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3 The Contents and Discontents of the Nature–Nurture Debate

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INTRODUCTION

Humans are a biological organism. Their psychology and behavior have been thought to have biological underpinnings. At the same time, humans are a highly social species and we inhabit cultures – e.g., normative ways of behaving and reacting to others' behavior – of our own making. Our experiences at least partly shape who we are. But which more importantly contributes to who we are and how we behave, biological influences or sociocultural-environmental influences? This question reflects the essence of the "nature–nurture debate," as traditionally defined.

This debate and its appropriate resolution have important implications. As traditionally defined, the debate has been presumed to speak to the malleability of our psychological dispositions. If we are largely a product of biology, it has been thought, our dispositions are relatively rigid and fixed. By contrast, if sociocultural and environmental influences dominate, our psychological dispositions may readily be altered, should the environments we inhabit change.

These implications are potentially very important. Psychologists and other social scientists should want to know what aspects of our psychological make-up are malleable and, if so, through what means. At the same time, in our view the nature–nurture debate is not profitably framed in the traditional way we describe above. The traditional framing implicitly assumes that "biological" and "environmental" causes – "nature" and "nurture" – constitute separable causes, as, say, pieces of a pie can be sliced apart and separated. If separable, we can, in principle, decide whether one or the other is larger (i.e., address which "piece of the pie" is larger). In fact, they are not separable. To say so is not to say that meaningful discussions of how nature and nurture, broadly construed, affect our psychological dispositions are not possible or profitable. It is to say, however, that the issues that can meaningfully be discussed must be reframed.

In this chapter, we present this reframing. First, we discuss why nature and nurture are not separable causes. To say that a feature is "biological" is not to say that it is fixed; indeed, many "biological" features are flexible. We illustrate this point with examples. In this context, we also discuss questions of heritability and why decomposition of trait variance into heritable and environmental components does not address the nature–nurture debate, as traditionally defined. Second, we identify a number of questions that *can* legitimately be asked within our reframing of nature–nurture issues, several of which concern key issues pertaining to the specific roles of nature and nurture. Finally, we discuss implications of these matters for potentially understanding gender, biology, and culture specifically.

NATURE AND NURTURE: SEPARABLE CAUSES?

An Assumption of the Traditional Framing: Biology and Environment Are Separable Causes of Phenotypic Outcomes

McLeod (2018) frames the nature–nurture debate in the traditional terms we refer to above and his discussion hence illustrates this framing:

> Nature is what we think of as pre-wiring and is influenced by genetic inheritance and other biological factors. Nurture is generally taken as the influence of external factors after conception, e.g., the product of exposure, life experiences and learning on an individual. The nature–nurture debate is concerned with the relative contribution that both influences make to human behavior, such as personality, cognitive traits, temperament and psychopathology. (www.simplypsychology.org/naturevsnurture.html)

He then goes on to contrast views within psychology that emphasize nature and nurture: Those according great importance to nature follow a "biological approach" that focuses on "genetic, hormonal, and neurochemical" explanations for behavior, whereas those that accord great importance to nurture include "behaviorism," which argues that "all behavior is learned from the environment through conditioning" (McCleod, 2018, p. 1).

As we note above, an implicit assumption to the claim that one can meaningfully assign relative contributions to nature and nurture is that such causes are separable. Otherwise, how could one make such assignments?

Why Biology and Environmental Causes Are Not Separable

Biology, Genetic Programs, and Open Programs

The quote above implies that what is "biological" is fixed and immutable – it's "pre-wired" and "inherited," and is furthermore contrasted with what is a "product of exposure" and "life experiences." Few biologists, however, would fully agree. Biology, after all, is simply the study of life and living organisms. Whatever life forms do or are capable of falls within the purview of biology. If particular biological organisms have the capacity to be shaped by "exposure" and "life experiences," those capacities are the subject of biology and, hence, are biological phenomena.

