Tastes of the Parents: Epigenetics and its role in Evolutionary Aesthetics

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ABSTRACT

Evolutionary Aesthetics is a bourgeoning and thriving sub-field of Aesthetics, the main aim of which is "the importation of aesthetics into natural sciences, and especially its integration into the heuristic of Darwin's evolutionary theory." Scholars working in the field attempt to determine through the adoption of an interdisciplinary research methodology whether and to what extent Darwinian evolution can shed light on our capacity to have aesthetic experiences, make aesthetic judgments (both of art and natural beauty), and produce literary, visual, and musical artworks. Notwithstanding Evolutionary Aesthetics' growing popularity in the past two decades, a look into the state of current research suggests a significant degree of haziness in the field from both epistemological-methodological and theoretical points of view. The main aim of the present paper is to make a first step towards a revision and extension of the discipline by assessing the role and potential of epigenetics in evolutionarily inspired aesthetic research. Epigenetics is among the youngest and most fascinating research fields in contemporary biology. But one of the most significant occurrences of the word "epigenesis" (the closest "ancestor" of contemporary "epigenetics") is in Immanuel Kant's third *Critique*, his aesthetic masterpiece. What might be the relationship between epigenetics and aesthetics? What is the role of epigenetic mechanisms in the development and functioning of aesthetic behavior in humans?

KEYWORDS

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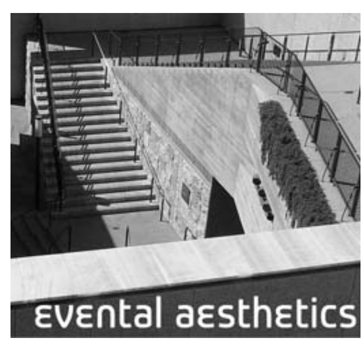

Biology and aesthetics: a twin birth in the eighteenth century[1]

The first uses of the words "aesthetics" and "biology" to indicate autonomous disciplinary branches within the humanities and the natural sciences respectively are traditionally traced back to the second half of the eighteenth century with Alexander Baumgarten on the one hand[2] and Theodor Georg August Roose[3] on the other — although Karl Friedrich Burdach, Jean-Baptiste Lamarck, and Michael Christoph Hanov are also given credit for coining the term "biology" more or less at the same time.[4]

The *simultaneous* birth of the two disciplines approximately two hundred and fifty years ago is not just a chronological coincidence. As Winfried Menninghaus argues, "From Alexander Gottlieb Baumgarten ... the founder of aesthetics as a separate branch of philosophy, to Kant and beyond, aesthetics is *molded* and *transformed* by this kind of overlap with biological discourses."[5] Aesthetics and biology have consistently interacted with each other since their first emergence, and Immanuel Kant's *Critique of the Power of Judgment* (1790), undoubtedly one of the milestones in the history of Western aesthetics, witnesses this mutuality in a most compelling way: whereas the first part of the work — "Critique of Aesthetic Judgment" — deals with the problems of beauty and aesthetic experience, the second part — "Critique of Teleological Judgment" — is devoted to the analysis of biological organisms, their fundamental properties, and the epistemology of life sciences.[6] Kant is persuaded of the relevance of his aesthetic theory for the understanding of biological phenomena. In recent years, a number of interpreters have also spoken in favor of an interpretation of the third *Critique* as a consistent whole, focusing on the continuity between its first and second parts.[7]

Evolutionary aesthetics: the state of the art

In the main works of Charles Darwin — the "father" of modern evolutionary biology and the first (together with Alfred Russell Wallace) to formulate a theory of evolution by means of natural selection — the aesthetic and the problem of beauty play relevant roles as well.[8] The *Origin of Species* (1859) is "aesthetically constructed," according to David Kohn;[9] and particularly in *The Descent of Man* (1871), Darwin frequently uses key concepts from philosophical aesthetics.[10] Drawing on Darwin's interest in aesthetics and the pervasive affinity between biological discourses and aesthetic reasoning, Evolutionary Aesthetics is today a bourgeoning and thriving sub-field of Aesthetics, the main aims of which are "the importation of aesthetics into natural sciences, and especially its integration into the heuristic of Darwin's evolutionary theory."[11] Scholars working in the field attempt to determine, through the adoption of an interdisciplinary research methodology, whether and to what extent Darwinian evolution can shed light on our capacity to have aesthetic experiences, make aesthetic judgments (both of art and natural beauty), and produce literary, visual, and musical artworks.

