

1 Introduction

What underlies or makes up the human mind has always been central to the nature–nurture debate. Despite historical philosophical arguments insisting that humans are substantially nature-determined (Plato and Hobbes) or, conversely, that humans are largely socially determined (Aristotle and Locke), today there is scientific consensus that both nature and nurture contribute to shaping the mind. The way in which nature and nurture work together, however, has yet to be settled, and integrative frameworks have emerged to address this gap in knowledge. This requires a broader perspective that includes both genes and culture, combining two seemingly disparate fields of research.

The study of individuals in connection to the cultural environment and to biology, separately, is not new. On the one hand, cultural psychology examines the impact of culturally shared social and environmental factors on the mind and behaviors (Markus & Kitayama, 1991; Segall, Lonner, & Berry, 1998; Shweder, 1991; Triandis, 2001; see also Kitayama & Cohen, 2010). As social beings, people are influenced by external factors – including diverse physical environments, social interactions, structures, institutions, values, and beliefs (Kim & Markus, 1999; Markus & Kitayama, 1991; Miyamoto, Nisbett, & Masuda, 2006) – the meaning of which is shared in a culture (Bruner, 1990). These factors jointly make up a culture and, in turn, can be considered the core of “nurture.” Cultural psychology has historically studied these nurture-focused explanations for differences in actions, traits, and thinking across cultures, drawing a clear link between nurture and psychological processes. On the other hand, biology has aimed to understand human behavior as well, but by focusing on the physical mechanisms that connect humans to, and also distinguish us from, other organisms. The field experienced a rather rapid leap with the completion of the Human Genome Project in 2003. By uncovering the sequences of DNA and unfolding processes that lead to phenotype expressions (Meaney, 2017), combined with various neural and physiological processes that predict human behavior (Eccles, 1964; Morrell, 1961), the fields of biology and neuroscience have enriched scientific understandings of how nature shapes individuals. Although through different routes, both cultural psychology and biology have aimed to understand why humans think and behave the way they do.

Yet despite great progress in understanding human behavior within each perspective, it is possible that unexplained variance considered “noise” in one field could be explained by looking to the other field. Therefore, with two distinct pathways illuminating the underlying mechanisms of the human mind and behavior, it is perhaps a logical next step to understand how these paths

may cross. Studying how cultural and biological factors interact may further our understanding of humans beyond what is possible in each field separately. Multidisciplinary work presents exciting new directions, but at the same time, it also introduces challenges that arise from combining different research methods and integrating disparate theoretical frameworks. Nonetheless, overcoming these challenges will ultimately enable us to understand the human mind to a fuller extent.

In this Element, we aim to provide a more nuanced understanding of human thought and behavior by using an integrated perspective of genes and culture. To do so, we first provide a review of gene–culture interaction research, covering key theories and empirical evidence that characterize this new area. Second, we discuss current issues in gene–culture interaction research, describing unique challenges that arise from integrating across fields. Finally, we conclude by highlighting future research directions, or opportunities for moving this new area forward.

2 Gene–Culture Interaction Review

This section reviews recent research within the framework of gene–culture interactions, including earlier frameworks and theories that led to its current form. First, we discuss preceding frameworks, such as the gene–environment interaction and gene–culture coevolutionary theory, and how the gene–culture interaction framework is related but also distinct. Then, we present empirical evidence demonstrating how cultural influences on various psychological processes, including cognitive processes, socioemotional behaviors, and well-being, can be moderated by genetic factors. After reviewing empirical work, we discuss key theories that lay an explanatory groundwork for gene–culture studies and provide new predictions for future research.

2.1 Overview of Frameworks

2.1.1 *Gene–Environment Interaction (G x E) Framework*

Contrary to the lay belief that genes wholly decide phenotypes, evidence from various fields, including biology, development, and cultural neuroscience, shows that genes do not solely determine characteristics. The environment can substantially influence genetic expression, with some genes never being expressed throughout an entire lifetime due to certain environmental conditions (Meaney, 2017; Rutherford, 2000). Given that both the environment and genes contribute to various phenotypic expressions or psychological outcomes, the gene–environment interaction (G x E) framework offers a useful and integrated perspective. More specifically, the G x E framework shifted the belief that

a map of genes would directly link to behavioral and clinical outcomes to the understanding that the environment interacts at various levels of DNA expression (Meyer-Lindenberg & Weinberger, 2006), and thus the importance of studying both genes and environments as well as their interactions has become apparent.