Ernst Mayr was one of the key architects of the modern synthesis of Darwinism and Mendelism, the broad theoretical perspective that proposes that biological evolution consists of changes in frequencies of different variants of genes (e.g., Mayr, 1942). He also introduced the concept of "the genetic program" to capture how, in the modern synthetic view, genes give rise to the apparent adaptive behavioral "purposiveness" of biological entities:

> The completely individualistic and yet also species-specific DNA code of every zygote (fertilized egg cell), which controls the development of the central and peripheral nervous systems, of the sense organs, of the hormones, of the physiology and morphology, is the *program* for the behavior computer of this individual. Natural selection does its best to favor the production of codes guaranteeing behavior that increases fitness … The purposive action of an individual, insofar as it is based on the properties of its genetic code, therefore is no more or less purposive than the actions of a computer that has been programmed to respond appropriately to various inputs. (Mayr, 1961, pp. 1,503–1,504; for another introduction of this concept, see Jacob & Monod, 1961; Peluffo, 2015)

This concept may seem to imply that, in fact, behavior is "pre-wired" into the organism and immutable, rather than responsive to life experiences. In fact, however, this claim is not true. First, as Mayr emphasizes in the quote above, "programming" leads individuals to "respond appropriately to various inputs." Those inputs come from the external world the organism inhabits. Hence, behavior, by this account, is necessarily responsive to environmental features and life experiences. Second and perhaps even more importantly, Mayr (1974) later explicitly distinguished "closed programs" and "open programs":

> programs which control the teleonomic processes in organisms are either entirely laid down in the DNA of the genotype ("closed programs") or are constituted in such a way that they can incorporate additional information ("open programs") … acquired through learning, conditioning, or other processes. (p. 103)

Open programs permit acquired behavior (the effects of "nurture"). But at the same time, they imply an "innate" component. A "program" itself – a function of DNA – specifies the kinds of "additional information" that can be incorporated to alter the program, and how the program is altered to affect responses to the environment. Systematic effects of nurture, in this view, demand a particular "nature." The two *jointly explain* behavioral outcomes, and necessarily so.

Instructively, B. F. Skinner, the intellectual founder of radical behaviorism, did not disagree. He considered psychology to be a natural science and, specifically, a branch of biology (see, e.g., O'Donohue & Ferguson, 2001). In this view, over time individuals were selected to have the capacity for behavior to be shaped by consequences; the capacity for acquired behavioral repertoires is itself "inherited."

Developmental Systems

Not all biologists embrace the metaphor of a genetic program. From a developmental systems perspective, the concept implies that genes play the role of master over cellular and, more broadly, organismic processes. In fact, however, cellular events unfold within a system of coacting elements, none of which constitutes a master controller (e.g., Griffiths & Gray, 1994; Oyama, 1985). The idea of a genetic program may imply various notions to the contrary: that genes contain the critical "information" required for phenotypic outcomes; these phenotypic outcomes are hence, in a sense, "preformed" (perhaps more accurately, "prespecified") in the genome; genes thus constitute *the* critical explanations of phenotypic outcomes; the idea of a genetic program therefore implies a kind of genetic determinism, even if it does not imply that phenotypic outcomes are completely impervious to environmental variation.

Developmental systems theorists have argued for different ways of conceptualizing processes than lead to phenotypic outcomes. Phenotypic outcomes are a product of development. Development itself is an outcome of organized processes that occur within a system of developmental "resources." Genes constitute some of those resources. But so do many nongenetic factors: e.g., at molecular levels, genes lack effects in absence of other cellular structures already in place, and even extracellular elements can affect outcomes (e.g., human skin does not develop normally in absence of consumed vitamin C); at more macro levels, some adaptive outcomes occur through experience with the current environment (e.g., as noted above, learning; see, e.g., Shea, 2011). It is not accurate, in this view, to give explanatory priority to genes by claiming that they embody outcomes via an information-based "program."

