Lamarck's Two Legacies: A 21st-century Perspective on Use-Disuse and the Inheritance of Acquired Characters

Ehud Lamm[1] and Eva Jablonka[1]

[1] The Cohn Institute for the History and Philosophy of Science and Ideas
Tel-Aviv University, Tel-Aviv 69978, Israel.

Abstract

Lamarck has left many legacies for future generations of biologists. His best known legacy was an explicit suggestion, developed in the *Philosophie zoologique* (PZ), that the effects of use and disuse (acquired characters) can be inherited and can drive species transformation. This suggestion was formulated as two laws, which we refer to as the law of biological plasticity and the law of phenotypic continuity. We put these laws in their historical context and distinguish between Lamarck's key insights and later neo-Lamarckian interpretations of his ideas. We argue that Lamarck's emphasis on the role played by the organization of living beings and his physiological model of reproduction are directly relevant to 21st-century concerns, and illustrate this by discussing intergenerational genomic continuity and cultural evolution.

Lamarck's two laws

Lamarck's major contribution to evolutionary thought was his suggestion that the inheritance of acquired characters drives evolutionary change. The idea that the effects of use and disuse – "acquired characters" – are inherited was not original to him; he took it for granted, as did most 18th- and 19th-century biologists (including Charles Darwin). However, his insistence that the effects of such inheritance go beyond within-species change and can account for the generation of new species, for patterns of diversity and for adaptation launched the theory of evolution (Burkhardt 2011), and has been the subject of experimentation, speculation and heated debate ever since. His proposal, which was popular during the last third of the 19th century but was rejected during most of the 20th century, is currently receiving serious consideration again (see Gissis and Jablonka 2011 for historical, biological and philosophical perspectives). We shall not review here the many studies that show that developmentally-induced variation can have heritable effects, since such reviews are being published regularly (e.g., Jablonka and Raz 2009; Turner 2011; Jablonka 2013; Rechavi 2013). Rather, we would like to show the continuities and discontinues between the two laws that Lamarck presented in his *Philosophie zoologique* (PZ) and 21st-century conceptions of physiological adaptation and heredity. We therefore start with Lamarck's famous two laws, as described in PZ:

"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 used; while the permanent disuse of any organ imperceptibly weakens it, 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 been long placed, and hence through the influence of the predominant use or the 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, PZ, part 1, p. 113; here as elsewhere in this paper PZ refers to the 1914 English translation of Lamarck's *Pilosophie zoologique*, 1809).

We suggest that the first law, which describes how characters develop through use and disuse, can be described in modern terms as the *law of biological plasticity*. The second law, asserting that the effects of these developmental “acquisitions” are inherited, can be described as the *law of phenotypic continuity*. We believe that these modern articulations of Lamarck’s ideas can contribute to discussions about heredity and evolution.

The law of biological plasticity

Lamarck’s view of the flexibility and responsiveness of living organisms (what we would today call phenotypic plasticity) was different from a simple notion of material flexibility. He devoted a lot of attention to the different ways in which living organisms are organized, and considered their forms of organization as fundamental for understanding how they react to stimuli (e.g., whether there is a localized or a coordinated response) and how they evolve. Lamarck regarded biological responsiveness as a fundamental defining property (a “primitive”) of living organization. The responsiveness of living things was for him the result of the combined effect of the types of chemical material from which biological entities are built (gelatinous matter in animals, mucilaginous matter in plants, in both cases organized as cellular tissue), and the self-organizing dynamics of fluxes of electricity and heat (which he called subtle fluids) that shape this material in a way that leads to its self-maintenance and complexification. This view of biological organization was at the heart of his approach to the origin life (part II of PZ) and to the evolution of psychological capacities (PZ, part III). It was a view that he had already developed in *Recherches sur l'organisation des corps vivants* in 1802, and which he quotes in PZ:

“…the function of the movements of fluids in the supple parts of living bodies, and especially in the cellular tissue of the simplest among them, is to carve out routes, places of deposits and exits, to create canals and thereafter diverse organs, to vary these canals and organs in accordance with the diversity of the movements or characters of the fluids causing them, finally to enlarge, elongate, divide and gradually solidify these canal and organs. This is effected by the substances which are

incessantly being formed in the fluids, and are then separated from them, and in part assimilated and united to the organs, while the remainder is rejected.
… *that the state of organization in every living body has been gradually acquired by the increasing influence of the movement of fluids* (firstly in the cellular tissue and afterwards in the organs formed in it), and by the constant change in the character and state of these fluids owing to the continual wastages and renewals proceeding within them". (PZ pp. 232-233; our emphasis)

What is central to Lamarck's view, both in his early and late works, is dynamic organization which is manifest in the activities that underlie the way that a living entity uses or disuses its organs and utilizes the resources in its environment. He believed that the gelatinous or mucilaginous states of matter, which alone could support living organization, have been (and continue to be) formed spontaneously; once this matter is exposed to fluxes of environmental caloric and electricity, the matter self-organizes into living, self-sustaining entities, which are endowed with the ability to nourish themselves, grow, and adapt to their conditions of life (see, for example, PZ p. 239).

