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Behavioral Epigenetics: The Last Nail in the Coffin of Genetic Determinism

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At a recent faculty meeting we were discussing topics for a Critical Questions in Psychology Seminar for our undergraduate honor students, and I suggested "nature versus nurture." Before I could elaborate on my idea, a colleague interjected in a slightly irritated tone, "Are we still debating 'nature versus nurture'? Hasn't that been resolved long ago?" Perhaps. Perhaps not. The ethologist Patrick Bateson [2002] seemed to imply so when he referred to how genes and environment interact over the course of development to produce the adult phenotype, as have many others. What has been resolved, it seems, is the erroneous dichotomy between nature and nurture and with it the extinction of extremists from both the nature and nurture perspectives. Any modern scientist who has given the issue even a modicum of thought recognizes that we can no longer ask "how much" of any phenotypic outcome is nature and "how much" is nurture, but ask instead how do nature and nurture interact to produce patterns of behavior, emotions, and cognition. We are all interactionists now. But there is still room for debate about the nature of this interaction, and David Moore, like many developmentalists, has ardently argued that the only way to understand how people (or any animal for that matter) end up the way they do is to study their development, with behavior emerging via the continuous and bidirectional interaction between the organism and all levels of its environment, both macro (family, community, culture) and micro (hormones, neurotransmitters, chemicals within the cell). This is a point Moore made explicit his excellent 2001 book *The Dependent Gene: The Fallacy of "Nature vs. Nurture."* In his most recent book, *The Developing Genome: An Introduction to Behavioral Epigenetics*, Moore reiterates his emphasis on the inseparability of genes/biology and experience/environment, but with a modern addition: *epigenetics* – the system, among other things, by which experience influences the activity of the genome. Thus, Moore not only presents a highly readable primer on modern epigenetics, especially as it relates to behavior, but does so by embedding it in a conceptual framework that a strict recitation of the facts about epigenetics would miss.

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The Biologizing of Development

There has been a steady biologizing of development over the past quarter century, as seen by increased theoretical and empirical attention to developmental neuroscience and to evolutionary accounts of ontogeny [see Bjorklund, in press]. Contemporary developmental psychologists cannot be biophobic. Moore argues, correctly I think, that epigenetics will be the next major focus in this trend, and he present facts, theory, speculations, and cautions about behavioral epigenetics in a book that will become a must-read for behavioral and social scientists concerned with how people come to be the way they are.

Moore divides his book into four parts. The first, consisting of seven chapters, provides readers with the basics of how phenotypes are constructed (via development, with genes always being expressed in a context), the processes of development (in terms of developmental systems theory), DNA (genes are probably not what you think they are), and the regulation of genes, which brings us to the mechanisms of epigenetics. In the second part of the book, Moore tells us in nine chapters what we know about epigenetics, including how early experience and prenatal diets alter DNA expression and thus behavior, as well as epigenetics' role in memory, disease, and psychopathology. Of these first 16 chapters, six are "Zooming in on" chapters (e.g., Zooming in on DNA, Zooming in on Epigenetics, Zooming in on Memory), providing greater background for the reader who would like to delve more deeply into the science behind a particular topic. Readers desiring only the "big-picture" perspective can skip these chapters and still come away with a wealth of knowledge about contemporary research in behavioral epigenetics while still feeling intellectually challenged and informed. The last two parts of the book are on inheritance (four chapters), which present research evidence and speculation of the heretical possibility that Lamarck was right, and implications, with chapters titled Caution, Hope, and Conclusions.

Epigenesis and Epigenetics

Epigenetics may be the new hot topic in biology, but it, or the related concept *epigenesis*, has a long history, dating back to Aristotle who used it to describe development as a series of steps. Philosophically, epigenesis can be contrasted with *preformationism,* which contends that development consists essentially of growth, or in more contemporary contexts, of following predetermined routes without influences from external sources. So, for example, when 17th century Europeans discovered that semen contained microscopic sperm, they deduced, quite correctly, that it was the joining of a male's sperm with a female's egg that produced new life. They inferred incorrectly, however, that in the head of each tiny sperm (or perhaps within the much larger egg) existed a small but fully formed human being who grew in size over the course of gestation [Gottlieb, 1992]. (Such views may not be as ridiculous as they sound, for scientists at the time did not know there were limits to how small biological units could be, and furthermore, most accepted the Church's view that the second coming was near, limiting the need for too many more generations, each tucked, Russian-doll style, into the testes of a microscopic boy.) Modern-day versions of preformationism propose not tiny homunculi, but rather that development is determined by genes, with adult phenotypes being essentially preordained. The counter modern epi-

