

PERSPECTIVES

Transgenerational epigenetic inheritance and social responsibility: perspectives from the social sciences

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Abstract

Research in environmental epigenetics explores how environmental exposures and life experiences such as food, toxins, stress or trauma can shape trajectories of human health and well-being in complex ways. This perspective resonates with social science expertise on the significant health impacts of unequal living conditions and the profound influence of social life on bodies in general. Environmental epigenetics could thus provide an important opportunity for moving beyond long-standing debates about nature versus nurture between the disciplines and think instead in 'biosocial' terms across the disciplines. Yet, beyond enthusiasm for such novel interdisciplinary opportunities, it is crucial to also reflect on the scientific, social and political challenges that a biosocial model of body, health and illness might entail. In this paper, we contribute historical and social science perspectives on the political opportunities and challenges afforded by a biosocial conception of the body. We will specifically focus on what it means if biosocial plasticity is not only perceived to characterize the life of individuals but also as possibly giving rise to semi-stable traits that can be passed on to future generations. That is, we will consider the historical, social and political valences of the scientific proposition of transgenerational epigenetic inheritance. The key question that animates this article is if and how the notion of transgenerational epigenetic inheritance creates new forms of responsibilities both in science and in society. We propose that, ultimately, interdisciplinary conversation and collaboration is essential for responsible approaches to transgenerational epigenetic inheritance in science and society.

Key words: transgenerational epigenetic inheritance; epigenetics of social adversity; social responsibility; race; class; gender

Introduction

Environmental epigenetics is a burgeoning life science discipline that is receiving significant attention not only from researchers within biology and biomedicine, but increasingly also from the social sciences [1–4]. For many social scientists who study the social and political dimensions of the biological sciences, environmental epigenetics represents an important opening of biological

reasoning towards accounting for the influence of the social environment on body and health on the molecular level. Such perspectives were mostly absent from genetic views on basic biology and disease aetiology [5]. Researchers in the social sciences often viewed such gene-focused models critically because they seemed to have little purchase on better understanding the unequal distribution of health and illness in society and tended to reduce such phenomena to the mere expression of underlying genetic traits.

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Gene-centric explanations were also significantly at odds with expertise in the social sciences that detailed the significant health impact of unequal living conditions and the profound influence of social life on bodies in general [6]. In contrast, research in environmental epigenetics that explores how environmental exposures and life experiences such as food, toxins, stress or trauma might shape trajectories of human health has been perceived to resonate with social science perspectives on the relationship between body, health and environment. Environmental epigenetics is understood as providing an important opportunity for possibly moving beyond longstanding debates about nature versus nurture between the disciplines and thinking instead in 'biosocial' or 'biocultural' terms across the disciplines [7–11]. Perspectives on the human body as "interconnected, plastic, permeable and responsive to changes in its surroundings" [12] that are currently emerging in environmental epigenetics, as well as in related fields such as social neuroscience, nutrigenomics or behavioural microbiomics [13] could thus create new innovative links between biology and social science and serve as starting points for the interdisciplinary exploration of the complex entanglements of social life and biological processes.

Yet, beyond enthusiasm for the novel interdisciplinary opportunities afforded by convergent perspectives in biology and the social sciences, it is crucial to also reflect on the scientific, social and political challenges that a biosocial model of body, health and illness might entail. In this paper, we thus contribute perspectives from the history of science (Meloni) as well as from the social studies of science (Müller) on this emergent conception of the body as biosocial and explore its social and political implications. We will specifically focus on what it means if biosocial plasticity is not only perceived to characterize the life of individuals but also as possibly giving rise to semi-stable traits that can be passed on to future generations. That is, we will consider the historical, social and political valences of the scientific proposition of transgenerational epigenetic inheritance. The key question that animates this article is if and how a possibly emerging notion of transgenerational epigenetic inheritance could create new forms of responsibilities both in science and in society and how these responsibilities could be addressed productively.

We will start by discussing historical links between a biosocial conception of the body and politics. Our aim is to show that the notion of a plastic body open to environmental and social influences was prominent in many biological and medical theories before the rise of modern genetics. Drawing on historical examples, we will highlight that notions of a plastic human biology were historically entangled with a wide range of political positions including, unfortunately, perspectives that viewed some groups in society as inferior to others, such as racist, sexist, classist or eugenic positions. We present these historical examples as cautionary tales that remind us that perspectives that emphasize a biosocial plasticity of the human body are not only able to support a greater awareness of social justice questions with regard to health and illness, but can also contribute to positions that further stigmatize and discriminate against socially disadvantaged and vulnerable groups.

In a second step, we will then explore if findings from contemporary environmental epigenetics also hold the potential to both empower and stigmatize individuals and groups that might appear as negatively affected by environmental exposures. We will review how notions of health risks across generations change as we move from a genetic to an epigenetic model of body, health and illness, and discuss which forms of scientific

and social responsibility might emerge with notions of transgenerational epigenetic inheritance. We propose that, ultimately, interdisciplinary collaboration is essential for addressing these challenges responsibly in science and society.