As is clear from PZ, Lamarck was working against a dominant vitalistic philosophy, and was reacting against the view that the environment was inherently antagonistic to the organism (Giglioni, 2013), a perception that remained typical in subsequent Darwinian and neo-Darwinian thinking. Xavier Bichat, whose views on this issue Lamarck explicitly rejected, had been concerned with the ability of fragile organisms to resist the destructive effects of the environment. These concerns led to various notions of vitalistic internal buffering, and were later replaced with more mechanistic alternatives, which paved the way to Walter Cannon's 20th century notion of homeostasis. However, the homeostatic notion of stability still fits a picture of external, destructive environment, emphasizes internal mechanisms that lead to *lack* of apparent macroscopic change, and, most significantly, regards biological organization as fragile. For Lamarck, in contrast, the interaction with the environment is essential for the adaptive adjustment of the organism, which is often associated with altered habits and morphology, and an increase in complexity (e.g., division of labor) and leads to an increase in stability.

The physiological activities of living entities, the practices to which parts of the organism are put, are the “uses and disuses” which Lamarck had in mind. Use and disuse, he thought, occur in both plants and animals, albeit in different ways because these classes of organisms have different forms of organization. In plants, which do not move and do not form habits (for Lamarck habits are mediated by a nervous system) changes are acquired through physiological activities like nutrition, absorption and transpiration, which are modulated by environmental conditions (the amount of light, caloric, moisture etc.) and through the dominance of some internal movements over others (PZ p. 108). In animals, the changes brought about by use and disuse are mediated by the nervous system and by the habits the animal forms, which are in turn mediated by felt needs, which are, according to Lamarck, the need for food, sex, general well-being, and avoidance of pain (PZ p. 352). What is altered in non-primitive animals as they face new challenges is their “inner feeling”, which requires a central nervous system and manifests itself fully only in animals that can move. The inner feeling is the precursor and the condition for the formation of the emotions that are found in more developed animals, and its specific effects depend on the internal organization of the nervous system and the animal’s morphology, both of which are tied to the activities of the organism. Lamarck’s notion of inner feeling is similar to the later physiologists’ ideas about an inner environment and homeostasis-preserving mechanisms, but the differences between his view and these later views are telling. His physiological notion of dynamic, plastic organization does not stress the buffering (canalizing) aspect of physiological adaptation; instead use and disuse lead to new habits, which make the organism more stable by becoming more complex, more differentiated.

Lamarck’s emphasis on flexible, plastic organization was adopted by French neo-Lamarckians. Laurent Loison (2011) argues that French neo-Lamarckism was initially structured by the notion of plasticity, which was at the core of the physiological investigations that were central to 19th- and early 20th-century French biology. Lamarck’s ideas were interpreted in the context of physiological research in zoology, teratology, microbiology and, most strikingly, botany, where ecological studies of plant populations and physiological studies in the laboratory showed the great scope and prevalence of plants’ adaptive plasticity. The adjustments of multicellular organisms and of microbes to changed conditions were interpreted by the French neo-Lamarckists in terms of individual plasticity –of use and disuse.

The notion of "acquisition" in the Lamarckian sense was closely linked to that of use and disuse, for it is through active use and disuse that living organisms "acquired" their new adaptations. A developmental acquisition was seen by Lamarck and his followers as the result of the response of the organism to a usually persistent environmental input that leads to a new phenotype (for example acquiring large muscles, acquiring a tan, learning to ski). However, although the term may seem intuitively clear, the usage of the term "acquired" is full of ambiguities, just like its mirror-image, "innate". Mameli and Bateson (2006) listed 26 partially overlapping meanings of "innate", and analyzed its many misuses and over-interpretations. Griffiths, who studied the way in which "innate" is used by lay people (i.e. the "folk biology" notion of innate), showed that it is identified with "inner nature", and this inner nature is characterized by *fixity* (innate traits are insensitive to environmental inputs), *typicality* (the individual is a normal healthy token of its species) and *teleology* (the trait is adaptive, deviations are pathological) (see Griffiths, 2002, 2011; Griffiths, Machery and Linquist 2009). As Bateson and Mameli, and Griffiths and his colleagues have shown through their analyses, although the terms seem to be dichotomous, the attributes of "innate" do not clearly distinguish it from "acquired". This can lead to conceptual muddles. For example, while the development of an acquired trait is by definition context sensitive, the acquired trait is usually a result of a typical organismal response, and is often, though not invariably, adaptive, involving the mobilization of already-evolved physiological mechanisms (Bateson and Mameli 2007; see also Lehrman 1953), Moreover, every trait in a living organism is sensitive to some context, and embryological development that unfolds in a species-typical manner can be, and often is, depicted as a cascade of inductions (Semon 1921; Waddington 1957). Hence, "typicality" and "teleology" do not distinguish between innate and acquired characters, and there are no unqualified "fixed" characters.

From Lamarck's point of view the most obvious distinctions one needs to make in order to clarify what "acquired" means are (i) that between passive acquisition and developmental (active) acquisition, and (ii) that between a developmental acquisition that depends on learning (which is special to animals and is based on neural learning mechanisms and motor behavior) and an acquisition that does not depend on the nervous system (which applies to all living organisms). To take simple examples, consider the distinction between the following three cases, each of which involves an "acquired" trait: a newly (acquired) shattered bone; an acquired crooked bone that resulted from the remodeling that followed a break in it; and an acquired skill in handling a dangerous item of prey (e.g. a scorpion) that resulted from a meerkat's learning process. The newly shattered bone is not considered as a biological acquisition, even though the bone has "acquired" a new shape, because there was no functional biological activity involved in the response to the breakage. On the other hand, a bone that has been remodeled after a break can be thought of as biological "acquisition": the healing-remodeling is based on mechanisms that, on average, enable the animal to cope with breaking-bone traumas (even if a particular instance of remodeling is awkward). Similarly, when an individual meerkat learns to handle a scorpion, the skill can be said to be developmentally acquired (through neural learning), because it involves biological activity. However, in this case the nervous system and motor behavior are involved, and this type of biological response demands, according to Lamarck, additional considerations to those involved in physiological acquisitions that do not involve the nervous system. Once a nervous system is in place, it becomes the organizing system of the animal, and its sensory and motor responses are controlled and coordinated by it. That is why animals do not adapt as directly to altered environments as plants; according to Lamarck, each change in animals' physiology is mediated by their nervous system and by their habits. This mediation means that external conditions have a less direct effect on animal physiology, and explains the greater physiological and morphological flexibility of plants.