Despite the growing popularity of Evolutionary Aesthetics — we have witnessed an increasing number of publications in the past two decades — there is a still significant degree of haziness in the field. Firstly, as Dissanayake persuasively stated,[12] more than a few scholars in Evolutionary Aesthetics conceptualize the aesthetic in a vague and partial way, frequently overlooking the relevant differences between the terms "aesthetic" and "artistic,"[13] reducing the aesthetic to the mere expression of adaptive preferences of one thing over others and considering these preferences to be mainly sexual or environmental.[14] Secondly, today Evolutionary Aesthetics' research program — as opposed to Darwin's comparative approach — is mainly restricted to *Homo sapiens*: so far there hasn't been much research on aesthetic or proto-aesthetic behavior in nonhuman animals although a trans-specific perspective would be very helpful for understanding the evolution of aesthetic behavior in humans.[15]

Thirdly, although the vast majority of scholars in principle declare a deep commitment to the rules and models of interdisciplinary research programs,[16] current research in Evolutionary Aesthetics does not always live up to expected standards mainly because scholars still seem to refer to a simplified version of evolutionary theory, largely structured along the model and patterns of so-called *narrow* Evolutionary Psychology.[17] As a result, most studies in Evolutionary Aesthetics focus on *shared* responses among aesthetic perceivers, attributing these responses to hypothetical universal human adaptations rather than exploring individual differences between perceivers — for example the influence of individuals' biographies and experiences — on the development of their aesthetic behaviors and attitudes. This is a critical point: actually, what makes an object — a face, a landscape, a flower, or an artwork — interesting and fascinating from an aesthetic point of view is mostly its *specialness*, its *sudden* and *surprising* appearance to the individual perceiver as worthy of being looked at, touched, listened to, or tasted. As will become clearer in the following sections, throughout this paper we adhere to a largely Kantian perspective on the aesthetic and the beautiful: we understand the aesthetic as something that escapes subsumption under any pre-established rule, norm, or principle — including "biological" norms, i.e., in this context, beauty-determining genes — and still demands "a universal voice." As Kant puts it:

> If one judges objects merely in accordance with concepts, then all representation of beauty is lost. Thus there can also be no rule in accordance with which someone could be compelled to acknowledge something as beautiful. Whether a garment, a house, a flower is beautiful: no one allows himself to be talked into his judgment about that by means of any grounds or fundamental principles.[18]

As members of the species *H. sapiens* and as a result of the specificities and constraints of their perceptual devices, although humans certainly have some general sensorial inclinations and predispositions towards what they find beautiful or worthy of attention, nevertheless aesthetic experience proceeds along largely unpredictable and individual tracks. Individual differences matter, specifically that individual variation that Charles Darwin himself aimed to make sense of with his theory of evolution by means of natural selection.[19]

All things considered, and taking for granted that going further on the interdisciplinary path between biology and aesthetics is a promising goal, it seems that Evolutionary Aesthetics requires an in-depth revision from both theoretical and epistemological-methodological points of view.[20] With this in mind, the main aim of the present paper is to make a first, fairly restricted but significant step in this direction by assessing the role and potential of the notion of "epigenetics" for a reviewed and updated Evolutionary Aesthetics.

Epigenetics is one of the youngest and most fascinating research fields in contemporary biology,[21] "portrayed by the popular press as a revolutionary new science — an antidote to the idea that we are hard-wired by our genes."[22] As Bird argues, however, the word has "several meanings with independent roots."[23] So what is epigenetics? And what is — or could be — the relationship between epigenetics and aesthetics? One of the most significant occurrences of the word "epigenesis" — which, as we will see, may be the closest "ancestor" of contemporary epigenetics — is in Kant's third *Critique*, his aesthetic masterpiece. What then might be the role of epigenetic mechanisms in the development and functioning of aesthetic behavior in humans?[24]