Caspi and colleagues (2002, 2003) set a milestone for the gene–environment interaction framework, which triggered an array of subsequent studies revealing that, even if exposed to similar adverse experiences or environments, only individuals with certain genes were more likely to develop antisocial behaviors or depression. For instance, those with the homozygous short allele of serotonin transporter polymorphism (5-HTTLPR) were much more likely to experience depression when they went through a greater number of stressful events, while those with the long allele showed a much weaker or no association between the number of stressful events and depression (Caspi et al., 2003). This line of research showed how genes and environment can jointly shape psychological outcomes. In other words, people with certain genotypes may be predisposed to react more strongly to environmental factors than people with other genotypes, and at the same time, people with the same genotype might react differently when exposed to different environmental factors.

As was the case in some of Caspi's research (2002), many G x E studies considered early childhood experiences related to parenting style as a prominent environmental factor. One reason for this focus on parenting might be the abundant research on child temperament and parenting style interactions in developmental psychology (Rothbart, Posner, & Hershey, 2006). Past research suggests that children with difficult temperament show more internalizing or externalizing behaviors when they experience negative parenting or caregiving (Blackson, Tarter, Martin, & Moss, 1994; Bradley & Corwyn, 2008; Rothbart & Ahadi, 1994), while those who receive positive and sensitive parental care exhibit higher social competence (Pluess & Belsky, 2009) and social skills (Pluess & Belsky, 2010; Stright, Gallagher, & Kelley, 2008) in later childhood or adolescence. Based on this previous research, more recent studies focused on the genotype of the children instead of their temperament (Stein, Schork, & Gelernter, 2008), but parenting style remained as one of the most studied environmental factors. The importance of parenting is also supported by other genetic studies. For example, rodent maternal behaviors, such as licking and grooming, are known to influence the DNA methylation process in the early life of offspring (Weaver et al., 2004). For humans, the perception of parental rejection was shown to be associated with differences in DNA methylation patterns (Naumova et al., 2016).

While the environment may influence how genes are transcribed (DNA to RNA) or translated (RNA to proteins), including the unfolding process of DNA to phenotypic variations such as histone modification and DNA methylation (Meaney, 2017), the detailed process of transcription or translation is beyond the scope of this Element. Nonetheless, it is important to note that not all genotypes are directly expressed to phenotypes, and the influence of the environment can work at many levels. Reflecting the bulk of existing G x E studies in the current literature, most of the research discussed in this Element will involve single nucleotide polymorphisms (SNPs) and repeat polymorphisms, common types of DNA sequence variations that occur naturally in populations, and how they interact with different environmental factors.

2.1.2 Gene–Culture Interaction (G x C) Framework

Although much research based on the G x E framework has focused on parenting style and adverse home life as part of the early childhood environment, the “environment” is not limited to what a family provides in the home; environmental influences can also be seen later in life. The gene–culture interaction (G x C) framework builds upon and extends the G x E framework by incorporating culture as a relevant environmental factor across the lifespan. Culture is a set of values, institutions, and social structures that are loosely connected and shared among people (Kitayama, 2002) and thus is a comprehensive meaning system guiding thoughts and actions. In other words, cultural contexts embedded in the environment can influence every aspect of daily life, from experiences in childhood to those in adulthood. Culture, therefore, provides specific context-dependent challenges and motivations to people, and without understanding these particular characteristics in different cultures, researchers may only achieve partial knowledge of the way genes and the environment interact. The G x C framework lays a foundation for understanding how people with one genotype would be more responsive to certain cultural values or structures compared to others with a different genotype, and how those with the same genotype might exhibit different patterns of thoughts and behaviors as well as mental health outcomes depending on their culture.

2.1.3 Dual Inheritance Theory/Gene–Culture Coevolutionary Theory

Boyd and Richerson (1985) proposed a foundational theory regarding the relation of genes and culture called dual inheritance theory, also known as

gene–culture coevolutionary theory (Chiao & Blizinsky, 2010; Fincher & Thornhill, 2012). The theory proposed that cultures have coevolved by interacting with genetic evolution. In other words, cultural values and traits are adaptive, and this adaptation influences and is influenced by genetic selection (Boyd & Richerson, 1985). Therefore, according to this theory, certain genotypes can lead people to attend to or show specific reactions to the environment, thus steering cultural selection. Culture as a form of environment may also influence genetic selection, for instance, if a genotype prospers because it imparts culturally rewarded or culturally valued traits (Odling-Smee, Laland, & Feldman, 2003).