Recently, some versions of developmental systems theory argue that, in fact, it is not meaningless to conceptualize the control of phenotypic outcomes in terms of information. In fact, genes do carry semantic content about phenotypic outcomes (e.g., Shea, 2011). For example, members of particular bird species reliably develop bills of particular shapes that, furthermore, reflect features of the environment to which they are adapted (e.g., the shape of flowers that specific hummingbirds feed from), and they do so reliably generation from generation. Shea (2011) introduces the concept of an *inherited representation* to discuss this semantic content and its high-fidelity transmission; genes constitute inherited representations. He argues, however, that nongenetic factors can also constitute inherited representations. Highly reliable features of the environment (e.g., the presence of vitamin C important to the development of human skin, as alluded to above) reflect inherited representation too. In human evolution, some nongenetic forms of highly reliable inheritance are social environments through which, for instance, individuals learn normative behavior (i.e., developing humans can "count on" encountering a group of conspecifics who will behave in particular normative ways, which constitutes a learning environment for the individual (Boyd & Richerson, 1985.) Adaptive evolution, then, not only consists of selection for genetic representations that support it; it also consists of selection for the presence of nongenetic representations that support it.

The development of some phenotypic features draws heavily on genetic inherited representations. The development of other phenotypic features may depend on genetic inherited representations, but also may draw heavily on nongenetic inherited representations. Though developmental systems theorists may reject what they perceive as unwanted surplus meaning implied by the metaphor of "genetic programs," in fact Mayr's (1974) distinction between closed programs and open programs aimed to make a very similar conceptual discrimination: Closed genetic programs draw very heavily on genetic inherited representations, whereas open genetic programs incorporate content carried by nongenetic inherited presentations.

Three Illustrations

Flexibility and contingency of the immune system. A primary function of our immune system is to recognize and protect us against potentially harmful foreign ("nonself") molecules and cells in our bodies. Innate immunity reflects capacities of our bodies to protect ourselves from harm by foreign molecules through processes that do not depend on prior exposure to those molecules. Disease-fighting white blood cells such as neutrophils, monocytes, and macrophages can be mobilized and destroy foreign molecules and cells with no recognition of them. Acquired immunity, by contrast, depends on prior exposure to foreign molecules and cells. When B cells (specific lymphocytes we possess) are exposed to a specific antigen (foreign material capable of stimulating an acquired immune response) the cells multiply and produce and release antibodies (structures that can attach to antigens) specific to the antigen. Antibodies defend against foreign antigens in a number of ways: They can directly render antigens harmless, they can prevent antigens from entering and infecting cells, and they can attract other immune system cells that ingest the invader (Tomar & De, 2014). In a very real sense, through antibody production the immune system experientially "learns" to defend against specific pathogens.

So, does acquired immunity reflect "nature" or "nurture"? Clearly, both. For any individual, the antibodies that circulate are ones specific to antigens that the individual has a history of being exposed to; they are the "product of exposure, life experiences and learning on an individual." At the same time, antibody production is performed by a highly specialized system that reliably develops in individuals, where development involves specific genes. While one can specify the ways that "nature" and "nurture" affect antibody production, one cannot meaningfully separate their relative impacts. The impact of experience (pathogen exposure) is only possible because of a highly specialized system not dependent on those experiences.

The acquired immune system illustrates ways in which "learning" processes themselves depend on systems that permit it. Again, the immune system learns to defend against specific pathogens in a very real sense. But that learning is achieved through a highly specialized system that can learn a very limited number of responses (antibody production) in response to very narrowly defined stimuli (foreign antigens). Though learning of antibody production is not psychological in nature, it nicely illustrates the fact that learning itself requires that systems that structure learning must be in place for learning to occur. Those systems may be highly specialized, enabling learning to occur within a very particular set of contexts.

The flexibility of reproductive systems. Human reproductive systems similarly illustrate the ways that experiences' impact on outcomes depend on the nature of systems. Women's fecundability – their capacity to conceive an offspring – is affected by energetic factors. One very important factor is energy balance: When women's caloric expenditure regularly exceeds their caloric consumption fecundability is downregulated, largely mediated by reductions in estradiol levels (e.g., Ellison, 2001; 2003). Extremes in energetic flux – large or small energy expenditures, even when consumption equals expenditure – similarly affect estradiol levels and thereby fecundability (Ellison, 2001; 2003). Experiences, then, affect reproductive capacities – but only because a "biological" system is sensitive to those particular kinds of experiences.