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genetic view stems from Conrad Waddington, who used the concept to describe development as the result of causal interactions between genes and the environment. Piaget [1967] adopted Waddington's idea stating that, "whenever one is dealing with a structure in the psychology of intelligence, its genesis can be traced to other more elementary structures which do not constitute absolute beginnings themselves but have a prior genesis in even more elementary structures, and so on ad infinitum. I say ad infinitum, but the psychologist will stop at birth … and at this level there is, of course, the whole biological problem because the neural structures themselves have their genesis, and so it continues" (p. 149). More recently, Gottlieb [2007] defined *probablisitic epigenesis* as the continuous and bidirectional interaction between all levels of the organism-environment (genes ↔ structure ↔ activity ↔ environment), which is the core concept underlying *developmental systems theory*. From this perspective, nothing arises fully formed, but has its origins in earlier structures or functions.

But *how* do experiences affect the expression of genes, thus influencing the development of structure and function? Through epigenetics. At its most basic level, according to Moore, "epigenetics refers to how genetic material is activated or deactivated – that is expressed – in different contexts and situations" (p. 14). A bit more technically, epigenetics is defined as "changes in gene function that do not alter its underlying structure of DNA but result in genes being switched on or off in a reversible way" [Puumala & Hoyme, 2015, p. 15]. Knowing what genes one has may be important, but what really matters is what those genes are doing. Are they producing proteins, and if so how much? It is epigenetic mechanisms that determine whether a segment of DNA is active or not, and such mechanisms are influenced by, among other things, experience. Epigenetic processes determine how experiences become biologically embedded, affecting an animal's morphology, physiology, and behavior.

Scientists have discovered many ways in which DNA is switched on and off. Moore describes the basic biology for the two best understood epigenetic mechanisms: *DNA methylation*, which generally results in deactivating DNA, and *acetylation*, which typically results in activating DNA. Biologists have known of these mechanisms for decades, believing they were responsible for influencing early development. For example, each human cell contains the full complement of chromosomes and DNA, used to construct head and shoulders, knees and toes, as well as all other parts of the body. Yet, once you have one head, a pair of shoulders and knees, and 10 toes, the genes associated with these structures turn off. The cells in your liver never decide to sprout a toe or two, even though they have the genes to do so. The reason they do not is because of DNA methylation. These genes (or stretches of DNA that regulate those genes) are prevented by epigenetic mechanisms from producing their once-vital product. Not long ago scientists believed that such methylation is highly stable and that epigenetic effects were essentially limited to the earliest stages of development. As it turns out, this is not necessarily the case.

Epigenetics and Early Experience

Moore describes research with humans and with nonhuman animals showing that early experience alters DNA methylation and thus gene expression, which is related to subsequent behavior. According to Moore, "this is why behavior epigenetics is so exciting: it is the link between our genes and our environments, the link that allows our

experiences to shape our brains and make us who we are" (p. 63). For example, Moore reviews research by Michael Meaney [2013] and his colleagues, showing that rat pups with mothers who engage in high rates of licking and grooming grow up to be less vulnerable to stress than pups with "low-licking mothers," and that these effects are mediated by methylation in areas of the brain associated with stress regulation.

Something similar happens in humans. For instance, high levels of childhood stress associated with poverty or abuse are related to poor physical and mental health later in life. This is a particularly important issue for Moore, who writes, "because I am a social scientist, I find it interesting and significant that early exposure to poverty is associated later in life with poor health and impaired psychological well-being, but I do not find such revelations to be especially surprising. *How* do these situations or events we experience early in life have their effects on us years later?" (p. 76). The answer, not surprisingly, is through epigenetic mechanisms. Moore reviews experiments in which the behavior and epigenetic markers (usually measured from blood) of groups of mice, rats, or monkeys that received stressful experiences early in life were examined later in life and compared to those of nonstressed control animals. Behavioral effects associated with early stress generally replicated findings of previous research (e.g., memory deficits, greater stress sensitivity), with behavioral effects being associated with differences in DNA methylation patterns. Such experiments, demonstrating unambiguous cause-effect relations, cannot be done with humans, but Moore summarizes the results of several correlational studies that report associations between childhood adversity (e.g., child abuse, poverty) and adult epigenetic markers. For example, in one study of 45-year-old men, researchers reported methylation patterns in approximately 1,200 DNA regions associated with childhood socioeconomic status, independent of adult socioeconomic status [Borghol et al., 2012]. Moore's identification of long-term effects of early stress via epigenetic mechanisms as a "hot" topic within developmental psychology is confirmed by the publication of more than a dozen papers on the topic since the 2015 publication of his book [see, for example, papers in Lester, Conradt, & Marsit, 2016, Witherington & Lickliter, 2017, and a review by Conradt, 2017].