Throughout the text we will use the term biosocial plasticity to denote notions of a body that is open to transformation in response to outside influences. We do so for two reasons. First, we want to be specific about what kind of plasticity of the body we are referring to when plasticity is spoken of in this text. While plasticity can also denote processes of developmental variability (e.g. in stem cells) that are not necessarily related to exposures and experiences in the environment outside the body, the type of biological plasticity that we are discussing denotes phenotypic changes that occur in response to environmental cues. Second, working with the term 'biosocial plasticity' is an explicit attempt to bridge biological discourse, which more often uses the term plasticity to speak about gene-environment interactions, and social science discourse, where the term 'biosocial' has gained momentum as a shorthand for denoting the complex interplay between biological matter and sociocultural processes. By adding 'biosocial' to the more common biological terminology of 'plasticity' we aim to contribute to possibly building a mutually accessible yet exact vocabulary across the two discourses to further potential collaborations.

Historical Perspectives on Biosocial Plasticity and the Inheritance of Acquired Traits

Epigenetics poses a number of important social and ethical questions that are far from being just theoretical or abstract. For instance: If epigeneticists claim that when I am eating, "I am eating for two" [14], implying that a future parent's diet has an impact on the offspring's wellbeing on the level of gene expression, how does this change notions of responsibility and risk, normality and pathology [15]? If the genome can be damaged through smoking or optimized through exercise, will we not monitor people's lifestyles more closely, thereby "creating ever more moralised domains and responsibilities" for health and illness [16]? And whose lifestyles will be monitored in particular? Not all bodies are considered equally permeable, and the degree of attention towards how the environment affects the body appears highly gendered, particularly when it comes to hereditary effects. If it is in the womb that many epigenetic effects are "programmed", should greater attention and more obligations be placed on pregnant women [17]? Might epigenetic knowledge indeed increase the momentum of current pre-conception health care initiatives that extend the timeframes of policing women's behaviour even into periods far before pregnancy [18]? And how might epigenetics impact the social perception of groups and individuals who have been subjected to negative exposures such as trauma, war or famine? Will they be perceived as harmed and therefore in need of reparation? Or will they be considered as damaged and possibly marked for life? [19]?

Compared to 20th century debates based on notions of mostly stable and unchanging genes, these questions are fairly new, while what is entirely new is the knowledge of the molecular mechanisms that now connect external exposure (toxins, food, stress) to changes in genomic expressions. However, the notions that bodies can be profoundly altered by environmental cues is much older and was pervasive in Western and non-Western medicine before and during the rise of the modern biomedical body that is conceived as much more separate from its

environment. Environmental themes in medical thinking have existed since the time of the first Hippocratic school, when food, winds or waters were deemed key factors in shaping not only individual bodies but whole group traits and characteristics [20]. Even the notion of the inheritance of acquired characteristics and the interplay of nurture and nature in shaping heredity, often attributed to Lamarck, are actually clearly outlined in ancient medical writings [21]. In the Hippocratic “On Airs, Waters and Places” we find, for instance, the description of a mythical population, the Macrocephaly (literally: the large-headed ones), whose unusually elongated skulls were considered the result of “usage”, that is, the effect of the local practice of fashioning the head with bandages to alter its original form. However, as the Hippocratic text notices, after the first generations had applied these efforts on the head, at a certain point “force” was no longer necessary as “nature cooperates with usage” so that the acquired trait is transmitted “naturally”—that is, “usage has nothing to do with it” (*On Airs, Waters, Places*, part 14 in [20], p. 161).

Our delving into historical examples to contextualize current developments is not to suggest that one can conflate all these different historical examples of thinking with biosocial plasticity into a smooth continuity of thought before and after the rise of modern biomedicine. Hippocratic themes in the ancient world were fairly different from those of eighteenth century Britain [22]. The inheritance of acquired characters in ancient authors lacked, for example, the creative power of the organism that some neo-Lamarckian authors speculated about [23]. It is also not the goal of this article to discuss continuities and differences between different forms of thinking with biosocial plasticity across history in minute detail. However, when it comes to the sociological implications of understanding the human body as deeply open to environmental influences, the ethical and political concerns raised by these in other respects indeed differing ideas also offer a number of important continuities. They do so particularly with regard to how they address social categories such as gender, race and class, as we shall argue in the two following sections.