Some scholars propose that the developmental onset of women's menses and hence fecundability is sensitive to social factors such as predictability of caregiving, quality of paternal care, and presence of non-paternal male adults in the home of upbringing (all hastening the onset of female menses; e.g., Ellis, Figueredo, Brumbach, & Schlomer, 2009 – though these ideas remain debated; e.g., Barbaro, Boutwell, Barnes, & Shackelford, 2017). Once again, if this is the case, "nurture" has impacts on outcomes only because specialized systems regulating reproductive development are sensitive to experiential inputs.

Behavioral learning. One key way through which experiences affect behavior is through learning. Though learning is typically thought of as a means through which "nurture" affects behavior, learning is only possible when an organism possesses a system through which learning may take place. Just as the sensitivity of antibody production depends on the presence of a system that renders its production sensitive to exposure to particular foreign antigens, behavioral sensitivity to experience via leaning depends on a specific system that renders learning possible. Learning, then, clearly involves both "nature" and "nurture."

One possible difference between the acquired immune system and some behavioral learning systems is the breadth of stimuli to which responses can be learned. Classical and operant conditioning are typically thought of as two kinds of learning that are highly general in nature. The equipotentiality hypothesis (see, e.g., Öhman, Fredrikson, Hugdahl, & Rimmö, 1976) proposes that any response an animal can make can be reinforced in the presence of any stimulus it can perceive. It furthermore proposes that linkage occurs through the same mechanisms or processes. In fact, however, many examples show that, in the extreme, the hypothesis is wrong. Fears of heights or snakes are learned effortlessly, whereas fear of electrical outlets is learned with difficulty (e.g., Cook & Mineka, 1990). Individuals can learn aversions to the taste of foods by ingesting food and experiencing nausea many hours later; aversions to virtually no other sensory inputs (e.g., touch, sight) can be learned when nausea follows perception, whether experienced immediately after or after a delay of hours (e.g., Garcia, Kimeldorf, & Koelling, 1955; Seligman, 1971).

More generally, Barrett (2015) argues that many important forms of human learning are adaptively specific to domains and not domain-general: learning about movements of objects within a constrained representation of how physical objects can potentially move, learning about animals and plants, learning precautions within the environment, learning normative behavior, learning the reputations of group members and how to respond to those reputations, and so on (see also Boyer & Barrett, 2015). The extent to which important forms of human learning invoke highly specialized adaptations (perhaps as specialized, in many cases, as the acquired immune system) or highly general learning systems continues to be debated.

Here, we discuss in some depth a specific example pertaining to a persistent socialization concern over students' academic performance. Governments and educators have been trying to identify factors affecting academic motivation and achievement. Recent evolutionary life history research points to a new direction by which nurture meets nature in solving this otherwise purely socialization issue (Chang et al., 2019). Animals routinely learn to find food and shelter by exploring their environments (Reader, 2015). Such learning may represent individual learning or trial and error or social learning by copying conspecifics (Chang, Mak, Li, Wu, Lu, & Chen, 2011; Marchetti & Drent, 2000). In either case, foraging or food exploration has been found to be conducted by animals either thoroughly or superficially (Wolf et al., 2007). Superficial explorers are found to search habitats that have more predators as well as more abundance of food sources (Both et al., 2005). They conduct food search fast and superficially under high predation risk. They also do not need to be thorough because of food abundance requiring little effort. By contrast, thorough explorers search food at safer locations that draw more conspecific food explorers. They take longer time and exert more effort to explore the heavily searched habitat thoroughly (Merchetti & Drent, 2000). The distinction between thorough and superficial exploration has been found in almost all animals and the difference is consistently linked with two distinct socialities. Superficial exploration is associated with boldness and aggression, whereas thorough exploration is associated with affiliative, prosocial, and inclusive sociality (Kurvers et al., 2010). The crucial factor separating these two kinds of foraging behaviors and two kinds of social behaviors is environmental safety and predictability.