From epigenesis to epigenetics: a look at the historical debate

The term "epigenetics" dates back to classical antiquity. In his *De Generatione Animalium*, Aristotle speaks in favor of an epigenetic view of embryonic development as opposed to preformationism. Whereas according to preformationism, all characters of the adult organism are simultaneously present in the fertilized egg and only need to grow into their full expressions, epigenesis interprets embryonic development as an incremental process that unfolds gradually over time and in close interaction with the environment. Asking whether the parts of the animal body "are all formed simultaneously — heart, lung, liver, eye, and the rest of them — or successively, as we read in the poems ascribed to Orpheus, where he says that the process by which an animal is formed resembles the plaiting of a net," Aristotle puts forward theoretical and empirical arguments (a result *inter alia* of his own biological research) to support the epigenetic view.[25] Aristotle's biology and his theory of epigenetic embryonic development exercised an extraordinarily deep influence on scientific debates in Europe until at least the seventeenth century. For example, William Harvey (1578-1657), the first scientist to describe extensively the systemic circulation of blood in animals (in his *Exercitatio Anatomica de Motu Cordis et Sanguinis in Animalibus* of 1628), explicitly referred to Aristotle in the embryological theory which appeared in *Exercitationes de generatione animalium* (1651), arguing that development proceeds as a cumulative formation and differentiation out of non-structured raw material.

At the end of the eighteenth century, while witnessing a renewed intensification of the debate between preformationist and epigenetic views of development, Immanuel Kant lent his support to Johann Friedrich Blumenbach's epigenetic understanding of embryonic development in the *Critique of the Power of Judgment*.[26] In turn, when Conrad Waddington (1905–1975) invented the term "epigenetics," he referred to the seventeenth- and eighteenth-century debate on epigenesis *versus* preformationism.[27] In his interpretation, preformationism and epigenesis were complementary.[28] But the traditional meaning of "epigenesis" — as it appeared in Kant and Blumenbach for instance — was renewed, partly retained and partly transformed, in light of modern genetics. In Waddington's words:

> We know that a fertilized egg contains some preformed elements — namely, the genes and a certain number of different regions of cytoplasm — and we know that during development these interact in epigenetic processes to produce final adult characters and features that are not individually represented in the egg. We see, therefore, that both preformation and epigenesis are involved in embryonic development.[29]

The conjunction between epigenesis and genetics resulted in the new field of *epigenetics*, originally defined by Waddington as "the branch of biology which studies the causal interactions between genes and their products, which bring the phenotype into being."[30]

Epigenetics today

In recent years, an increasing number of biological phenomena has been explained in terms of epigenetics, including seemingly unrelated processes such as paramutation in maize, the position effect variegation (PEV) in the fruit fly *Drosophila melanogaster*, and the "imprinting" of specific paternal or maternal *loci*, i.e., specific locations or positions of a gene, in the mammalian genome. In a broad sense, epigenetics is the bridge between genotype and phenotype, a set of molecular mechanisms that change the final outcome of a *locus* without changing the underlying DNA sequence.[31] More specifically, epigenetics may be defined as the study of any potentially stable change in gene expression or cellular phenotype that occurs without changes in Watson-Crick base-pairings of DNA.[32]

As is commonly acknowledged, Waddington's original approach to epigenetics — which he defined as the discipline dealing with the mechanisms of interaction between genes and their intra-cellular and extra-cellular surroundings to produce a phenotype — was still fairly genecentric. Trying to overcome Waddington's original formulation, contemporary "epigenetics gradually expands the range of molecular processes influencing the genome, thereby decentralizing the sovereign role of the genome."[33] It is not just genetics that matter for the development and functioning of an organism. Contemporary epigenetics mainly focuses (albeit not exclusively) on the transgenerational transmissibility of epigenetic modifications as a second, autonomous, non-DNA-based inheritance system.[34] No evidence of this idea of epigenetics as a non-genetic inheritance system can be found in Waddington's work.