Dual inheritance theory gained support from numerous empirical studies showing how a specific feature of culture interacts with certain genes (Chiao & Blizinsky, 2010; Mrazek, Chiao, Blizinsky, Lun, & Gelfand, 2013). For instance, research on level of lactose tolerance across Europe showed a positive association between dependence on milk products and lactose-tolerant population (Beja-Pereira et al., 2003), suggesting a historical coevolutionary link between cultural practices in milk production and people's biological ability to digest milk efficiently in these regions. In other research, Chiao and Blizinsky (2010) showed that countries with higher historical pathogen prevalence tended to be more collectivistic. The authors proposed that this positive association might be explained by the high frequency of serotonin transporter polymorphism (5-HTTLPR) short allele carriers. Furthermore, the frequency of short allele carriers in the population is actually negatively correlated to the rate of anxiety and depression, despite these carriers showing a higher tendency to express depression and anxiety (Lesch et al., 1996). Fincher and colleagues (2008) suggested that collectivistic values might have a buffering effect against not only pathogens but also environmental stress, therefore leading to the high frequency of people with short alleles in collectivistic cultures (Chiao & Blizinsky, 2010).

One criticism of research on human evolution and its developmental processes is that some older perspectives lacked explanation beyond simply claiming that it was adaptive (Gould & Lewontin, 1979), when findings in this area could be better explained by incorporating cultural factors (Andersson et al., 2014; Bogin, Bragg, & Kuzawa, 2014). For example, human reproduction and caregiving practices are distinct from other primates in that allocare and resources are transferred among not only those who are genetically related but also to non-family members and those without a close genetic relationship (Bogin et al., 2014). The authors suggest that this unique practice is a product of human culture and genes, called biocultural reproduction. The products of

gene–culture coevolution are not limited to reproduction and caregiving practices and may also extend to language and religion (Ferretti & Adornetti, 2014). In other words, various practices in our lives may result from the coevolution of genes and culture rather than solely one or the other.

Although both dual inheritance theory (gene–culture coevolutionary theory) and gene–culture interaction acknowledge the importance of genes, culture, and their interplay, gene–culture interaction framework differs from dual inheritance theory in that it focuses on how the interplay manifests in individuals' daily lives. While dual inheritance theory provides a broad framework of how cultural evolution and genetic evolution co-occur by focusing on a macrolevel of analysis, the $G \times C$ framework attempts to understand how genetic and sociocultural factors jointly shape psychological processes and behaviors at the micro- or individual level (Kim & Sasaki, 2014). In other words, dual inheritance theory aims to understand the distribution of certain genes within specific cultural groups while the $G \times C$ framework aims to explain various psychological tendencies and behaviors through the interaction between certain genes and cultures. The findings we discuss in this Element have relevance for broader processes of genes and culture, including gene–culture coevolutionary theory. However, we focus primarily on the combined effect of gene and culture in various psychological processes and behaviors at the level of the individual via the $G \times C$ framework.

2.2 Empirical Evidence of Gene–Culture Interactions

In this section, we discuss empirical evidence that supports the gene–culture interaction framework. Although not exhaustive of the research done in this area, we review notable studies in various psychological domains, from early cognitive processes to long-term mental health outcomes. Through these studies, we can see how genes and culture jointly affect psychological outcomes and the importance of considering their interactive effect rather than trying to partition the proportions of nature versus nurture.

2.2.1 Perception and Attention

The earlier steps of cognitive processes include the perception of, and selective attention to, stimuli in the environment. A good deal of research in cultural psychology has shown how culture can influence people's perception and attention. For example, Masuda and Nisbett (2001) showed that East Asians and North Americans differ in their locus of attention such that East Asians tend to focus more on background information, while North Americans tend to

attend more to focal objects. Within each culture, individual differences represent natural variation between individuals (Na et al., 2010), and according to the G x C framework, at least some individual differences may be explained by certain genotypes that are more or less susceptible to cultural influence. Therefore, numerous studies prompted by the G x C framework started to address these individual variances within a culture by focusing on genes that should theoretically link to certain individual differences.