Separately, neuroscience research has neuroanatomically linked foraging search, known as area-restricted search (ARS), to goal-directed learning (Hills, 2006). Molecular evidence from the prefrontal cortex and striatum suggests that dopamine and glutamine are involved in modulating both goal directed learning and spatial focus in ARS (Hills, 2006). Synaptic activities in the basal ganglia correspond similarly to foraging behavior and goal-directed learning (Sheth, Abuelem, Gale, & Eskandar, 2011). The neuro and molecular mechanisms that initially evolved to modulate ARS are later co-opted to control goal-directed learning (Hills, 2006). "What was once foraging in a physical space for tangible resources became, over evolutionary time, foraging in cognitive space for information related to those resources" (Hills, 2006, p.4).

Together these two lines of research suggest that learning, which is otherwise treated as a pure nurture issue, is programmed by nature to respond to the environment. Additionally, research suggests that environmental safety and predictability that separated thorough from superficial foragers continue to differentiate academic achievers from underperformers (Chang et al., 2019). Adolescents growing up in dangerous neighborhoods or chaotic families, or having negative life events, were shaped by such environmental unsafety and unpredictability to adopt antagonistic sociality and superficial learning (Chang et al., 2019). This finding is based on cross-cultural evidence from nine countries (China, Columbia, Italy, Jordon, Kenya, Philippines, Sweden, Thailand, and the United States; Chang et al., 2019).

Finally, this evolutionary insight (nature) does not contradict but corroborates socialization (nurture) theories and findings. Extensive research has been conducted to identify factors affecting children's academic performance. Based on meta-analyses as well as traditional reviews of these studies, the following factors are among those that matter the most: lacking attention to details (Jacob & Parkinson, 2015), the lack of motivation and effort (Cerasoli, Nicklin, & Ford, 2014), and distraction by Internet use (Anderson, Steen, & Stavropoulos, 2017). These learning-impeding factors all seem to mirror superficial exploration that is unable to attend to details, that is easily distracted, and that is uninterested in the learning. Other studies have highlighted environmental conditions such as residential change (Anderson & Leventhal, 2017), parental absence (Berg, Rostila, Saarela, & Hjern, 2014), familial disruption (Hampden-Thompson & Galindo, 2015), and antagonistic classroom norms (Chang, 2004) in affecting children's academic performance. These factors represent various proxies of environmental unsafety and unpredictability that, consistent with the evolutionary prediction, lead to antisocial behavior and superficial or ineffective learning. Widely reported comorbidity between externalizing behaviors and academic underperformance among school children (Gershoff, 2002) especially supports the coevolution between antagonistic sociality and superficial learning (Wolf et al., 2007).

Heritability Studies: Partitioning Genetic and Environmental Variance

Behavioral genetic studies seek to partition total population variance in a psychological trait into that associated with genetic variation and that associated with environmental variation. The heritability of a trait (h^2) is the proportion of the trait's variance that is associated with allelic variation. The remainder of the trait's variance is that proportion associated with environmental variation (though some of that variance is almost always simply variation that is measurement error). Virtually every psychological feature that varies across people has non-negligible heritability; 50 percent heritability is not uncommonly estimated (e.g., Turkheimer, 2000).