The term currently employed to describe the active "acquisition" of new capacities and characters during development is *phenotypic plasticity*. The most comprehensive and nuanced discussion of plasticity to date is that of West-Eberhard's (2003). Like Lamarck, West-Eberhard sees plasticity as a "primitive", a defining feature of life: "… it is reasonable to conclude that phenotypic plasticity has been a property of living organisms since their origin" (West-Eberhard 2003, p. 180). She notes that plasticity does not necessarily mean that altered conditions bring about a modification of the organism's macroscopic phenotype. The response of an organism to a change in its conditions of life can be either a modification of its phenotype, or the active maintenance of its macroscopic state (for example its level of blood sugar) in spite of the changed conditions, a process that requires changes in the nature and/or activity underlying mechanisms (e.g. hormonal mechanisms), and hence requires plasticity at an underlying microscopic level. West-Eberhard therefore defines plasticity broadly, as:

"…the ability of an organism to react to an internal or external environmental input with a change in form, state, movement, or rate of activity. It may or may not be adaptive (a consequence of previous selection). Plasticity is sometimes defined as the ability of a phenotype associated with a single genotype to produce more than one continuously variable alternative form of morphology, physiology and/or behavior in different environmental circumstances (Stearns 1989). It refers to all sorts of environmentally induced phenotypic variation (Stearns 1989).

Plasticity includes responses that are reversible and irreversible, adaptive and nonadaptive, active and passive, and continuously and discontinuously variable". (West-Eberhard, 2003 p. 33).

In addition to the qualifications mentioned in the quotation (passive and active, reversible and irreversible, continuous and discontinuous), West-Eberhard discusses additional, equally important qualifications: maturational and non-maturational developmental responses; learnt responses (whose development requires a psychological description), and responses that do not require such description; open-ended plasticity, which accommodates novelty (such as the ability of a handicapped goat to walk on its hind legs), and plasticity that leads to a pre-defined range of responses (such as the development of different castes in social insects). Open-ended plasticity is of particular interest, because the novelty produced is, by definition, not the result of past genetic selection for the new trait, and the novel trait cannot be assumed to exist in a latent state within some underlying "genetic program".

West-Eberhard calls the developmental reorganization that is involved in the generation of novel phenotypes *phenotypic accommodation* (West-Eberhard 2003). It is mediated through general biological properties such as mechanical flexibility and the multiplicity of partially-overlapping regulatory elements, and through exploration and selective stabilization processes that are based on the generation of numerous variations and interactions, from which only a small subset are eventually stabilized and manifested. Examples of exploration-stabilization mechanisms can be found at every level of biological complexity, from the cellular to the social/cultural. Selective stabilization underlies spindle formation within the cell (Gerhart and Kirschner 1997), the stabilization of synaptic connections during development and learning in animals (Changeux et al. 1973, Edelman 1987), trial-and-error learning (Skinner 1981), and the stabilization of cultural practices (Sperber 1996). For West-Eberhard, some open-ended plasticity processes that enable organisms to cope with unpredictable conditions, may be part of *all* accommodation processes (even those that involve "typical" reactions of the organism) because an organism always faces some unpredictability: the environment is always somewhat erratic, and development is always somewhat "noisy".

West-Eberhard defines phenotypic accommodation as the "adaptive mutual adjustment among variable parts" (West-Eberhard 2003 p. 51), a definition which resonates with Lamarck's belief that physiological adaptation through use-disuse leads to new forms of (self) organization. As we noted already, for Lamarck, as for West-Eberhard, dynamic organization is a key concept, and adjustment to adverse conditions implies successful coping with environmental challenges. The well-being of the individual and its reproductive success require either that the organism adjusts to the environment, or that it adjusts the environment to itself. Lamarck focused on organismal adjustments, and for obvious reasons (lack of information) did not differentiate between different types of plastic strategies, something which is of great interest today. For example, Jablonka and Lamb (1995, p. 172) distinguished between four types of plastic response to challenge: (i) a non-stressful response (within the typical reaction range of the organism, for example, the response of a plant to a change in day-length); (ii) a stressful, specific but familiar response (e.g., reaction to a predator); (iii) a response to a general, non-acute and familiar stress (e.g., mild starvation); and (iv) a response to catastrophic conditions to which one cannot adapt physiologically or behaviorally (e.g., acute starvation, drastic heat-shock). Each of these types of accommodation employs different types of genomic and developmental mechanisms and leads to the generation of different types of heritable non-genetic or genetic variations (Lamm and Jablonka 2008; Shapiro 2011).

Another way in which organisms can adapt to the environment and affect evolution is by altering the environment they experience. They do this by migrating to a different location, or by modifying their environment, for example by building burrows or nest, a practice known as "niche construction" (Odling-Smee et al 2003). The processes of migration and niche construction began to be emphasized in the last quarter of the 20th century, partly as alternatives to the Lamarckian model with its emphasis on phenotypic accommodation. Unlike use and disuse, migration and niche construction do not change the organisms involved directly; rather, they affect the selection pressures that the organisms and their descendants face, indirectly leading to changes in the progeny through natural selection.

