by the capacity of the living organism to conform to the physicochemical characteristics of its environment. This notion had physiological roots, and was used to reinforce the idea that, just as Claude Bernard had emphasized, the organism was a self-adjusting system. Individual plasticity was therefore necessary in order to maintain the integrity of the "milieu intérieur," the internal environment, a key concept in Bernard's view of homeostasis.

The mechanism of adjustment was never clearly articulated by these scientists. In general, they believed that the intimate relationship of an organism with its environment (biotic and abiotic) was a sufficient cause to explain the transformation. The physiological working of the body was the way through which the environment affected morphology.

In this theoretical framework, the adaptations of living things were explained as individual physiological acclimations. This means that phyletic evolution was totally reduced to individual changes, and thus the organism was the only relevant level for studying the operations of evolutionary mechanisms. Alfred Giard (1846–1908), holder of the first chair of "évolution des êtres organisés" at the Sorbonne, emphasized this point many times (see, for example, Giard 1904). But to have any evolutionary significance, these individual transformations had to be at least partially hereditary. That is why all of these scientists assumed that the inheritance of acquired characters was a fact.

The Notion of Heredity: Explaining Continuity

Natural selection was not well understood in France at the end of the nineteenth century (Conry 1974). Most biologists accepted it, but always by reducing its evolutionary role to almost nothing. Natural selection was seen as being responsible for destroying the unfit, but certainly was not responsible for the creation of the fittest. Because of this common, negative interpretation of natural selection, adaptation was explained using physiological arguments. It was necessary to accept soft inheritance, because otherwise phyletic adaptation could not be explained. Such acceptance was natural for these biologists, because the phenomenon of reproduction was identified with simple budding. There was strict protoplasmic continuity between organisms from generation to generation, and thus an inevitable morphological re-formation. Reproduction was indeed a *re-production*, because of the continuity of the protoplasmic material (Perrier 1881).

This view was reinforced by merotomy experiments: when a unicellular organism was cut into pieces, those pieces that contained the nucleus were able to develop and re-form the initial organism with its specific shape. It seemed that the chemical composition of protoplasm was the only factor that was necessary to bring about morphological features. There was no need to imagine hypothetical particles like pangenes or gemmules. Félix Le Dantec (1869–1917), a famous disciple of Giard, played a central role in constructing a developmental notion of heredity in France. After 1895, when he stopped working as an experimental biologist, he constructed a theoretical system to explain life as a mechanical process, and the evolution of such a system as a neo-Lamarckian phenomenon. In one of his major books, published in 1907, he argued that there is a necessary link between protoplasmic chemistry and morphology, suggesting it as a new theorem of general biology (Le Dantec 1907).

When considering unicellular organisms such as bacteria, this notion of heredity as phenotypic continuity was quite convincing, but major problems arose when this notion was applied to multicellular organisms. These problems were clearly recognized by August Weismann (1834–1914), and led him to reject the inheritance of acquired characters (1883, translated into French 1892; see Weismann 1892). According to Weismann, it was impossible to think of a mechanism through which modifications of the soma could be incorporated into the germ line. This was one of the *theoretical reasons* that led Weismann to develop his germplasm theory during the 1880s and the 1890s. However, French biologists did not pay much attention to

Weismann's conception. For a long time his critique was considered irrelevant, because his explanatory system seemed to be an excessively metaphysical, speculative construction. The theory of the germplasm was indeed very different from the positivist expectations of the French scientists of the second half of the nineteenth century (Canguilhem, 2002).

Because of their belief in a universal and complete determinism (France was the country of Pierre-Simon Laplace, and his influence was evident then and even more so later in the century), and because of their conception of the organism as an indivisible totality, French biologists were convinced that, in one way or another, environmentally induced phenotypic modifications could reach the germ cells and become inherited. The Bernardian concept of "milieu intérieur" seemed to be a sufficient foundation for this notion of heredity. The precise mechanisms, once again, were never a matter of interest for these biologists.

Moreover, evolutionary mechanics was identified as a simple process which could be understood and articulated by using two seemingly simple concepts: plasticity and heredity. At least until the first years of the twentieth century, an evolutionary explanation based on these concepts seemed to be sound because, unlike the notion of natural selection, it did not appear to raise major theoretical problems. At the same time, it seemed that, unlike the germplasm theory, it was easy to experimentally test the proposed evolutionary mechanisms.