Impressionable Mothers

A stunning example of such kinds of continuities is the notion of maternal impression, which has stubbornly crossed different cultural and medical frameworks from ancient and early modern biology into the early twentieth century. ‘Maternal impression’ describes the idea that the thoughts, emotions and experiences of a pregnant woman could ‘imprint’ on the physiology of her unborn child [24–27]. Stories of maternal imprints as a result of observing events, objects, statues and people are widespread in ancient and early modern medicine. Many stories describe the effects of experiencing or witnessing a traumatic event (as we would put it in our contemporary terminology) on a pregnant woman, such as being present at a public execution or encountering a wild animal. Maternal biology was considered plastic enough to be impressed by the power of the emotions and thoughts engendered by these disturbing events. This in turn would affect the physiology of the developing foetus. This is why the doctrine of maternal impressions often came with specific prescriptions regarding the behaviour of pregnant women. A popular medical textbook in the 18th century, for example, recommended that “[a pregnant woman] ought to discreetly suppress all anger, passion, and other perturbations of mind, and avoid entertaining too serious or melancholic thoughts; since all such tend to impress a depravity of nature

upon the infant’s mind, and deformity on its body”, (Maubray, 1724, cited in [28], p. 42). The idea of maternal impressions and the plastic and mediating nature of female bodies was thus intimately connected to moral prescriptions about how women were supposed to conduct themselves in order to ensure the well-being of their offspring.

It is telling that as recently as 1915, an unnamed editor of the *Journal of Heredity*, a key publication of the genetics (and eugenics) movement, felt the urgency to contrast the superstitious nature of “what is commonly called maternal impression, prenatal culture, ‘marking,’ and so on” with emerging genetic ideas of inheritance. It is disconcerting, the editor claimed, that we still find nowadays in popular science publications on baby care claims such as that “[t]he woman who frets brings forth a nervous child. The woman who rebels generally bears a morbid child.” Or that “self-control, cheerfulness and love for the little life breathing in unison with your own will practically insure you a child of normal physique and nerves.” The unsigned editorial had two main goals. One was scientific: showing that most of the changes to the embryo occur at a period when the mother is still unaware of her pregnancy and in such a general form that she is unable to intervene directly in any way. However, there was also a more subtle and complex moral aim: not only to free mothers from the burden of a moralistic responsibility “which [they] need not bear”, as the editorial states, but, more substantially, to avoid any distractions from the eugenic movement and its key messages of hard heredity. From the perspective of a truly selectionist approach to eugenic matters, a focus on prenatal life that attributed to mothers not only the burden but also the power of shaping heredity through their behaviours was just a waste of energy [29]. The text is still worth reading today as an interesting conundrum regarding the often undecidable back and forth between moral assumptions and scientific claims, and the ambiguous positioning of notions of both biological fixedness and biosocial plasticity with regard to gender and heredity. Was a genetic view of heredity a liberation for women from an unjustified responsibility to the foetus? Or was it instead an impoverished view of pregnancy that subtracted agency from the maternal body?

The notion of maternal impressions and its history illustrate how scientific discussions about the role pregnancy played in heredity were also always debates about the social role of mothers and their moral obligations towards their unborn children. However, at the same time, it becomes visible that at any point in history, including today, social conventions and norms of motherhood and maternal responsibility have also shaped scientific questions and research designs in the first place, making some research questions more likely than others [4, 30]. Scientific and social understandings of the role of maternal bodies and lives for the health and well-being of their offspring hence are always co-produced and never independent of each other.

Biosocial Plasticity and the History of Racism

Historically, notions of biological plasticity have not only played a role in explaining differences between individuals—for example between those whose mothers had witnessed traumatic events and those whose had not—and in gendered notions of morality, but they were also used to explain so-called ‘racial’ differences. Especially in ancient and early modern times, claims about the assumed ‘superiority’ of certain human groups were not necessarily considered to be the result of a fixed and invariable heredity (what we would consider today as genetic

inheritance), but as consequences of the accumulated effects of climate and location on body and mind. Often, populations living in tropical areas were viewed as inferior because they were considered to have been rendered 'lazy' or 'luxurious' by the effects of a constant hot and humid climate [31]. Many authors before the 17th century considered that any of these so-called 'racial' traits could be, albeit with effort, changed through relocation to another place, as humans were considered to—like plants—change their characteristics when moved to another terrain [32]. This connection of place and physical traits was, at that time, both a source of anxiety (the fear of degeneration in hotter climates and through specific foods) and hope (the chance of regeneration through the 'right' climate and the 'right' foods), particularly among the colonizing nations. These anxieties informed, for example, colonial practices of rejecting indigenous lifestyles and foods [33].