Phenotypic continuity: a historical notion of heredity

It is clear that the focus on plasticity illustrated by Lamarck's first law is of central importance in 21st-century biology, and it is equally clear that today "plasticity" carries meanings and implications that were unthinkable 200 years ago. Our present knowledge about the processes that underlie plasticity and inheritance also enables us to understand better how "acquired" traits may be passed on to descendants, as suggested in Lamarck's second law.

The modern concepts of heredity and inheritance are derived from the legal context dealing with the transfer of ancestral properties, such as land and money. "Heredity" was first incorporated into biology in 1807, but the term was used in several different and inconsistent ways during the 19th century. Different things were said to be inherited: external things belonging to ancestors, such as property; physical parts of ancestors; the potential for developing traits, and the initial conditions that are necessary or enabling for such development. This multiplicity of meanings led Johannsen (1911), in an influential paper in which he defined central terms such as phenotype, genotype and gene, to criticize the vague and metaphoric notion of inheritance. Instead, Johannsen advanced an ahistoric, explicitly non-developmental notion of the genetic potentialities that are transmitted between generations:

“The genotype-conception is thus an “ahistoric” view of the reactions of living beings – of course only as far as true heredity is concerned. ... I suggest that it is useful to emphasize this “radical” ahistoric genotype-conception of heredity, in its strict antagonism to the transmission- or phenotype view. …Certainly, evolution of types of tools, instruments and implements of all kinds is – at least partially – going on by means of selective factors combined with tradition, the latter not only conserving the valuable types but actively stimulating their improvement. But all this has nothing to do with the biological notion of heredity.” (Johannsen 1911, p. 139-140)

He then concluded: “Heredity may then be defined *as the presence of identical genes in ancestors and descendants*” (Johannsen 1911 p. 159; his italics). According this view, which has become very influential and guided thinking about heredity and evolution for most of the 20th century, only genotypes can be inherited; a phenotypic trait is a characteristic of an organism resulting from the interactions between an internal initial potential (genetic-developmental) and the external environment, and it is only the genetic potential that is inherited in a “real” biological manner (for discussion see Jablonka and Lamb 1995, 2005). Following the discovery of DNA, the genotype became identified with the DNA sequence present in the cell, and biological inheritance became identified exclusively with DNA replication.

Clearly, Lamarck’s notion of inheritance does not conform to Johannsen’s definition: for Lamarck inheritance is an aspect of development and hence is by definition “historical”. However, it is important to note that Lamarck’s notion is not an early variant of a pangenesis theory like that which Darwin later developed (and named). Darwin postulated that tiny gemmules that are formed during development and represent the trait (and the variations it acquires during development) accumulate in the reproductive organs and are passed on to offspring where they seed the construction of similar traits. Pangenesis theories thus account for the inheritance of developmentally acquired modifications, so it is tempting to read Lamarck’s second law as being a vague version of something like pangenesis. Until recently, pangenesis models were rejected because of the acceptance of the germline-soma barrier proposed by August Weismann in the 1880s, and Johannsen’s insistence that the genotype alone is inherited (see Jablonka 2013; Rechavi 2013 for recent evidence for the germline inheritance of acquired variations). However, the pangenesis view of heredity was not part of Lamarck's ideas. Lamarck did not propose a theory of heredity, and during his time the notion of heredity as a specific kind of process that applies to all characteristics of the organism, both species-typical and the specific characters of individuals, was still crystallizing. Lamarck was committed instead to a view of physiological continuity, of heredity as inter-generationally-extended development. According to him, ancestors transfer acquired changes in organization at the same time as they pass on developmental aptitudes and tendencies: "just as reproduction transmits *acquired forms* both internal and external, so too it transmits at the same time *an aptitude for certain specialized types of movements and corresponding habits*." (PZ p. 346; our italics). Characters are the products of development and must be "acquired" ontogenetically. For Lamarck, transmission is not a process of forming or copying distinct gemmules or determinants, but a developmental re-construction process that involves a response to recurring environmental conditions and leads to gradual, systemic changes in organismal form and aptitude.

The Lamarckian way of thinking about heredity is non-intuitive for many biologists today. However, West-Eberhard has presented a view of heredity that is similar in some respects to the one implied by Lamarck, and may help clarify his viewpoint and show its relevance to our current, extended notion of heredity. Like Lamarck, West-Eberhard is committed to the idea that "all order proceeds from order". She thus stresses the evolutionary significance of what she terms the continuity of the phenotype, namely "*the unbroken and overlapping* phenotypic connections between generations mediated by parentally-constructed offspring phenotypes (e.g., eggs, spores, seeds, and effects of later development)" (West-Eberhard 2003 p. 93, our italics). Instead of thinking about parents and offspring as self-contained individuals connected by the transmission of the parental genotype to the offspring, West-Eberhard suggests that we notice that there is an unbroken chain of intermediary phenotypes, consisting, for example, of the unfertilized egg, the egg after its fertilization by sperm, larvae, juveniles, and adults. Each of these is an organized and plastic entity. Genes always operate in the context of an already organized entity that was shaped by previous events and generations. All the intermediary phenotypes, like phenotypes in general, are plastic. Development, according to West-Eberhard, results from the reaction of intermediary (bridging) phenotypes to genetic and environmental stimuli, potentially including additional maternal stimuli. Since the zygotic genome interacts with other preexisting components in the fertilized egg, it is constrained by the parentally-constructed structure.