A gene–culture interaction study on perception was done by Ishii and colleagues (2014), examining how people recognize the disappearance of facial expressions. Past studies have shown that East Asians are more sensitive to the disappearance of others' smiles due to the interconnected nature of collectivistic cultures and attention to social approval, compared to North Americans, whose individualistic culture emphasizes self-approval and satisfaction more (Ishii, Miyamoto, Mayama, & Niedenthal, 2011). While this general tendency differs across cultures, the authors propose that the sensitivity to those stimuli might differ depending on serotonin transporter (5-HTT), more specifically, 5-HTT gene-linked polymorphic region (5-HTTLPR). 5-HTT is known to play an important role in serotonergic neurotransmission regulation, which is deeply involved in cognition and emotional states. There are two types of alleles – short (s) and long (l) – of 5-HTTLPR, and short allele carriers show reduced binding of 5-HTT to the brain (Heinz et al., 2000). Short allele carriers are also known to show heightened attention to fear-relevant stimuli, higher sensitivity to emotional stimuli, as well as greater susceptibility to environmental stimuli in general (Beevers, Wells, Ellis, & McGeary, 2009; Caspi et al., 2003; Osinsky et al., 2008). Combining the expected effects of culture and genetic predisposition, the researchers predicted that among Japanese, those with the short allele of 5-HTTLPR would be more sensitive to the disappearance of a smile compared to 5-HTTLPR long allele carriers due to a greater sensitivity to relationship-threatening cues. However, among North Americans, there would be little to no difference between the short allele group and long allele group since the disapproval of others is less of a threatening cue. The results were in line with their hypothesis, thus providing support for the gene–culture interaction in perception of facial expressions, a relatively early stage in cognitive processes.

Another study that taps into gene–culture interactions on cognition was done by Kim and her colleagues (2010b) on how locus of attention differs by culture and could be moderated by genotype. A well-documented phenomenon is that there tend to be cultural differences between Eastern and Western cultures in locus of attention, whether people pay more attention to focal or contextual

information in the environment. Due to the tendency to adopt a holistic style of reasoning, East Asians are prone to attend to the entire field, including background information, while North Americans who typically adopt an analytic style of reasoning, are prone to attend to focal objects more than background information (Nisbett, Peng, Choi, & Norenzayan, 2001). In addition to this cultural difference, research on cognitive flexibility found that 5-HT activity level influences the ability to attend to relevant stimuli while ignoring irrelevant information (Schmitt et al., 2000). Therefore, taking into account the role of 5-HT_{1A}, an autoinhibitor of 5-HT release, Kim and her colleagues examined whether the effects of 5-HT_{1A} interact with culture on locus of attention. They speculated that people homozygous for the guanine (G) allele, compared to those with cytosine (C) alleles, of 5-HT_{1A} would adhere more to the culturally dominant attentional locus – Westerners attending more to focal objects and East Asians attending more to background information. Indeed, the researchers found a linear trend among European Americans in the degree of attending to non-focal information such that people homozygous for the G allele paid the least attention to contextual, background information and those homozygous for the C allele paid the most attention, such that those with the heterozygous genotype were in between them. On the other hand, Koreans showed the opposite trend such that those homozygous for the G allele paid the most attention to contextual, non-focal information, and those homozygous for the C allele paid the least. In sum, cognitive processes, including the perception of and attention to stimuli, show different patterns depending on the genotype and the culture of people. By incorporating two seemingly distant fields, we are stepping forward in understanding how and why people think differently or similarly when faced with the same stimulus or situation.

2.2.2 Self-processes

Going beyond cognitive processes, studies from various fields support the interaction effect of genes and culture on how people construe the self. It would not be an exaggeration to say that one of cultural psychology's main areas of study has been the difference in the concept of self between the Eastern and the Western world. Building on cross-national research by Hofstede (1984), Markus and Kitayama (1991) showed there are striking differences in how people from different cultures conceptualize the self as relatively more independent, or distinct from others, versus more interdependent, or connected to close others. As was the case with cognitive processes, researchers soon investigated how genetic factors could moderate these processes.