It may seem that heritability estimation is a way to assess the relative contributions of "nature" and "nurture." But no such straightforward interpretation of heritability is possible. First, even features that possess no variation may be strongly affected by genetic inheritance. Indeed, as alluded to above, most species-typical features (e.g., in humans, possessing a heart, lungs, liver, two legs, two eyes, and on and on) develop in species-typical ways because genetic representations strongly influence these outcomes. (Hence, when people do not possess, say, two legs, it is usually due to an accident or amputation, not genetic variants.) Second, as also alluded to above, even nongenetic variation typically arises due to foundations that are, in part, informed by genetic representations. People have different antibodies because they have been exposed to different pathogens (environmental variation across individuals), but the mechanisms through which they generated different antibodies (themselves species-typical) developed through processes in which genes played crucial roles. The same is true of variable psychological outcomes. Third, variation that is so-called "genetic" may crucially involve environmental influence. For instance, physical differences (e.g., in body size and shape), influenced by genetic alleles, may lead individuals to have different experiences, which then affect psychological outcomes. Even some variation in neural processes affected by genetic variants (e.g., variation in sensitivity to certain rewards and punishments) affects psychological outcomes, at least in part, because they affect the specific life experiences of individuals. It would be wrong to think that the genetic variation in psychological traits solely reflects the fact that different psychological outcomes are "coded" into the genes (e.g., Turkheimer, 2000; see also Tooby & Cosmides, 1990, on "reactive heritability"). (Broadly, "heritability" estimation is a statement about correlation – association between trait variation and genetic variation – which cannot be simply interpreted in causal terms, e.g., simple "genetic effects.")

Of course, we do not imply that behavioral genetic studies cannot inform our understanding of development. Especially as these studies come to identify the functional roles of genetic variants that affect traits (which are almost always very numerous, with each variant having little impact; e.g., Chabris, Lee, Cesarini, Benjamin, & Laibson, 2015), scientists may come to better understand the processes that affect trait development. Here, we simply make the point that behavioral genetic studies cannot allow us to assess the relative contributions of "nature" and "nurture."

LEGITIMATE QUESTIONS WITHIN THIS REFRAMING

As we noted at the outset, psychologists should be interested in questions of how nature and nurture, broadly construed, affect psychological outcomes. Indeed, answering these questions constitutes core tasks of psychological science. We argued, however, that these questions should not be construed within a traditional framing of the "nature–nurture" debate, which assumes that the relative contributions of nature and nurture can be cleanly cleaved. We presented a reframing of this debate, in which the contributions are not cleanly separable. Within this framing, legitimate questions can be asked. We turn to discuss such questions.

Norms of Reaction: Flexibility versus Fixed Outcomes

Phenotypic features may differ with regard to their plasticity. Highly "rigid" outcomes are ones insensitive to environmental encounters during development. When single outcomes are relatively stable in the face of environmental variation, the outcome is said to be highly canalized (e.g., Waddington, 1957). Many human morphological features are relatively canalized: having two eyes and two ears, having five fingers or toes at the end of each limb, having two hemispheres of the brain connected by the corpus collosum, and so on. Some behavioral features may be highly canalized too, such as the patellar reflex.

Many others are more "plastic," shaped by experience. As emphasized above, however, the latter features do not lack an evolved, "biological" component. Just as the immune system has been specially designed by selection to "learn" to produce antibodies to specific antigens to which the system has been exposed, behavioral learning systems too have been selected (see discussion above on "open programs").

Even when outcomes are highly plastic, the systems that produce plasticity are often highly canalized and hence reliably develop.

Specificity versus Generality of Environmental "Inputs"

Learning systems may differ greatly in the extent and range of the environmental "inputs" to which they are sensitive. In one sense, the adaptive immune system is sensitive to a wide range of different inputs: It can produce antibodies in response to just about any foreign antigen that is not detected as "self." In another sense, however, the inputs are narrowly defined: They must be antigens; the system is not sensitive to variations other than variation in antigen structure. In the same way, some behavioral learning systems are sensitive to very specific kinds of inputs. Specialized language syntax learning may be an example (though "grammar" may not be as "universal" in precisely the same way that Chomsky [1965] proposed).

We noted above that classical and operant conditioning are often thought to involve highly general processes (see, for instance, our earlier discussion of the equipotentiality hypothesis). At the same time, some scholars argue that many important forms of human learning involve highly specialized systems (e.g., Barrett, 2015; Boyer & Barrett, 2015). That is, just as the acquired immune system involves "learning" but in a highly specialized way (such that the system is responsive to inputs of a highly specific nature, with outputs also being highly specific), psychological learning processes may also depend, in many instances, on highly specialized systems. Earlier, we listed a number of examples. As we also noted, the extent to which important forms of human learning invoke highly specialized adaptations (perhaps as specialized, in many cases, as the acquired immune system) or highly general learning systems continues to be debated.