Hence, what West-Eberhard calls “the continuity of the phenotype”, the unbroken chain of phenotypic connections, underlies the re-construction of developmental acquired ancestral organization in subsequent generations. Although she emphasizes organized bridging-phenotypes that are developmentally plastic, whereas Lamarck stressed the transfer of changes in organization and developmental aptitudes from ancestors to descendants, the affinities between the two approaches are obvious: both view heredity as inter-generationally-extended development, and physiological continuity is central to their notions of heredity.

A few examples may clarify this picture and help show the continuity between development and heredity. West-Eberhard notes that maternal gene transcripts in the egg are still used after embryonic development begins. More dramatically, in the frog species *Xenopus* the zygotic genes are not expressed at all for several hours after fertilization, when the blastula contains 4000 cells (West-Eberhard, 2003, p. 96). Moreover, maternal effects can accumulate over several generations. For example, in migratory locusts the maternally-transmitted effects of adult crowding accumulate for several generations before the migratory phenotype becomes fully expressed (West-Eberhard, 2003, p. 98). Hence, maternal and, more generally, ancestral developmental effects demand an extension of the notion of inheritance and a return to an “historic” view of heredity.

“Biological inheritance” includes more than extended maternal effects, however. In addition to inheritance through DNA replication (the “ahistoric” aspect), heredity today is seen as encompassing developmental inheritance and infective inheritance (the inheritance of factors acquired from the environment, such as viruses, pieces of DNA or RNA, and prions, which are thereafter vertically transmitted). Developmental inheritance includes: (i) The inheritance of phenotypic variations that are not dependent on variations in DNA sequence. These include epigenetic variations, behavioral variations, and symbolic variations (Jablonka and Lamb 1995, 2014). (ii) The inheritance of changes in DNA that are regulated and directed by control systems that respond to developmental signals and environmental cues (Lamm and Jablonka 2008, Shapiro 2011, Lamm 2014). These phenomena are often interpreted as supporting Lamarckian inheritance, although some of them (especially those focusing on the germline inheritance of epigenetic variations) resonate more with the neo-Lamarckian (pangenesis) heredity theories of late 19th-century and early 20th-century biologists (described in Robinson 1979) than with Lamarck's physiological view of heredity. However, since developmental variations acquired in one generation can have physiological effects on the next generation that lead to similarity between parents and offspring, the various mechanisms of heredity form a continuum. For example, exposing a pregnant rat to the chemical vinclozolin can affect her physiological state in ways that alter the somatic-physiological and the behavioral development of her offspring, change the chromatin in their germline, and lead to the transmission of the altered acquired states to future generations (Guerrero-Bosagna, Settles, Lucker and Skinner 2010).

For Lamarck, inheritance was not simply a parent-offspring relation; it involved the environment, the habits that an individual develops during its ontogeny, and the cumulative effects of the habits formed by ancestors. This multi-generational phenotypic continuity characterizes developmental inheritance more generally, and has evolutionary implications. Alexander Badyaev and his colleagues studied phenotypic accommodation in the house finch *Carpodacus mexicanus*, a bird which since the 1940s has greatly expanded its range, having spread from its original habitat in California to both the hot and humid areas of Alabama and the cold and dry areas of Montana. These expansions were accompanied by physiological adaptations in each population, leading to significant and divergent differences between the two sexes. Analysis has shown that the adaptations occurred through changes in the physiology and laying behavior of the mother, i.e., through environmentally-induced maternal effects. The birds adapted during their own lifetime, with females that migrate from one environment to another getting progressively better-adapted to their new environment with age, and the adjustments continue to get better in subsequent generations (Badyaev 2009). Badyaev has suggested that the next evolutionary stage may involve the stabilization of hereditary transmission through epigenetic germline inheritance, with final stabilization occurring when genetic variations that confer even greater stability on the birds' development displace the epigenetic variations, a process that West-Eberhard (2003) calls genetic accommodation. Although this progression of heredity-stabilizing mechanisms is not the only possibility (genetic accommodation can occur without the intervention of maternal effects and epigenetic germline-inheritance, and epigenetic germline-inheritance need not be preceded by maternal effects), such progression is likely because epigenetic inheritance stabilizes the environmentally induced and accommodated changes, thus guiding selection that leads to their genetic accommodation.

Discussion: The benefits of an interdisciplinary framework

The complexity inherent in the phrase "the inheritance of acquired characters" problematizes not only the notion of inheritance, but also that of "character", and consequently also the notion of the "individual" to which a "character" is attributed. Some notions of "character" are straightforward: an organism (e.g., a human) can be said to have morphological characters (a round head, long limbs, broad shoulders), physiological characters (high sugar level, low cholesterol, normal blood pressure) or characters described by behavioral/psychological attributes (active, alert, emotionally-dependent). Of course the categories overlap, because morphology and physiology are closely related, and the psychological can be seen as a special aspect of the physiological. In all these cases there is an obvious overlap between "character" and a developmentally constructed phenotype, but this is not always the case. Is a developmental alteration in a specific DNA sequence, such as that resulting from a programmed, environmentally-induced genetic change in yeast, a character? If we view the genome as a developmental system (Lamm 2011, 2014), the answer is clearly positive, while from an "a-historic" point of view, the answer is negative.