While, in theory, biosocial plasticity was considered to give rise to both degeneration or regeneration, in colonial contexts, plasticity was mostly understood as a source of degeneration and served to legitimize claims of European superiority. This biased outcome was partially a product of theories that proposed that the colonized were simultaneously *more and less* plastic than the colonizers. This strategic usage of biosocial plasticity in colonial contexts remained an important trope in the nineteenth century, when other views of the plastic body and heredity, for instance Lamarckism, took shape. The colonized were considered more plastic because they were deemed more at the mercy of their physical environment than colonizing Europeans; at the same time, they were considered as less responsive to attempts at regeneration. Even non-Lamarckians adopted this language. For example, the evolutionary theorist Alfred Wallace claimed that the "remotely ancient representatives of the human species"—which is how he referred to the indigenous inhabitants of colonized lands—"were in their then wild state much more plastic than now to external nature" [34, p. 42]. That means that while plasticity was referred to as the origin of 'racial' inferiority, plasticity as a potential source of acquiring equality was, at the same time, denied [35]. The idea that the colonized had, in the past, lost all their potential for change, e.g. in response to beneficial living conditions, because of acquired habits that had become engrained into their bodies was one of the key themes of nineteenth century plasticity-based forms of racism [19]. Here we find a two-step process of argumentation that is characteristic of how notions of biosocial plasticity were historically used to further racist and eugenic arguments: first, by attributing to distinct groups in society a specific vulnerability to outside influences. Second, by arguing that these groups have been exposed to negative influences in ways that render intervention mostly meaningless because the attributed 'biological damage' is framed as hardly reversible. This sequence of arguments illustrates the profoundly ambiguous relationship between notions of biosocial plasticity and processes of racialization. On the one hand, they contributed to a weakening of notions of racial stability and inborn essences through which modern racist thought has prevalently proceeded. On the other hand, they have contributed to the ongoing racialization of social groups and the re-inscription of racial categories. They have done so, in particular, by arguing that certain human groups have shared a common social experience that has hardened into a biological reality which now defines their embodied identity [36]. A closer look at these historical formations also teaches us to carefully consider how contemporary biosocial research could both destabilize and reaffirm notions of race.

Degeneration, Not Regeneration

Another important point to bear in mind in current discussions about biosocial research is a curious asymmetry between the focus on positive and on negative environmental effects. With the exception of a few studies that highlight the positive effects of enhanced environments or the possibility of resilience [37], biosocial research today mostly focuses on the vulnerability of certain individuals and groups to social and environmental harms [19]. This imbalance is certainly related to the need to argue for research funding, which might privilege the study of negative effects as part of the study of disease aetiology. However, at the same time, history casts a long shadow and we cannot understand the current focus on harm over improvement as entirely separate from historical precursors. Indeed, historically, discussions about the plasticity of heredity were much more strongly characterized by a focus on *degeneration* [38] than explorations of *regeneration*. This is, for example, obvious in the case of maternal impressions, where the womb was typically seen as the bearer of a potential misfortune for the foetus, rather than a possible source of improvement. "The wrong maternal passions could produce monsters, but there is no legacy, from this era, of thinking that the right maternal passions could improve the virtue, health, or form of the fetus beyond what it would attain if it merely remained uninfluenced and uncorrupted" [39, p. 22–23]. However, the uneven focus on degeneration was a much more widespread bias in perspective. Especially from the early nineteenth century onwards, doctors, biologists and social reformers studying the relationship of environment, body and inheritance mostly focused on the *pathogenic* qualities of specific environments that were considered to render their inhabitants socially irredeemable and hence a lesser category of citizen over the course of generations (see Meloni 2016 for a detailed elaboration on this topic) [19]. Degenerationists believed that a pathogenic environment acted as a so-called "racial poison", that is, "a substance, of whatever nature, which injures the offspring through the parent or parents, and is thus liable to *originate* degeneracy in healthy stocks" [40]. There were many conditions that were regarded as such poisons and which were assumed to weaken the germ-line: the overpopulated metropolis of the industrial revolution, particularly its slums; alcohol; prostitution; sexual diseases. Degenerationists proposed that, if biological heredity is open to environmental influences, then the present germline of historically disadvantaged social or ethnic groups would reflect the "debilitating effects of having lived for centuries under deprived conditions", as a critic of plastic heredity put it in the context of Soviet debates on eugenics in 1920s (Filipchenko, quoted in [19]). From this perspective, the biological effects of accumulated disadvantage explained the 'incapacity' of various non-White or other socially disadvantaged groups, such as the "undeserving poor" [41], to catch up with the benefits of societal progress. Vicious cycles of social disadvantage were thus explained as an effect of biology, not social oppression, discrimination and stigma.

A very obvious champion of this argument was the Belfast-born Neo-Lamarckian embryologist Ernest William MacBride (1866–1940; see [42]). A prominent figure in the British Eugenics movement, MacBride relied on notions of environmental effects to create a 'racial' typology in which Northern 'races' were at the top. 'Races' for MacBride were to be understood as "the embodiment of a whole hierarchy of memories." Since they "acquired their characters as a reaction to their different environments" [43, p. 241], as MacBride claimed, the Nordic race learnt its "indomitable courage" in the struggle against the

“bleak climate of their old home” [43, p. 243]. Conversely, the Mediterranean race, formed in a less invigorating climate, was “characterized by a mercurial temperament, prone to quarrel and quick to take revenge.” Africans, of course, were “thoroughly tropical animal[s]” [43, p. 242, 244–245]. These debates were far from being just speculative: these racial stereotypes were meant to offer a platform to shape social policy and public health strategies.