SOME IMPLICATIONS FOR UNDERSTANDING WOMEN, MEN, BIOLOGY, AND CULTURE

In a variety of ways, this reframing of nature–nurture issues has implications for understanding the sexes. Within particular species, males and females possess many sex-typical features that are shared as well as some that are specific to each sex. For instance, the sex-typical reproductive systems of men and women differ. Men produce many small gametes (sperm) and, once reproductively capable (i.e., capable of producing viable sperm), they typically maintain that capability through the life span. Women produce many fewer but larger gametes (eggs). Fertilization itself is internal to females. And even after reproductive onset, women's fecundability varies. As noted above, women's reproductive capacity is sensitive to energetic states. And even when naturally cycling, women are conceptive only a few days out of a month, perhaps two months of every year. They are not conceptive when pregnant or during several months of lactation, though during these states women allocate a considerable amount of energy consumed into reproduction (feeding and sustaining an offspring). And reproductive senescence (leading to menopause) typically precedes their more general somatic senescence. These contrasting features of male and female reproductive systems are perhaps most profitably thought of as sex-typical sex-specific features rather than "sex differences." But they likely have implications for how men and women experience the world, due both to variations in "nature" and to variations in "nurture."

Take, for instance, the fact that adult women are not continuously conceptive, even when naturally cycling. Given the implications of being potentially conceptive and not being potentially conceptive, it would be remarkable if women experienced the world exactly the same under these two states. And, indeed, they do not. When conceptive during a cycle, women's sexual motivations typically increase (e.g., Roney & Simmons, 2013). And, perhaps as compensation, their food-seeking motivations diminish (e.g., Roney & Simmons, 2017). Especially when they are romantically involved, they may become more concerned about relationship features when non-conceptive (e.g., Grebe, Gangestad, Garver-Apgar, & Thornhill, 2013; Grøntvedt, Grebe, Kennair, & Gangestad, 2017) and more attracted to particular male features when conceptive (e.g., Gangestad, Dinh, Grebe, Del Giudice, & Thompson 2019). (See also Thornhill & Gangestad, 2008.) Though one can understand these variations functionally in light of women's conceptability, at a proximate level they are likely affected by hormones that vary across the cycle (notably, estradiol and progesterone; e.g., Roney & Simmons, 2017). At the same time, of course, to say that physiology has psychological impacts is not to deny that the way that women experience events – their "nurture" – has impacts. Again, "nature" and "nurture" are not separable causes.

We offer an example of nurture meeting or extending nature with the phenomenon of gender "equality" – the extent to which, on average, men and women possess equal access to material resources and control over resource distribution. Initially "nurtured" in the post-industrial age among Western, White, middle-class populations, the concept of gender equality has since emerged in most developed and developing societies. This has sometimes been celebrated by a (misconceived) narrative of good nurture taking over or changing bad nature.

Our argument is that nurture extends but does not change nature, and without evaluative qualification, gender equality and inequality represent both nature and nurture.