The nature of the "individual" is crucial to our judgment of the character-status of an attribute. If the individual of interest is a lineage, a statistical (collective) attribute can be thought of as a character. For example, the frequency of recombination in a particular chromosome, which is high in one lineage and low in another, is a lineage-character. If the individual is a more or less coherent community of organisms, a holobiont, then the potentially varying constituent-partners can be thought of as a character of the focal partner (the one which is the major focus of interest). Thus, if we think about humans and their many microbial gut symbionts as a "human-holobiont”, then for the human part of the partnership, having a particular type of symbiont or combinations of symbionts is a character, which has been actively constructing during the human’s development (with an initial contribution coming as part of the maternally-produced bridging phenotype); similarly, for a bacterium within the holobiont, its human partner contributes to its multi-faceted phenotype (Gilbert 2011). Moreover, an ecologically constructed niche can be seen as one of the characters of an individual organism or group of organisms. The beaver’s dam, for example, can be thought of as developmentally and behaviourally constructed character, which has distinguishing qualities that depend on the beavers’ construction methods and the local environment, including the dam that was acquired from the parents (Odling-Smee et al. 2003). Here, the character – the type of dam – of individual groups of beavers is socially constructed. If we turn to culture, we recognize that cultural practices are composite characters: they are made up of behavioral and social-niche components (e.g., artefacts and tools), which are characters both of the individual and of the social system of which it is part. Moreover, social institutions and social systems such as firms can have collective characters (e.g., efficiency, or civility).

A framework that emphasizes plasticity and phenotypic continuity, and therefore stresses the connection between development and heredity, the interconnected mechanisms of transmission, and the multiple levels of individuality, requires an interdisciplinary approach. This is because every character, whether heritable or not, is the result of development, which always has genetic and epigenetic inputs, and in humans also behavioral and symbolic inputs. Heredity and evolution therefore need to incorporate multiple mechanisms of “acquisition” and transmission, as well as several levels of individuality. We will illustrate this by showing how this framework impinges on genomic research and on the study of cultural evolution.

Genomic developmental continuity

In eukaryotes the genome consists of chromatin, which is composed of DNA wound around various histone proteins, together with associated non-histone proteins and RNA molecules. Chromatin has a three-dimensional structure that is related to gene expression, and DNA that is inaccessible to the reading machinery because of its structure is not expressed. The conformation of chromatin is dynamic and changes during the life of the cell, depending on cellular activities and functions. Recognizing the importance of the organization and dynamics of chromatin is crucial for understanding both heredity and evolution (Lamm 2011). When cells divide, components of chromatin (in addition to the DNA sequence) are reproduced in the daughter cells, and in this way the three-dimensional conformation of chromatin is partially “copied”; its structure is later elaborated and completed by mechanisms operating in the daughter cells (reviewed in Lamm 2014). The inheritance of chromatin conformation agrees with the views of heredity discussed earlier, both with Lamarck’s vague proposal and with the modern idea of the continuity of the phenotype proposed by West-Eberhard. In addition to enzymes and other maternal contributions (e.g., non-coding RNA molecules and regulatory factors) that are transmitted to the zygote, parental chromatin structure affects the chromatin structure and gene expression in the zygote, and is an important part of what West-Eberhard calls a bridging phenotype.

The factors and processes that maintain variant chromatin structures over time, and thereby lead to cell memory or cell heredity, are *epigenetic* mechanisms. One type of epigenetic mechanism is DNA methylation. Methyl groups can be attached to the cytosines of the DNA, and although they do not alter the coding properties of the sequence, patterns of cytosine methylation affect the probability of transcription. Crucially, changes in DNA methylation patterns can be induced by the environment, and are copied when DNA is replicated. If the patterns of DNA methylation or their phenotypic effects are taken to be “characters”, then the discovery and elucidation of this molecular copying mechanism provides support for a neo-Lamarckian model for the inheritance of acquired characters.

DNA methylation is only one of several mechanisms of epigenetic inheritance. Other mechanisms involve the re-production of histone modifications, the three-dimensional templating of proteins such as prions, which are transmitted through cell division, the transfer and re-production of small RNA molecules that act as regulators of gene expression, and the transmission of components of autocatalytic positive-feedback loops that are passed on from mother to daughter cells during cell divisions and reconstruct parental cellular activities (reviewed and discussed in Jablonka and Lamb 2014)

In addition to transmission within a cell lineage, the same molecular epigenetic mechanisms are known to have roles in the maintenance and transmission of changes at higher levels of biological organization. They sometimes underlie the inheritance of behavioral characters by routes that by-pass the germline (reviewed and discussed in Jablonka and Lamb 2014). In particular, acquired stress-induced behavioral phenotypes, which are associated with changes in chromatin and the regulation of gene expression in fear and reward centers in the mammalian brain, are reconstructed in the offspring. For example, rat pups raised by mothers who give them little grooming and licking grow up to be fearful and readily stressed adults, while pups raised by mothers that groom and lick then a lot grow up to be adventurous and relatively stress-free adults. These differences in behavior are reflected in the structure of the chromatin in the rats' brains, and are reproduced when the females treat their offspring in the same way as they themselves were treated by their mothers (Kappeler and Meaney 2010).

Epigenetic mechanisms can also influence changes in DNA sequences. For example, certain types of small RNA molecules inhibit transposon movements, so a developmental change that reduces the production of these small RNA molecules can enhance transposition, thereby leading to changes in the organization of DNA. Hence, even the reliable transmission of DNA sequences can be developmentally altered, and genetic and epigenetic continuity are tightly linked (Lamm and Jablonka 2008; Lamm, 2011, 2014).