Epigenetics and the Emergence of New Scientific and Social Responsibilities

Why is it important for the epigeneticists of today to be aware of these histories of biosocial plasticity, heredity, public health and social policy? With the emergence of environmental epigenetics, arguments about the plasticity of the body and the effects of environmental exposures and social experiences are acquiring new valence today. An emergent “biology of social adversity” [44] is investigating the multigenerational effects of toxic exposures, famine, violence and trauma. Related fields, such as the Developmental Origins of Health and Disease (DOHaD; [45]), work to increase the scientific and public awareness of emergent arguments about the importance of parental preconception health for the well-being of future generations and for public health more broadly. Initial translations into policy campaigns, such as the First 1000 Days initiatives [46], point to the possibly significant policy impact of these knowledge claims. Thus, it is pivotal for researchers in environmental epigenetics to understand that their work is inevitably embedded in a social and political world where conceptualizations of the body as plastic and malleable by its biosocial environment have a longstanding and complex political legacy that includes reinforcing stigmatization and discrimination against socially vulnerable groups. At the same, we should inquire if concepts and models that have been developed in the second half of the 20th century in order to address social, ethical and political dimensions of genetic research might need to be readjusted to fit the novel forms of risk and responsibility that epigenetic perspectives on body, health and illness bring about. The proposition of transgenerational epigenetic inheritance in particular might create a demand to rethink notions of responsibility and justice [47] across generations as it suggests novel timescapes of exposure and experience that interlink “multigenerational lives—past, present, and future—” [48, p. 17] in complex ways.

From Genetic to Epigenetic Risks and Responsibilities

The Human Genome Project (HGP) was an important milestone, not only for biology and for advancing our basic biological understanding of life itself, but also for a more comprehensive and systematic engagement with the social, political, ethical and legal implications of biology. In the course of the HGP and the expansion of genetic and genomic research more generally, governments in North America, Europe and elsewhere implemented policies that dedicated a small but significant percentage of all funding for genomics research to so-called ELSI or ELSA projects (Ethical, Legal and Social Implications/Aspects). These projects investigated genetics and genomics research in the specific social and political context of the late 20th and early 21st century. A main motivation for these investments into social science and humanities research as part of funding for the genomic sciences was the worry that the analysis of the human genome could lead to the resurrection of a biology of human difference that culminated in the scientific, social and

political atrocities of the social hygiene movements and of fascist regimes in Germany and elsewhere in the first half of the 20th century. For example, while the UNESCO statements on race in 1950 and 1952 aimed to show that the scientific community was dedicated to the social and political equality of all people, genetic research often continued to investigate human difference along traditional categories of social stratification such as race [49]. Could this research be undertaken without once again contributing to the division of humanity and the possible discrimination of specific human groups? How could genetic differences and their health effects be studied without possibly exposing individuals to social stigma? Social science and humanities analysis was understood to be integral to efforts to investigate, identify and discuss social, ethical and political issues as they arose as part of genetics and genomics research. Issues that have been and are of ongoing concern to scholars in the social studies of science and related fields include, for example, if genetic research might lead to new forms of genetic essentialism and genetic discrimination, i.e. if individuals or groups in society might come to be defined and limited by, for example, a genetic mutation they carry [50, 51]. Other studies have been exploring what it might mean socially and politically if new forms of at-risk status are generated by genetic testing technologies: Which new forms of being affected as individuals, families and groups are being created through the availability of genetic tests? Are individuals empowered or imperilled by these new types of risk information [52, 53]? Still others investigate how genetic types of health information contribute to the formations of new norms of what counts as rational and responsible behaviour with regard to health risks, disease prevention and care for the self, family and society [54, 55]. This type of research is an important contribution to understanding how genetic research impacts society, which kinds of distinctions between human beings it might create, and what kinds of political and legal frameworks are needed to mitigate potentially negative impacts, particularly on vulnerable groups in society.

Yet, as genetics is increasingly complemented by epigenetic perspectives on health and illness, notions of health risks shift in ways that create novel and distinct social and political questions. To explain this shift, we will briefly compare the specific characteristics of genetic and epigenetic notions of health risks and elaborate why this difference is central for understanding the new forms of social and scientific responsibility that arise with epigenetic approaches to health, illness and inheritance.