However, in the 1970s and 80s, the terms "epigenesis" and "epigenetics" were extensively used by neuroscientists such as Jean Pierre Changeux,[35] Gerald Edelman,[36] and Stanislas Dehaene[37] in a sense somewhat close to Waddington's. Changeux's theory of the epigenesis of neuronal networks by selective stabilization of synapses is primarily intended to make sense of the interactions that take place between the brain and its physical, social, and cultural environments in the course of development. This theory therefore links variations in synaptic connections within the brain as well as variations in behavior between individuals with differences in the environments to which they are exposed. Changeux uses the two terms "epigenetics" and "epigenesis" interchangeably; but in the context of his synaptic discussion, "epigenesis" refers to the processes not directly under genetic control by which the environment affects the organization of synaptic connections in the postnatal period of brain maturation by either stabilizing or eliminating synapses, depending on the activity of the neural networks.[38] Synaptic epigenesis is of particular significance in the context of *H. sapiens*' brain development because, in Changeux's view, it enables social and cultural evolution as a result of the extraordinary extension of the postnatal period of brain maturation, a unique adaption with consequences of the highest relevance for our species. Inspired by Changeux's achievements, Stanislas Dehaene's recent work has shown that it is precisely thanks to epigenetic processes — processes that take place *over the course of individual development* — that we acquire highly cultural abilities such as reading and writing.

Changeux's and Dehaene's epigenetic theories on the postnatal development of the human brain have been fruitfully applied to aesthetics. Drawing on the idea that reading and writing are epigenetically acquired skills, Desideri has recently argued that human aesthetic behaviors — specifically our aesthetic preferences and rules of selection, which take the form of highly flexible, plastic, and context-dependent patterns of aesthetic orientation towards the world — stabilize in an epigenetic way, actively shaping the "inner landscape" of our aesthetic minds.[39] In other words, far from being encoded in our genome or the result of an innate psychological module inherited from our Pleistocene ancestors — as the vast majority of evolutionary aestheticians seem to claim, heavily relying on *narrow* evolutionary psychology — human aesthetic schemes seem to be actively *shaped and molded* as fruits of the experiences we undergo most frequently in our physical, social, and cultural environments.[40] Repeated rules of selection, habits, choices, and preferences for certain tastes, smells, figurative styles, and so on stabilize in the brain's epigenome throughout the individual lifespan, allowing a person to distinguish and exercise a judgment between beautiful and ugly things, between cuteness and awkwardness, and so forth.

The question is now: are these epigenetically stabilized aesthetic schemes and rules of selection also transgenerationally transmissible? In other words, is it possible to draw a connection between the *Waddingtonian* meaning of epigenetics as it has been taken up by Changeux and Deheane and applied to the brain — i.e., "epigenetics" as the interplay between the actions of genes and the experience unique to each individual — and the *molecular* meaning of epigenetics, where the latter is more focused on the transmissibility of epigenetic modifications? In order to answer this question, we need to look in more detail at the molecular level of epigenetic processes.

The regulative genome: the epigenome

Each mammal possess some hundreds of different cell types deriving from a single fertilized egg. The differentiation of each cell type is achieved not via changes in the organism's DNA sequence but through the coordination of subsets of genes.[41] In order to achieve the proper temporal and spatial regulation of these genes, the cell employs a set of epigenetic mechanisms, including DNA methylation and histone modifications.[42]

DNA methylation is the most commonly studied epigenetic mark in the mammalian genome. It consists of the transfer of a chemical group (methyl group) to a cytosine, which is one of the four DNA bases (the "rungs" of a DNA "ladder") in the DNA strand.[43] DNA methylation patterns should be faithfully inherited during mitosis, i.e., the process by which a cell divides into two identical daughter cells. The failure to maintain the correct methylation patterns leads to aberrant cell functioning, which is often observed in human neurodevelopmental defects; neurodegenerative, neurological, and autoimmune diseases; and cancers.[44]

Another form of epigenetic regulation is the modification of histones: the small proteins involved in "packaging" DNA within the nucleus of each cell into structural units called nucleosomes.[45] Biologists use the term "chromatin" to refer to the complex of DNA and the histones that package it. Histones can be modified in a number of ways by adding chemical groups,[46] which alter the histones' interaction with the DNA molecule in a manner that influences gene activity and DNA transcription. Roughly, DNA transcription is the process by which DNA is copied into messenger RNA during the production of proteins, which make up the structure of the body.[47] If, as Nessa Carey writes, we may conceive of our DNA as a script, then:

> DNA methylation represents semi-permanent additional notes ... histone modifications are the more tentative additions. They may be like pencil marks, that survive a few rounds of photocopying but eventually fade out. They may be even more transient, like Post-It notes, used very temporarily.[48]

Whereas the genome is all the DNA in the nucleus of a cell, the complex profile of DNA methylation and histone modifications is known as the epigenome.[49] The interplay between DNA methylation and histone modifications underlies the so-called "epigenetic memory" of each somatic cell. In the last decade, our understanding of the different epigenetic layers and their participation in gene expression has rapidly improved. Following Changeux's and Edelman's work on the epigenetic processes that shape the mammalian brain, today's researchers have identified the biochemical mechanisms underlying these modifications. For example, in a recent paper Tsigelny et al. used molecular genetics to map the expression patterns of the genes involved in synaptic epigenesis over the lifespan of a rat. They noticed that a huge change occurs at birth when many genes that were active in the embryo are switched off and thousands of other genes involved in the regulation of chromatin modifications become active as the animal goes through the dramatic experience of birth.[50]

Reprogramming genomes and inherited epigenomes: towards an environmental inheritance

As mentioned in the previous section, every mammal develops from a single cell, the zygote, which is made up of an egg and a sperm, each of which contains a haploid genome. When fertilization occurs, the genomes of both egg and sperm already have their own epigenetic "states," the characteristics of which are determined by the parents' epigenetic conditions.[51] This means that each zygote receives a male *imprinted* genome from the father and a female *imprinted* genome from the mother. After fertilization, these epigenetic marks are usually stripped off very quickly as the zygote undergoes the extensive reprogramming which allows a new, complex, multicellular organism to develop. However, during the past decade, a handful of studies carried out in mammals suggested that some *loci* can escape reprogramming and that epigenetic changes due to environmental stimuli can therefore be inherited, passing from the parents to at least one generation of offspring.[52] A key study of this sort of "environmental" inheritance showed that the exposure of pregnant female rats to an endocrine disruptor affected male fertility in subsequent generations and that these effects were associated with epigenetic changes in the germ line.[53] Other studies also reported the occurrence of an epigenetic transgenerational inheritance in the next generation,[54] but results were very controversial about the occurrence of effects through more than one generation.[55] Transgenerational inheritance of epigenetic marks has also been reported as a consequence of the exposure of male parents to stresses.[56] For example, offspring of male mice that had been fed a low-protein diet showed changes in the expression of genes involved in cholesterol biosynthesis and DNA methylation.[57] Similarly, it has been suggested that abnormal phenotypes in humans, even those caused by stressors such as low nutrient intake, might be passed on for many generations through epigenetic marks on the gametes of one parent.[58]

At present the most remarkable evidence for the possibility of epigenetic inheritance in the mammalian genome is the study conducted by Brian Dias and Kerry Ressler, who showed that when mice are taught to fear an odor, both their offspring and the next generation are born with the fear of the same smell. Dias and Ressler modeled an ecologically relevant exposure by pairing an odor with mild foot shocks, thereby training mice to fear the odor of acetophenone — which is recognized by the receptor Olfr151 — and then measured the behavioral response to this odor in the offspring. As a control, they used a different odor (propanol) that was not paired with shocks, which acts on a different receptor, Olfr6. The authors found that when mice were trained with acetophenone, their offspring as well as the subsequent generation showed a heightened startle response in the presence of acetophenone but not in the presence of propanol. When ancestors were instead trained with propanol, their descendants were fearful in the presence of propanol but not acetophenone. In the molecular analysis, the authors found that the gene coding for Olfr151 (but not Olfr6) was differentially demethylated when the mice were trained to fear acetophenone in respect to the control odor. This is an exquisite demonstration that DNA methylation in sperm can be targeted in specific *loci* in response to a specific exposure and that sperm's methylation signature is transferred to the next two generations, indicating that the methylation signature evades erasure at both the primordial and post-fertilization phases. Dias and Ressler also provided strong evidence that these changes are even transmitted through the germ line during *in vitro* fertilization. Sperm from a specific odor-conditioned mouse resulted in the transmission of an anatomical feature: the increased size of odor-specific glomeruli in the offspring's olfactory bulb.