Cultural continuity

Societies and culture change over time, and exhibit dynamics that transcend those of individuals. It is therefore natural to try to capture these dynamics using evolutionary tools. Attempts to do so have been very controversial, however. Joseph Fracchia and Richard Lewontin (1999), for example, insist that such approaches use "simplistic ad-hoc notions of individual acculturation and of the differential survival and reproduction of cultural elements. It is unclear what useful work is done by substituting the metaphor of evolution for history" (p. 52). One of the approaches they have in mind incorporates the idea of cultural memes, which was introduced by Richard Dawkins (1976). The memetic account is based on the premise, shared by other accounts of cultural evolution, that culture can be broken down into semi-independent units, which are supposedly analogous to genes. The fate of these units (e.g., a catchy tune, food hygiene) is then studied using modified and enriched models of population genetics that take into consideration not only vertically transmitted information, but also information transmitted by peers and teachers. In addition to looking at the effects of selection, drift, migration and random variation, which are used in conventional population genetics, these models incorporate processes that are specific to the generation, acquisition, and transmission of cultural information. These include "guided" variation, based on individual trial and-error learning; blending inheritance, which takes place when an individual adopts the average of several cultural variants it encounters; and the preferential acquisition of variants because of their content (content bias), or the status of the model (prestige bias), or in order to conform (conformity bias). Although more complex than the methods used in traditional population genetics, most practitioners of this approach readily accept that viewing culture this way is still a gross simplification, yet they argue that it is a worthwhile idealization (Heinrich, Boyd, and Richerson 2008).

We agree with Fracchia and Lewontin (1999) that human historical processes are impossible to understand by studying how individual memes spread in populations, idealization or not. Cultural evolution models may be appropriate for very localized scenarios (Mesoudi 2011), and may also be applicable to animals that lack rich mental lives. However, since both the acquisition and transmission of social-cultural practices are developmental processes of construction, models of cultural evolution must also incorporate the factors that affect physiology and behavior, and contribute to the persistence of practices. For example, in order to understand the socio-cultural persistence of urban poverty, models have to incorporate the long-term epigenetic effects of conditions such as malnutrition in utero and psychological stress in early development, as well as multiple familial and social factors. And since the relations between the dynamics of the individual's development and the dynamics of the social system (e.g., social hierarchies, institutions, norms) must be addressed, an approach that is focused on plasticity and intergenerational continuity, and takes into account more than one time scale (those of the individual, the family, the community, etc.), is a more productive approach for understanding cultural change. One proposal for such an approach has been outlined by Tavory et al. (2014).

*   *   *

Lamarck’s ideas, as analyzed and discussed in this paper, go beyond traditional conceptions of “Lamarckism”, which became synonymous with the inheritance of acquired characters and with a specific, pangenetic model of what such inheritance entails. We have argued that this traditional, mainstream perspective fits much better with later, 19th- and 20th-century neo-Lamarckian notions of heredity, and that it obscures some key aspects of Lamarck’s own ideas. Two legacies of Lamarck – the role of phenotypic organization and plasticity, and the continuity of modified phenotypes in heredity – which were presented in his two PZ “laws”, remain highly relevant today. These Lamarckian legacies are inherent in and unify the approaches used in many biological disciplines, including medical epigenetics, behavioral epigenomics and cognitive-sociocultural coevolution. Because it is now recognized that understanding biological heredity and evolution needs a broad interdisciplinary approach, Lamarck’s original way of thinking has become far more relevant than it was thought to be during most of the 20th-century.

Acknowledgment: We thank Marion Lamb for her many contributions to this manuscript.

Bibliography

Badyaev, Alexander V. “Evolutionary significance of phenotypic accommodation in novel environments: An empirical test of the Baldwin effect.” *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364, 2009: 1125–1141.

Bateson, Patrick and Mameli, Matteo.” The innate and the acquired: useful clusters of residual distinction from folk biology?” *Developmental Psychobiology* 49, 2007: 818-831.

Burkhardt Jr., Richard W. “Lamarck, Cuvier, and Darwin on animal behavior and acquired characters”. In: *The transformations of Lamarckism*. Snait Gissis and Eva Jablonka (eds), pp. 33-44. Cambridge MA: MIT Press, 2011.

Changeux, Jean-Pierre, Courrege, Philippe, and Danchin, Antoine. “Theory of epigenesis of neuronal networks by selective stabilization of synapses.” *Proceedings of the National Academy of Sciences USA*, *70*(10), 1973: 2974-2978.

Dawkins, Richard. *The selfish gene*. Oxford: Oxford University Press, 1976.

Edelman, Gerald M. *Neural Darwinism: the theory of neuronal group selection*. New York: Basic Books, 1987.

Fracchia, Joseph, and Lewontin, Richard C. Does culture evolve? In *The return of science: evolutionary ideas and history*. Special issue 38, *History and Theory*, 1999: 52–78.

Gerhart, John, and Kirschner, Mark. *Cells, embryos, and evolution: Towards a cellular and developmental understanding of phenotypic variation and evolutionary adaptability*. Malden, MA: Blackwell, 1997.

Giglioni, Guido. “Jean-Baptiste Lamarck and the place of irritability in the history of life and death.” In *Vitalism and the scientific image in post-enlightenment life science,* *1800-2010*, Normandin, Sebastian and Wolfe, Charles T. (eds) 19-49.Berlin: Springer, 2013.

Gilbert, Scott. “Symbionts as an epigenetic source of heritable variation.” In: *The transformations of Lamarckism*, Gissis Snait and Jablonka, Eva (eds), pp.283-293. Cambridge MA: MIT Press, 2011.

Gissis, Snait. B., and Jablonka, Eva (eds). *The transformations of Lamarckism: from subtle fluids to molecular biology*. Cambridge, MA: MIT Press, 2011.