Genetic Risk

The genetics of the late 20th century introduced a new category of risk—genetic risk—and with it new possibilities for its assessment and management, e.g. through genetic testing. Social scientists and humanities scholars who study these novel developments proposed that by providing these means to assess genetic risk, genetic research opens up possibilities for both empowerment and discrimination [56]: a potential for empowerment because genetic testing allows for new knowledge as a basis for preventative action or other life decisions for at-risk individuals; and a potential for discrimination because it also allows for genetically ‘damaged’ individuals to be identified. In the worst-case scenarios of cultural imaginaries during the HGP, it was feared that genetic science could possibly lead to structures of extreme societal stratification based on individual genetic heritage—concerns illustrated popularly by the 1997 movie “GATTACA”, which portrayed a society in which only the genetically superior were allowed access to education, the job

market and procreation. Social science studies of those who live with the knowledge of a genetic mutation, for example a BRCA 1 or 2 mutation, show that their experience of genetic knowledge and testing technologies is also often characterized by this ambivalence [57]. On the one hand, the possibility of genetic testing is perceived as a life-saving technology. On the other hand, worries about continued access to health insurance or discrimination on the job market if the information about their risk became known are also part of their experiences [53]. These worries are, depending on the national context, more or less substantiated [58, 59].

At the advent of the HGP, it was assumed that genetic risk would explain the distribution and clustering of common diseases such as cardiovascular disease, diabetes and cancer. However, it is widely recognized that this hope did not come true [60] and, despite the existence of personal genomics products and projects such as 23andMe, genetic risk as a public discourse and as a health care concern is today largely confined to a few specific high-risk groups, such as families with histories of breast and ovarian cancer or Huntington's disease (although, of course, this might change in the future should a larger number of relevant mutations be identified through new technological or other scientific advances). What is crucial is that these groups and families can be found in different social locations in society, with different class and ethnic backgrounds.

Discourses about the social responsibilities connected to genetic risk thus also remain largely confined to at-risk families and the genetic clinics that work with them. Common discussions about responsibilities in this context concern, first, the flipside of the opportunity to know one's risk and engage in prevention, for example, whether specific family members have the right not to know about or not to engage in medical prevention in cases where risk has been established [61]. Second, questions arise about whether one must inform other family members of a possibly at-risk status and if one's reproductive choices should be influenced by genetic risk information [62]. And third, the first two points often become linked to larger discussions about whether at-risk individuals have an obligation towards society to address their health risks in a responsible way, which is often equated with practices of knowing and sharing risk information and engaging in prevention, in order to save health care costs and be responsible citizens [57]. Social science research indicates that discussions of guilt and individual failings remain largely confined to these three levels of responsibility. They do not become, however, linked to the disease risk itself: whether one does or does not carry a genetic mutation is largely interpreted as fate and hence beyond individual control.

Epigenetic Risk

What changes now if we move from a genetic to an epigenetic perspective on risk? Epigenetics introduces new forms of risk that are not linked to the gene per se, but to its relationship with the environment. Just like the environment itself, epigenetic risk is thus dispersed and omnipresent. In a sense, it concerns everyone. Everyone lives in an environment that might affect their epigenome. However, epigenetic risk is, at the same time, strongly related to the social conditions of our lives: the contexts we live in and the ways we live in them. This leads to a key difference between genetic and epigenetic risk: as epigenetic risk becomes linked to life circumstances, it holds the

potential to discriminate between people along traditional categories of social segregation that impact their life circumstances [63, 64].

In the beginning of this section, we revisited how the genetic sciences of the late 20th century worked hard to explicitly set themselves apart from one of their historical precursors: eugenics. Eugenics assumed that different groups in society had different biological properties. Positive eugenics, which was prominent, for example, in South America, assumed that better life circumstances would improve human biology and hence worked on improving hygiene, medical care and education to improve the population. Negative eugenics, which is what we mostly think of when we say eugenics, aimed to exclude those who were deemed biologically inferior from reproduction, often violently, while encouraging other groups to reproduce [65]. Historians of science have shown that it was key for the emerging genetic sciences after WWII to emphasize how they were different from eugenics (see [49] for a critical overview). A key message of the HGP, for example, was: On a genetic level, all humans are pretty much the same. Post WWII genetics also cast itself as a humanitarian project that lent unity to the human race after the atrocities of the first half of the 20th century. With regard to the health sciences, the major research object it produced—the genetic mutation—turned out to mostly work within this framework, as it appeared as dispersed among different groups in society. Nevertheless, a focus on genetic mutations also enabled new forms of discrimination and stigmatization by introducing novel at-risk groups (as discussed in the previous section), and in some cases forged associations between specific genetic health risks and distinct social groups, as illustrated, for example, by the long-held assumptions that African-Americans have a higher risk of cardiovascular disease due to genetic factors, a hypothesis that has come to be increasingly challenged in the life sciences [66].