Moore also describes and discusses research looking into epigenetic effects on memory, the epigenetics of cancer, and the relation between epigenetics and various forms of psychopathology (e.g., depression, schizophrenia, anxiety). Moore cautions that epigenetic research is a long way from discovering "cures" for cancer or depression, and we must be cautious in making too much of what little we currently know about the role of epigenetics in health-related fields. Yet, he is optimistic. Moore states, "using currently available data, the advice that can be gleaned is no different from advice attentive people would have given before learning about epigenetics at all: eat a healthy diet with plenty of vegetables, stay calm, nurture friendships, avoid toxins. What we now understand is *how* these kinds of factors produce the effects they do, and this information will likely be useful to future healthcare professionals and, ultimately, to the people they are trying to help" (pp. 221, 222).

Lamarck Revisited

As exciting as the findings are about how experiences influence gene expression and the potential role that epigenetics may play in understanding disease and psychopathology, some of the most exciting research Moore describes concerns the *in-*

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heritance of epigenetic markers and the consequences that this has not only for understanding development, but also evolution. Moore reports experimental studies with nonhuman animals and correlational studies with humans showing transmission of behavior (e.g., reactions to stress, tendencies toward obesity) and associated DNA methylation patterns across generations (e.g., from grandparents to grandoffspring). Such epigenetic inheritance has been reported in both the female and male lines. In other words, experiences of grandparents (e.g., grandmothers when they were pregnant, grandfathers during childhood) influence the development of their grandchildren. Some of these effects seem to reflect adaptations (e.g., women experiencing famine during a portion of pregnancy having children with "thrifty phenotypes," thus conserving calories) whereas others reflect pathology (e.g., exposure to pesticides by male rats produces sperm abnormalities and grandsons that are relatively unattractive to females), and it is not known how frequently such epigenetic inheritance occurs. However, the fact that epigenetic effects can be transmitted across generations questions the basic assumptions of the modern synthesis and Weismann's contention of the total separation between the soma and germline. Moore states:

> *There is only one kind of inheritance*, and it requires the transmission of both genetic and nongenetic developmental resources. [E]pigenetic effects can be "inherited" *even if the epigenetic marks are not transmitted through the germline.* What matters in evolution is that characteristics be transmitted from generation to generation, regardless of how that happens; from this perspective, then, it does not matter whether experiences produce epigenetic effects that are maintained via the germline, or whether the epigenetic effects are transmitted some other way. Regardless of exactly how it works, it is now clear that some epigenetic effects can be passed from generation to generation. (p. 155)

Conclusion

Not long after the publication of the first drafts of the human genome in 2001 [International Human Genome Sequencing Consortium, 2001; Venter et al., 2001], scientists recognized that genes are only part of the story. Identical twins, and even cloned animals, are different from one another at birth, and these differences cannot be attributed to genes. Instead, they are caused by epigenetic effects. Moore describes clearly the mechanisms of epigenetics, as well as research and theory on this important topic and what the future may hold. But he does so always with the developmentalists' perspective in mind: bodies, behaviors, and minds develop over time via the interaction of endogenous and exogenous factors. Genes are essential, of course, but they are only a component in the overall system. Genes are always expressed in a context, and it is through the mechanisms of epigenetics that the experiences we have in those contexts get embedded in our biology.

Scientists in all fields debate, often vehemently, about matters at the fringes of their discipline, so that, to an outsider, it might appear that there is little agreement about core issues. Developmentalists are no exception [see e.g., Bjorklund, 2016; Witherington & Lickliter, 2016]. However, there seems no longer to be any serious debate about the core of the nature-nurture issue, and recent findings from behavioral epigenetic research, presented so lucidly in Moore's book, put the last nail in the coffin of genetic determinism. As Moore writes, "the truly complex reality is

that neither genetic nor environmental factors *independently* cause phenotypes" (p. 59). Details still need to be worked out, and research in epigenetics will be central in deciphering how genes and environment interact over the course of ontogeny to produce phenotypes, the central concern of developmental biologists and psychologists.

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