The Impossible Link between the Notions of Plasticity and Heredity

A conception of the evolutionary process based on the notion of heritable, plastic responses has to deal with at least three theoretical problems. The first is the well-known problem of adaptability. How can one explain that individuals have the ability to respond adaptively to environmental changes? Adaptability has to be explained, and cannot be taken for granted: a complete theory of evolution has to make the origins and evolution of adaptability understandable. This point was clearly stated by Weismann (1892:350). The answers of the French neo-Lamarckians were quite complicated, and differed depending on the scientist one focuses on (for detailed discussion of different views, see Loison 2008a). But for most of them, this property of the living was just a physiological characteristic inherent in life processes (see, for example, Costantin 1901); there was no need for a specific explanation of plasticity. Furthermore, the question of the *origin* of a natural phenomenon (in this case, natural adaptiveness or adaptability) was seen as going beyond the limits of scientific inquiry (Costantin 1898).

The second problem is to explain the inheritance of acquired characters in multicellular organisms. As I described earlier, this, too, was taken for granted because of general physiological considerations. Indeed, it was impossible for these biologists to construct a precise hypothesis of heredity without renouncing their metaphysical conceptions. Thus, this problem was never clearly articulated in France during these years (Loison 2008a).

The third problem, on which I focus here, is the link between the notion of plasticity and that of heredity. These two notions were at first seen as complementary, but this simple articulation hid a very complicated theoretical issue. This was pointed out by the British zoologist Edwin Ray Lankester in 1894. In a short paper he emphasized the self-contradiction inherent in the statement "the inheritance of acquired characters." He wrote:

> And it seems to me, that in considering this we are led to the conclusion that *the second law of Lamarck is a contradiction of the first.* [. . .] What Lamarck next asks us to accept, as his "second law," seems not only to lack the support of experimental proof, but to be inconsistent with what has just preceded it. [. . .] Since the old character (length, breadth, weight) had not become fixed and congenital after many thousands of successive generations of individuals had developed it in response to environment, but gave place to a new character when new conditions operated on an individual (Lamarck's first law), why should we suppose that the new character is likely to become fixed after a much shorter time of responsive existence, or to escape the operation of the first law? Clearly there is no reason (so far as Lamarck's statement goes) for any such supposition, and *the two so-called laws of Lamarck are at variance with one another*. (Lankester 1894:102, italics added)

The "two so-called laws of Lamarck" were the basis of every Lamarckian theory at the end of the nineteenth century, both in France and in England. These "laws" were published by Lamarck in 1809 to explain the deviations from the progressive sequence of evolution. The lateral branches of the chain of being were the consequences of an adaptation process resulting from environmental changes. Lamarck stipulated:

> *First Law*: In every animal which has not passed the limit of its development, a more frequent and continuous use of any organ gradually strengthens, develops and enlarges that organ, and gives it a power proportional to the length of time it has been so used; while the permanent disuse of any organ imperceptibly weakens and deteriorates it, and progressively diminishes its functional capacity, until it finally disappears.
> *Second Law*: All the acquisitions or losses wrought by nature on individuals, through the influence of the environment in which their race has long been placed, and hence through the influence of the predominant use or permanent disuse of any organ; all these are preserved by reproduction to the new individuals which arise, provided that the acquired modifications are common to both sexes or at least to the individuals which produce the young. (Lamarck [1809] 1963:113)

These two laws show the same theoretical structure as the one I discussed for neo-Lamarckians' evolutionism: the first law implies plasticity; the second, heredity. But for Lamarck these processes were of secondary importance, because evolution was mostly driven by a progressive internal, mechanical force. For most of the French neo-Lamarckians, this march of progress did not exist, and evolution was only about environmental adaptation. Because of this reframing of Lamarckian evolutionism, they had to face the problem of the contradictory relationship between the notions of plasticity and heredity. "Inheritance" presupposed the stability of a character in heredity in spite of environmental changes. If that were so, heredity was "stronger" than plasticity. On the other hand, the notion of "acquired" presupposed phenotypic change as a result of environmental actions. If that were so, plasticity was "stronger" than heredity. A neo-Lamarckian organism should have been able to stabilize its form and, *at the same time*, should have been capable of adaptive response. This theoretical problem was not explicitly formulated in France until 1911 (Cuénot 1911). But even though the problematic character of the Lamarckian statement was not explicitly recognized, the *tension* between the notions of plasticity and heredity led to various attempts of reconciliation.