Griesemer, James, R. “Reproduction and the reduction of genetics.” In *The concept of the gene in development and evolution, Historical and epistemological perspectives*, P. Beurton, R. Falk, and H-J. Rheinberger (eds), 240-285. Cambridge: Cambridge University Press, 2000.

Griffiths Paul, E. “What is innateness?” *The Monist* 85, 2002: 70-85.

Griffiths, Paul E. “Our plastic natures.” In *The transformations of Lamarckism*, Snait Gissis and Eva Jablonka (eds), 318-330. Cambridge MA: MIT Press, 2011.

Griffiths, Paul E., Machery, Eduard and Linquist, Stefan. “The vernacular concept of innateness.” *Mind and Language* 24, 2009: 605-630.

Guerrero-Bosagna, Carlos, Settles, Matthew, Lucker Ben, and Skinner, Michael K. “Epigenetic transgenerational actions of vinclozolin on promoter regions of the sperm epigenome.” *PLoS ONE* 5(9), 2010: e13100. doi:10.1371/journal.pone.0013100

Henrich, Joseph, Boyd, Robert and Richerson, Peter J. “Five misunderstandings about cultural evolution.” *Human Nature* 19, 2008: 119–137.

Jablonka, Eva. “Epigenetic inheritance and plasticity: The responsive germline.” *Progress in Biophysics and Molecular Biology* 111, 2013: 99-107.

Jablonka, Eva and Lamb, Marion J. *Epigenetic inheritance and evolution: The Lamarckian dimension*. Oxford: Oxford University Press, 1995.

Jablonka, Eva and Lamb, Marion. J. *Evolution in four dimensions: genetic, epigenetic, behavioral, and symbolic variation in the history of life*. Cambridge, MA: MIT Press,. revised edition, 2014.

Jablonka, Eva and Raz, Gal. “Transgenerational epigenetic inheritance: Prevalence, mechanisms, and implications for the study of heredity and evolution.” *Quarterly Review of Biology* 84, 2009: 131–176.

Johannsen, Wilhelm. “The genotype conception of heredity.” *American Naturalist* 45, 1911: 129-159.

Kappeler, Laurent and Meaney Michael J. “Epigenetics and parental effects.” *BioEssays* 32, 2010: 818–827.

Lamarck, Jean-Baptiste. B. *Zoological Philosophy: An exposition with regard to the natural history of animals*. Translated by H. Elliot. Chicago: University of Chicago Press, 1984 reprint of 1914 edition. First published as *Philosophie zoologique, ou exposition des considérations relatives à l’histoire naturelle des animaux*, Paris, Dentu, 1809.

Lamm, Ehud. “The metastable genome: A Lamarckian organ in a Darwinian world?” In *The transformations of Lamarckism*, Snait Gisssis and Eva Jablonka (eds), 345-355. Cambridge MA: MIT Press, 2011.

Lamm, Ehud. “The genome as a developmental organ.” *Journal of Physiology* 2014 (in press).

Lamm, Ehud and Jablonka, Eva. “The nurture of nature: hereditary plasticity in evolution.” *Philosophical Psychology* 21, 2008: 305-319.

Lehrman, Daniel S. “Critique of Konrad Lorenz’s theory of instinctive behavior.” *Quarterly Review of Biology* 28, no. 4, 1953: 337–363.

Loison, Laurent. “The notions of plasticity and heredity among French Neo-Lamarckians (1880 – 1940): From complementarity to incompatibility.” In *The transformations of Lamarckism,* Snait Gissis, and Eva Jablonka (eds), 67-76. Cambridge MA: MIT Press, 2011.

Mameli, Matteo and Bateson, Patrick. “Innateness and the sciences.” *Biology and Philosophy* 21:2, 2006: 155-188.

Mesoudi, Alex. *Cultural evolution: How Darwinian theory can explain human culture and synthesize the social sciences.* Chicago: University of Chicago Press, 2011.

Odling-Smee, John F., Laland, Kevin L., and Feldman, Mark W. *Niche construction: The neglected process in evolution*. Princeton, NJ: Princeton University Press, 2003.

Rechavi, Oded. “Guest list or black list: heritable small RNAs as immunogenic memories.” *Trends in Cell Biology*, 24, 2013: 212-220.

Robinson, Gloria. *A prelude to genetics*. Lawrence, KS: Coronado Press, 1979.

Semon, Richard. *The mneme*. London: Allen and Unwin, 1921. (translation of the 3rd 1911 edition by Louis Simon 1921).

Shapiro, James. A. *Evolution: A view from the 21st century*. Upper Saddle River, NJ: FT Press Science, 2011.

Sperber, Dan. *Explaining culture: A naturalistic approach*. Oxford: Blackwell, 1996.

Tavory, Iddo, Ginsburg, Simona and Jablonka, Eva. “The reproduction of the social: A developmental system approach.” In *Developing scaffolds in evolution, culture, and* *cognition*, Linnda Caporael, James Griesemer and William Wimsatt (eds), 307-325. Cambridge, MA: MIT Press, 2014.

Turner, Bryan M. “Environmental sensing by chromatin: an epigenetic contribution to evolutionary change.” *FEBS Letters* 585, 2011: 2032-2040 (*Epigenetics Special Issue*).

Waddington, Conrad H. *The strategy of the genes*. London: Allen and Unwin, 1957.

West-Eberhard, Mary-Jane. *Developmental plasticity and evolution*. Oxford: Oxford University Press, 2003.