Dias and Ressler's most intriguing conclusion is that although the environmental stimulus does not access the genome directly, it induces *behavioral* changes that are passed down. The authors' data suggests that epigenetic, transgenerational, germline-transmitted adaptations to threats occur in a predictable and organized fashion similar to that of other physiological responses. Hence it seems that there are mechanisms which can translate adult experience and environmental exposures into inherited phenotypes without affecting the genotype. And it seems we must rethink our understanding of phenotypic adaptation as well as entrenched ideas on how species respond to new challenges. The research we have described — which unravels the molecular link between experience and the gamete epigenome and explores the relationship between gametes and the development of behavioral brain circuitry in response to experience — poses a formidable challenge to several other research fields, suggesting that epigenetics may serve as a link between apparently distinct disciplines from molecular genetics[59] to psychology[60] and aesthetics.[61]

Epigenetics and aesthetics: overcoming narrow evolutionary psychology

Mammals seem to be equipped with mechanisms that respond specifically and efficiently to novel experiences, such as odors and predator threats, and transmit this information effectively to their offspring without the need for the typically slow process of natural selection. Even if the molecular machinery involved in such a process is unclear, the germ line can serve also as a vector for transmitting information from adults across generations, making future studies necessary to determine how common these environmental-based epigenetic changes are and which types of "knowledge" can be fixed into our genome through epigenetic marks. From the perspective of Evolutionary Aesthetics, although we know that the human brain does not possess distinct regions, genes, or gene complexes which are specifically responsible for processing and decoding aesthetic stimuli,[62] it is possible that such stimuli are processed by brain areas whose molecular pathways, structure, and functioning are modified at an epigenetic level by the environment.[63]

In the last two decades, a considerable amount of literature has been published on the emergence and functioning of human aesthetic behavior, including preferences, rules of selection and tastes. Evolutionary aestheticians have suggested that *Homo sapiens* has evolved general standards of beauty directly derived from the fitness value of the opposite sex and environmental aesthetic preferences correlated with survival chances in specific habitats.[64] The mainstream position in Evolutionary Aesthetics is that our aesthetic preferences are in a certain sense "encoded" in our brains as a legacy of the adaptive aesthetic choices (mate choices and habitat choices) made by our ancestors in the Pleistocene era.[65] More than a few scholars in Evolutionary Aesthetics have argued for the existence of a proper "aesthetic module" innate to the brain, carefully forged by natural selection over the course of evolution.[66]

However, given the work of Anjan Chatterjee and others, the existence of a brain module devoted to aesthetics seems unlikely.[67] In that case, a key concept for a more effective understanding of the emergence, functioning, and inheritance of our aesthetic behavior may be epigenetics. On the one hand, following Changeux and Dehaene, it seems reasonable, lacking any evidence of aesthetic genes or aesthetic modules innate to the human brain, to conceive the development of our aesthetic customs as a plastic and incremental process that takes place over time. In this sense, it seems that our aesthetic dispositions are in no way fixed at birth (even though of course they are constrained by our evolutionary history as a species). From this perspective, brain epigenetics can be used to account for the extraordinary variability in human aesthetic behavior.

On the other hand, however, following the most recent research on the transmissibility of epigenetic modifications from the parents to the offspring and beyond, we can explain how at least some of the epigenetically stabilized preferences and schemes may be inherited and propagated, leading to changes in aesthetic behavior over generations. From the latter perspective, epigenetics could provide an interesting window onto the relationship between the unique components of aesthetic schemes and shared predispositions constraints. In other words, epigenetics could provide an analysis of how aesthetic experience — in its multifaceted declinations and components, both local and shared — structures itself over the course of an individual lifetime. After all, the word "aesthetics" comes from the Greek "*aesthesis,*" which means "sensation," "perception"; and as Dias and Ressler showed, sensorial preferences and repulsions (olfactory ones at least) are developed and inherited *in an epigenetic way* in mammals. Their study may be a starting point for future research on the epigenetic development and transgenerational transmission of (proto-)aesthetic rules and schemes in humans.