Although in botany the program of the experimental transformism showed some real success, some plants could not be experimentally modified. Costantin recognized this as a fact. If the period of time was long enough, then plasticity seemed to fade in favor of the almighty "ancestral heredity" (the accumulated effect of the environment on organisms [Costantin 1899:120]). A new character could evolve only if a drastic change in abiotic conditions happened, because it was necessary to break the old and powerful balance between the organism and its environment. Hence, for some of the French botanists, evolution became a saltationist phenomenon: most of the morphological transformations occurred only during the rare periods of organic plasticity, under extreme, stressful conditions. This theoretical tension started the phase of theoretical schizophrenia which had been intensifying from the 1910s to the late 1930s.

In zoology, Le Dantec developed the idea that plasticity could be a vital property which decreased as the complexity of the organism increased. Biological evolution was then identified with the universe's thermodynamic transformation: plasticity should follow the same laws as entropy, but in the opposite direction (Le Dantec 1910). Only the simplest organisms could be transformed by the environment; for others, heredity had become stronger than plasticity. The general idea that evolution seemed to be a process which was about to stop was further developed by one of Le Dantec's colleagues at the Sorbonne, the zoologist Maurice Caullery (1868–1958) (Loison 2008b). As time went on, Caullery became more and more skeptical about the possibility that an acquired character could be effectively inherited. Since he did not understand that natural selection may play a creative role in evolution, he believed that the inheritance of acquired characters had to be the main evolutionary mechanism, but that it had operated only in the past (Caullery 1931). On the one hand, fossils showed that organisms were already very complex during the early eras of life. For Caullery that meant that a progressive evolution had occurred in the *past* because of the efficiency of the inheritance of acquired characters. And, on the other hand, experiments failed to demonstrate that *present* evolution was driven by the physiological effects of the environment. That is why he believed that Lamarckian processes were the main factors of evolution only during the first stages of life's transformation.

These examples show that the tension between plasticity and heredity was not a simple one. At first, French biologists were interested in life's transformations: they focused on phenotypic plasticity. Plasticity seemed to be the best explanation of the variation of individual organisms. However, around 1900, as genetics was starting to develop, they had to pay much more attention to the possibility that variations could be inherited. That is why they became more and more focused on explaining the persistence of induced characters. But the respective weights of plasticity and conservative heredity remained an unsolved question which had been first underestimated by these biologists. This tension was theorized at that time by the very vague notion of balance (*équilibre*): organisms were torn between past causes (because of their heredity) and present causes (because of their plasticity). This state of theoretical schizophrenia finally led French neo-Lamarckism to an explanatory impotence: after the 1930s, adaptation was no longer a phenomenon that could be explained by the present laws of nature. Hence, for some biologists, adaptation belonged to mechanisms that acted in the past (Caullery), while for others adaptation simply did not exist (Rabaud 1922).

Conclusion

To conclude, I would like to emphasize three points. The first is a historical point. During their later careers, Costantin, Le Dantec, Caullery, and others reached a theoretical impasse which prevented transformism from becoming an experimental theory of evolution. According to them, because of the progressive intensification of the power of heredity, the important steps of evolution happened in the past, and could not be reproduced in the present. Thus, experimental science had nothing to tell us about (past) evolutionary mechanisms. This important renunciation transformed French neo-Lamarckism from an experimental practice (experimental transformism, 1880–1910) to a metaphysical and dogmatic position (1910–1940). Subsequently, because of its explanatory impotence, this type of evolutionism slowly disappeared.

The second point is a more philosophical one. The failure of this version of Lamarckism seems to show that it is impossible to construct a consistent theory of evolution that is founded *only* on the two notions of plasticity and heredity. Note that this was not the case for Lamarck's own theory, since he used additional assumptions and notions, nor is it true for the current epigenetic notion. Epigenetic explanations take place (or have to take place) within the framework of the Darwinian synthesis.

This leads us to the third point, which is a more scientific one. Epigenetic inheritance is a phenomenon which does exist (Jablonka and Raz 2009). Its importance *in natural conditions* is a scientific question that will be discussed by scientists in the next few years. As I see it, however, the main challenge to epigenetic inheritance is theoretical: it is to find an articulation within the classical assumptions of Darwinian evolutionism. Like other kinds of inheritance (ecological, for instance), it is important to understand how and how much these epigenetic phenomena could affect fitness, and thus have an evolutionary role.

Acknowledgments

I would like to thank Eva Jablonka and Snait Gissis for their very kind invitation to the international workshop commemorating the publication of the *Philosophie zoologique* (1809). It was for me a unique opportunity to meet very interesting people and to have fruitful discussions.

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