In hundreds of millions of years of evolution, most sexually reproductive species practice polygyny, and 95 percent of all mammalian animals are polygynous (Clutton-Brock, 1989). Gender inequality stems from humans evolving from a long line of polygynous species and having practiced polygyny throughout much of their evolution including the civilized history (Zhu & Chang, 2019). In a polygynous mating system, sexual selection favors sexual dimorphism resulting in gene-based dimorphism (e.g., a colorful male peacock tail) and, very often, resource-based inequality (e.g., men control resources). In both cases, sexual selection is the cause and explanation of gender inequality. According to sexual selection theory (Darwin, 1871/2019; Trivers, 1972), differential parental investment of the two sexes drives intrasexual competition, mainly among the less investing sex (males), and mate choice, mainly by the more investing sex (females). These two processes lead to wide-ranging sexual dimorphic phenotypes, which in human evolution may extend to intangibles, namely such cultural values as gender inequality and male chauvinism (Dawkins, 1982). Because ancestral humans have a long lineage that primarily practiced resource-based (in contrast to gene-based) polygyny (Puts, 2010), gender inequality mainly concerns uneven distribution of resources driven by intrasexual competition among males. When some males control more resources than others and females who depend on said resources are willing to share them with co-wives, polygyny arises alongside an unequal relationship between the sexes. Through male hunting and female gathering, the human-specific gender division of labor shapes or reinforces resource-based gender inequality because male hunters control meat- and protein-based resources (Marlowe, 2000). In short, gender inequality is evolutionarily derived from uneven distribution of resources, even among males. This evolutionary view is consistent with socialization views regarding gender inequality (e.g., Roberts & Soederberg, 2012).

Gender equality also has evolutionary roots, albeit with a shorter history than that of mammalian evolution. In the 2 million years of human evolution, humans have repeatedly faced new challenges and overcome them with new solutions. Most notably, premature birth, which constitutes an adaptive workaround solution to the coevolution of bipedalism and increased cranial size, puts selective pressure on alloparenting (care of offspring by individuals other than genetic parents), including paternal assistance in the nest (Lu, Zhu, & Chang, 2015; Low, 2005). Likely coinciding with concealed ovulation and human pair-bonding and monogamy, fathers assuming childrearing responsibilities and domestic roles may represent the first evolutionary step toward reversing gender inequality. Paternal assistance in the nest enables women to leave their offspring and garner additional resources (Marlowe, 2003). In hunter-gatherer societies, women joining hunting expeditions to assist or replace men while men take care of children is not uncommon (Marlowe, 2003). Consistent with gender-role theory (Eagly, Wood, & Diekman, 2000), this transformation of gender roles is fundamental to the development of gender equality. Furthermore, women's participation in the labor force decreases their reliance on men for resources and increases their need for paternal involvement in raising their offspring, thereby contributing to gender equality through gender-role undifferentiation and resource allocation. As noted by Newson and Richerson (2009), modernity is a result of women becoming increasingly engaged in paid labor outside the home and spending less time in familial contexts. Subsequent human societal development, including industrialization, imposed monogamy, and gender equality, results from women leaving the nest to enter the resource-garnering workforce and men assuming domestic roles (Lu, Zhu, & Chang, 2015; Zhu & Chang, 2019). However, remnants of the considerably longer history of mammalian polygynous evolution continue to permeate human societies today in the form of gender inequality.

Neither gender equality nor gender inequality on various dimensions is "fated" by biology. Gender equality is modifiable, to be sure. At the same time, in order to understand how gender equality is modifiable, one must appreciate the nature of the systems that affect it. In terms of concepts we introduced earlier, gender equality is the outcome of open programs. Open programs themselves yield effects of "nurture." But open programs themselves are products of "nature." As we have stressed repeatedly, the effects of "nurture" can only be understood through nature.

SUMMARY

Human behavior is a product of biological influences and sociocultural-environmental influences. But which more importantly contributes to who we are and how we behave? In our view, this question is not the right one to ask. It assumes that "nature" and "nurture" are separable causes. They are not. One can meaningfully ask a number of questions often thought to follow from the nature–nurture debate: How flexible or plastic is human behavior within particular contexts? To what extent are environmental inputs that shape behavior general or specific? These questions remain debated. More generally, one can and should ask what specific roles nature and nurture play in giving rise to human behavior. In our view, answers with regard to each will invariably invoke the other. "Nature" shapes behavior partly by affecting how environmental events direct behavior. And "nurture" shapes behavior because "nature" permits it to do so.

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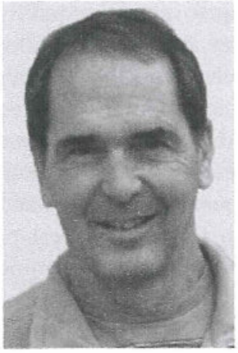

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