One of the most widely observed cultural differences is in self-construal (Markus & Kitayama, 1991), with many Western societies showing independent social orientations and Eastern societies, especially East Asian countries, showing stronger interdependent social orientations (Singelis, 1994). Despite these broad cultural differences, individuals can also show important variation within the same culture (Na et al., 2010). Kitayama and his colleagues (2014) examined whether these individual differences could be due to one of the hypothesized plasticity genes – the dopamine D4 receptor gene (DRD4). DRD4, which is a repeat number polymorphism rather than a SNP, plays a role in regulating the dopamine pathway, which is related to the reward-processing areas of the brain (Delgado, 2007; Dreher, Kohn, Kolachana, Weinberger, & Berman, 2009). Although previously known as the risk-seeking gene, DRD4 is now more widely understood to be related to reward sensitivity in general (e.g., Stice, Yokum, Burger, Epstein, & Smolen, 2012). Variation in the DRD4 polymorphism may thus be associated with sensitivity to reward, which, in turn, could influence how much people adhere to cultural norms, where adherence is usually associated with social rewards. More specifically, Kitayama and colleagues (2014) hypothesized that those with the plasticity DRD4 genotype, with 2- or 7-repeat alleles (2R or 7R), would endorse the culture-dominant social orientation more compared to those with the non-plasticity DRD4 genotype, with 4-repeat alleles (4R). The results showed that among 2R or 7R DRD4 carriers, there was a significant difference in the extent of independence endorsement between European Americans and Asian Americans, but no such difference was found among the 4R DRD4 carriers. These findings suggest that cultural norms about how to construe the self may be more meaningful to people with certain genetic tendencies. Although a cultural way of being may be widespread in a particular place, individuals can vary in the extent to which they internalize it.

Self-processes are not just confined to the concept of self alone but can be extended to how the self is viewed in relation with others (Markus & Kitayama, 1991). Attachment style is one of the foundational processes through which we develop relations between the self and close others and may have interesting implications in gene–culture research. LeClair and colleagues (2016) uncovered individual differences in attachment style depending on culture and genotype. Past literature showed that East Asians, especially Japanese, tend to have higher attachment anxiety and avoidance, while Americans show more secure attachment styles (Ishii et al., 2011; Rothbaum, Weisz, Pott, Miyake, & Morelli, 2000). Previous research has also shown that people with certain genes, including the oxytocin receptor polymorphism (OXTR), can be more or less susceptible to certain

environmental influences (Kim et al., 2010a; Luo et al., 2015). OXTR rs53576 consists of G and/or A alleles, therefore one can carry one of the three genotypes – GG, AG, or AA – with the homozygous G allele carriers known to be more susceptible to particular features of cultural environments (Kim et al., 2010a). Taking these past findings into account, LeClair and colleagues (2016) predicted that those with the G allele would tend to have a more culturally common attachment style, and indeed they found that G-allele Japanese showed more avoidant attachment styles, while G-allele Americans showed a more secure attachment style. Overall, this study demonstrated that those with more socially sensitive genotypes tended to have an attachment style that is more common in their culture. Self-processes, including the concept of self or social orientations and attachment styles, are the basis of how people view the world and form relationships. Therefore, understanding the factors that influence self-processes may further our knowledge of psychological processes with implications much beyond the self.

2.2.3 Socioemotional Behaviors

Cognitive processes are an important part of psychology, but the emotional processes linked to cognitions, as well as the actual behaviors that result from them, are also crucial for a more complete picture of the mind. Socioemotional behaviors, including empathy and emotion regulation strategies, take a unique place in the intersection of genes and culture. Past literature has shown cultural differences in emotion processes (Mesquita & Walker, 2003), patterns of emotional experience and expression (Cohen & Nisbett, 1994; Fischer, 1999), as well as dominant emotions (Butler, Lee, & Gross, 2007; Kitayama, Markus, & Matsumoto, 1995). Considering the tight relation between physiological processes and emotions (Cannon, 1927), it is easy to see how genes, in interaction with sociocultural factors, may influence these processes and behaviors.

Empathy is understanding others' emotions and sharing their emotional states, and therefore, it taps into how much people can “feel” others. Due to the central component of connectedness with others, empathy has been investigated in relation to interdependent self-construal. Indeed, studies have shown that there is a positive correlation between interdependence and empathy (Joireman, Needham, & Cummings, 2002), and priming self-construal modulates empathic neural responses to the suffering of others (Jiang, Varnum, Hou, & Han, 2014). From a biological perspective, empathy is known to be linked with oxytocin, with past studies showing that administration of oxytocin increases emotional empathy (Abu-Akel, Fischer-Shofty, Levkovitz, Decety, &