Although the molecular nature of inherited epigenetic marks is still unknown in most cases, recent innovative technologies make this problem tractable, enabling us to fully characterize epigenetic marks across the entire genome. However, even if DNA methylation is still the most popular candidate for the molecular basis of transgenerational epigenetic inheritance via gametes, future studies should be focused not only on epigenetic marks but also on the processes and factors that may bring brain-induced epigenetic changes into gametes. For the latter, microRNAs and RNA piwi-interacting RNA (piRNA) seem at present to be the best candidates.[68]

Stephen J. Gould argued that "human cultural evolution, in strong opposition to our biological history, is Lamarckian in character. What we learn in one generation, we transmit directly by teaching and writing."[69] He was right, but it is also possible that we transmit at least a part of what we learn in one generation — for instance, aesthetic schemes and rules or some of their basic components — via our inheritable epigenome: a second inheritance system that functions alongside cultural transmission.[70]

Towards a new evolutionary aesthetics

At a conference held at the University of Uppsala in March 2015, epigenetics was presented as the "meeting point between nature and nurture," the intersection zone between biology and culture.[71] It is in consideration of its "hybrid" nature — on the boundary between organism and environment, genes and the world, internal biological dispositions and external environmental influences — that epigenetics may play a significant role in a renewed and updated Evolutionary Aesthetics.

Modern and contemporary explanations of human aesthetic experience have traditionally oscillated between two conflicting foci: a subjective understanding (Humean for instance), claiming that beauty is not a quality of things themselves but exists merely in the mind which contemplates them; and an objectivistic understanding, according to which beauty should be conceived as a property of objects, which compel people to agree on their aesthetic value. Neither of these explanations fully accounts for the complexity of aesthetic experience. Although there can obviously be no aesthetic experience without a subject — for the simple reason that the aesthetic is a certain kind of relation between the individual subject and the world — and although aesthetic tastes vary significantly between individuals, it seems that under certain conditions, we tend nevertheless to converge upon the same aesthetic values and judgments. Why and how is this possible?

Answering this question requires getting rid of traditional dichotomies — such as nature/culture, universalism/relativism, and objectivism/subjectivism — the overestimation of which has created most of the pitfalls that aesthetic theory has fallen into over the course of its history. In Evolutionary Aesthetics, the dichotomy between an "innate" account (i.e., in this context, based on genes) and the "externalist" reduction of the aesthetic to a matter of cultural differences is, as we have been suggesting in this paper, a *misleading* dilemma.

Undercutting dualisms, particularly the dualistic view of nature *versus* culture, was one of the main features of John Dewey's philosophy, particularly his aesthetics. Largely inspired by Charles Darwin's biological views, Dewey always regarded the live creature interacting with its environment as the starting point of his philosophical investigations. In this sense, as he argued in *Art as Experience* (1934), Dewey understood the emergence and unfolding of aesthetic experiences in humans as a strongly "relational" process, a matter of inherent interaction and perceptual trade between the organism involved and its surroundings. According to Dewey, the environment with which the organism interacts and in relation to which aesthetic experience unfolds is both physical and socio-cultural. Nature and culture are so fully integrated, Dewey says, that in the aesthetic experience, each disappears. In *Art as Experience,* we find the following general definition of experience, which also applies to the specific case of human aesthetic experience:

> Experience is a matter of the interaction of organism with its environment, an environment that is *human as well as physical, that includes the materials of tradition and institutions as well as local surroundings*. The organism brings with it through its own structure, *native and acquired*, forces that play a part in the interaction ... [E]very experience is constituted by interaction between "subject" and "object," between a self and its world.[72]

There is no room for dichotomies in Dewey's approach. In perfect syntony with Darwin's views, Dewey sees culture as the result of a continuous and cumulative interaction with the environment. Both culture and nature contribute to the unfolding of the aesthetic experience to such a point that the distinction between the two concepts seems to dissolve. As Dewey remarks, the dichotomies between nature and culture, the mind and the world, subject and object collectively constitute "a bias, and one, which, most unfortunately, is just the one most fatal to aesthetic understanding."[73] Dewey's view could not be closer to the recent perspectives emerging from the field of epigenetics, which show how our "culture," defined in a broad sense, leaves a physical trace on our (epi-)genome — i.e., on our "biological nature" — modifying its phenotypic expression and thus undercutting the dichotomies between genotype and phenotype, biology and culture. Indeed, epigenetics provides a new, effective lens through which we can appreciate from *within* evolutionary theory this synergy between the organism and its physical, social, cultural environment.