Environmental epigenetics and particularly the proposition of transgenerational epigenetic inheritance, however, already challenges the aspirational *ideal* of sameness that was foundational to modern genetics [19]. Social location comes to matter for physical and mental health outcomes through its effects on gene expression—potentially across generations. While studies often aim to point out the health impacts of possibly unjust living conditions, at the same time they run the risk of defining already disadvantaged groups in society as biologically different and disadvantaged. Jörg Niewöhner [67] referred to this as a potential “molecularization of biography and milieu” that might emerge with epigenetics. This ambivalence is a challenge that epigeneticists will have to face, particularly as research from their field becomes increasingly important for public health [68].

Epigenetic Responsibilities

As with genetics, insights from epigenetics can present both means of empowerment—to understand the links between social location and health outcomes—but also means of possible discrimination [69, 70]. Individuals and groups exposed to certain socio-material experiences are understood to be marked as biologically different at the level of gene expression. As we have shown, historically marking specific social groups as biologically different has mostly been to their disadvantage. Rather than leading to the betterment of their living conditions, it has often served to legitimate existing social hierarchies [71].

In contemporary environmental epigenetics, numerous studies using animal models and human cohorts currently explore how trauma, deprivation and exposures affect physical and mental health in later life and across generations. While their insights are unquestionably important, from a social science perspective a key question is: Will these studies contribute to the betterment of living conditions or increase the stigma and discrimination that disadvantaged groups are often already facing? Certainly, the answer to this question will highly depend on the social and political development of our societies, which has in many countries taken a downturn when it comes to the commitment to social solidarity, inclusion and the sharing of wealth and resources across societal strata. However, scientists, too, have an important responsibility to consider the social context of their work when they design and conduct their studies and interpret their results. The biological in general and the molecular in particular hold a certain power: in our societies, phenomena that can be traced to the materiality of the biological and the molecular are often considered to be more real and credible than descriptions based on other data alone [4]. Even if certain correlations between life circumstances and health might have been known before, they gain weight as there is molecular 'proof'. That goes hand in hand with a certain responsibility on the part of life science researchers. Exactly what phenomena am I making real with my research? Which categories do I use to describe and label that which I seek to explore? Which silent assumptions about the social world might I integrate into my research designs and the interpretation of my results, possibly without further reflection? Have I considered the possible social and political implications of my work in the way I communicate my results?

However, the degree to which life science researchers—individually and as research communities—can engage with such questions is highly dependent on the social organisation of the scientific system as such, particularly on its reward and incentive structures [72]. Currently, the scientific system and its funding and career structures tend to encourage a focus on fast-paced scientific work that aims to score well in terms of quantitative performance metrics such as the Journal Impact Factor [73]. As has been discussed in much greater detail elsewhere, one of the often-detrimental effects of this orientation are specific time-regimes of work that discourage scientists from engaging in activities that will not be easily translatable into the next high-impact paper [74]. This effect is particularly pronounced for current postdoctoral and tenure-track scholars who are in the process of building a career in science and who constitute the next generation of the scientific leaders of the field. Yet, socially and politically important and challenging fields such as environmental epigenetics clearly point to the limits of the kinds of work that can be accomplished within the current normative structure of science. Time-pressured and impact-factor-oriented modes of work make it difficult for life scientists (and researchers in other fields, too!) to devote time to reflection, interdisciplinary exchange, experimental re-designs and the slow work of crafting and communicating research results cautiously and responsibly.

Nevertheless, as research in environmental epigenetics is so intimately tied to the social world, it will be crucial to enable processes of exploring its social and political dimensions before, during and after the research process. Research funders will play a particularly important role in this process, as will institutional leaders, in both funding and rewarding careful research proposals that also include explorations across disciplinary boundaries that seek to responsibly account for the biosocial

nature of research in environmental epigenetics. Particularly for research that explores the biological impact of unequal living conditions and experiences across generations—may it be in a model organism or in cohort studies—it will be of uttermost importance to engage with its inherent connections to questions of social and environmental justice. Below, we want to highlight just two aspects that are particularly important to consider at the intersection of social justice and transgenerational epigenetic inheritance.

Individual and Collective Responsibility

Social and bioethical studies of science [63, 75, 76] have indicated that exploring the molecular aspects of a social issue often leads to locating the responsibility for addressing this issue on the level of individual instead of the level of society. In the case of environmental pollution, for example, the polluted landscapes and elements might fade out of perspective and the focus rests on the specific chemical that individuals need to avoid contact with in order to ensure their own health and well-being and/or that of future generations [77]. In the case of nutrition, food often becomes viewed as an individual choice instead of a complex social phenomenon [78]. The focus on the molecular thus often tends to shift attention away from the complexities of society to the actions of the individual. While this can be politically powerful in terms of enabling individual agency, it also means that more collective questions and answers are often neglected. Swedish political scientist Maria Hedlund [75] reminds us that it will be pivotal to discuss epigenetic responsibility on the collective level—that environmental pollution is not considered as something that needs to be managed by the individual, but as something for which states and companies are held responsible. Similarly, questions of nutrition and lifestyle cannot be negotiated at the scale of the individual alone. Socially stratified patterns of food intake also need to be understood as expressions of distinct social hierarchies and the unequal distribution of social, political and economic resources. Approaches that seek solutions on the individual scale alone often end up holding the most vulnerable members of our society responsible for improving their own health and that of future generations without addressing the structures that significantly contribute to creating the problem [68]. The environmental epigenetics research community can contribute to a more complex understanding of epigenetic responsibilities across generations by considering how they themselves frame the problems they seek to address, which contexts they consider in their experimental designs and how they interpret their findings.