Recent studies have suggested that the relative emotional impact of certain artistic styles — i.e., the fact that certain figurative styles or sound patterns trigger stronger emotional responses than others — may be interpreted in light of "epigenetic memory," in which associations between experiences and emotions are formed.[74] In the same way, the stabilization of individual preferences and the sedimentation of aesthetic patterns within a population may be understood as a case of epigenetic transmission with the potential of reversibility. Aesthetic preferences and behaviors are thus neither genetically inherited nor solely the result of cultural transmission but the fruits of interactions between the organisms and their surroundings. Other studies discuss epigenetic mechanisms which influence the production and secretion of hormones and neurotransmitters (e.g., dopamine) as potential foundations of artistic creativity and perception.[75] The way seems to be open for a broader interdisciplinary research program working on the boundary between philosophical aesthetics, psychology, evolutionary biology, and molecular biology.

Although Dewey was very critical of Kant's aesthetics, describing Kant's theory as "a thoroughly anemic conception" of the arts and aesthetic experience, the considerations we have developed so far on the basis of the most recent research in epigenetics point conclusively to Kant.[76]

As we briefly discussed in the introduction, Kant's *Critique of the Power of Judgment*, while inaugurating the new course of aesthetics as an autonomous discipline within the broader field of philosophy, simultaneously attests to an intrinsic intertwinement between aesthetic reasoning and biological reasoning. Kant claims that the same transcendental, regulative principle — the principle of purposiveness —

grounds both our understanding of biological entities and our aesthetic judgments.[77] In other words, when dealing either with organisms or with beautiful objects (whether the latter are natural or artistic), the human mind works more or less according to the same principles.

Moreover, as Elisabeth Schellekens has remarked, Kant provides a clearly "relational" account for the aesthetic experience, overcoming the object/subject dichotomy.[78] Despite his emphasis on the "uniqueness" of the interaction between the human mental faculties which occurs during aesthetic experience — the "free play" of imagination and understanding — Kant does not claim that the aesthetic resides solely in the subject of experience.[79] Rather, the free play *within* the subject is triggered by something in the *object's* character, namely its form. In other words, according to Kant, as a consequence of the absence of "rule[s] in accordance with which someone could be compelled to acknowledge something as beautiful," aesthetic judgments must be grounded in the subject's experience of pleasure.[80] Nevertheless, such judgments demand a "universal voice" on the basis of a shared common sense.[81]

In one of the most fascinating passages of his third *Critique*, Kant writes that the experience of beauty is *ein glücklicher Zufall*, "a happy accident": the experience of beauty is contingent, singular, and reversible, but it demands objective agreement.[82] As a new facet of the intertwinement between biology and aesthetics which has its roots in the history of both disciplines, epigenetics may help us understand how the exemplar contingency and singularity of beauty emerge and how the perspectival experience of the individual person contributes to the emergence of shared schemes and preferences at the intersection between our biologically evolved nature and the environment and culture in which we are embedded.

Notes

1 The authors have both contributed to the conception and design of the entire work; Mariagrazia Portera is responsible for paragraphs 1, 2, 3, 4 (second part), 7 (first part), 8; Mauro Mandrioli is responsible for paragraphs 4 (first part), 5, 6, 7 (second part). We would like to thank Alessandro Minelli for his insightful comments that helped improve the manuscript.

2 See Alexander G. Baumgarten, *Aesthetica/Ästhetik* (Hamburg: Felix Meiner Verlag, 2007).

3 Theodor Georg A. Roose, *Grundzüge der Lehre von der Lebenskraft* (Braunschweig: Christian Friedrich Thomas, 1797).

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