Studying Harm without Exploring Reversibility

We have outlined that in the history of biosocial approaches to body, health and inheritance, studies often focused on the negative effects of certain exposures, with much less attention given to exploring reversibility and the effects of positive environments. As we briefly discussed before, a similar trend has become visible in contemporary environmental epigenetics research. While it is of course of uttermost importance to understand the detrimental effects of environmental toxins, trauma or other biosocial exposures, it is equally important to consider the possible social impact of scientific research focused often almost exclusively on harm. Bioethical discussions about genetic testing posed the question of whether testing should be available if there is neither a cure nor the possibility of prevention, as for example in the case of Huntington's disease [79].

While insights from environmental epigenetics holds the prospect of banishing or avoiding detrimental exposures in the future [63, 75], the question emerges of whether there is a retrospective responsibility towards already affected individuals to invest more in studies of reversibility. On a societal level, it needs to be considered if a message of damage without hope of reversibility might contribute to the stigmatization of individuals and groups, potentially across generations. While studies of reversibility alone are no cure for the possibility of discrimination [80] and potential suggestions of social or medical interventions based on notions of reversibility will need to be carefully scrutinized regarding their social and political impacts, more attention to questions of reversibility in the study of (heritable) epigenetic effects can be an important step.

Interdisciplinary Collaboration as a Practice of Responsibility

We have highlighted these two questions as they are particularly important challenges for science and society in the context of environmental epigenetics in general, and specifically with regard to the proposition of transgenerational epigenetic inheritance. They are challenges that life science researchers need to become more aware of, but, at the same time, we believe that they do require engagement from across the disciplines in order to be addressed productively. Together with a growing number of social scientists, humanities scholars and life scientists, we propose that epigenetic research and, particularly, work on such a sensitive topic as transgenerational epigenetic inheritance needs interdisciplinary exchange and collaboration to thrive responsibly. To date, there are a few initiatives where scholars from these different fields have to come together to work on integrating social science perspectives that foreground questions of social responsibility, justice and equity into research designs and the interpretations of studies [70]. These forms of collaboration require bringing together expertise from disciplines that might appear radically different and which might focus on topics that seem very distant from each other at first glance—such as gene regulation, methylation patterns, cellular signal cascades, social structure, war trauma, racism, gender discrimination or agrarian economics. But it is the power and the challenge of a field like environmental epigenetics that it works on topics that intersect the social and the biological world so profoundly that all of these different types of expertise might need to interact to make sense of the complex phenomena that environmental epigenetics seeks to describe. Thus, we argue for forms of engagement that build on combining different types of expertise and exchanging perspectives, but that are, at the same time, open to transformative processes that might profoundly alter the viewpoints with which each participant has entered the engagement. In recent decades, interdisciplinary collaboration, particularly in an ELSI/ELSA mode, was often conceived of or could practically only be conducted as a form of social science research alongside life science inquiry. The social sciences' contribution was thus often limited to offering a critique of life science research from the outside or to addressing possible downstream problems after the facts had been established. This continued separation has been criticised by many social scientists as insufficient for addressing the inherent social and political character of life science research (see e.g. [81, 82]). A field such as environmental epigenetics that brings together the social and biological in such complex ways makes it even more apparent that such a mode of engagement built on critique from the outside alone and persistent disciplinary

separation is not enough. Hence, we envision more integrative processes of collaboration in which scholars from different disciplines participate in the design, conduct and interpretation of experiments and studies. Becoming aware of the troublesome histories of biosocial research must be an essential part of such processes in order to not repeat historical injustices.

Responsibility literally means the 'ability to respond'. Responsibility is thus in its essence a doing, a practice. The practice of *responding well* to the challenges and potentials of environmental epigenetics and transgenerational epigenetic inheritance will require pooling our resources across the disciplines and working together to understand life and inheritance in all its social and biological complexity. It will require developing a new language that goes beyond simple notions of determinism, whether social or biological, and that can begin to address the interplay between social and biological life as always already a scientific and a political question. The intent, then, of interdisciplinary conversations and collaboration is to render scholars in different disciplines articulate in ways that allow them to speak across disciplinary divides to explore the biosocial aspects of life in ways that live up to these inherent political responsibilities.

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