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# Nature, Nurture, and Their Interplay: A Review of Cultural Neuroscience

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## Abstract

Cultural neuroscience research examines how psychological processes are affected by the interplay between culture and biological factors, including genetic influences, patterns of neural activation, and physiological processes. In this review, we present foundational and current empirical research in this area, and we also discuss theories that aim to explain how various aspects of the social environment are interpreted as meaningful in different cultures and interact with a cascade of biological processes to ultimately influence thoughts and behaviors. This review highlights theoretical and methodological issues, potential solutions, and future implications for a field that aspires to integrate the complexities of human biology with the richness of culture.

## Keywords

cultural psychology, cultural neuroscience, gene–culture interactions, gene–environment interactions, genetics

It is not nature *or* nurture. Nor is it nature *and* nurture. . . . Life emerges only from the interaction between the two: There are no genetic factors that can be studied independently of the environment, and there are no environmental factors that function independently of the genome. Phenotype emerges only from the interaction of gene and environment.

—Meaney (2001, p. 51)

Although some may believe the nature-versus-nurture debate to be obsolete in academic discourse, it lives on through a number of persistent lay beliefs about the causes of human behavior. These beliefs are rooted in intuitions about explanation more broadly. Particularly in “WEIRD” populations (composed of “White Educated Industrialized Rich Democrats”; Henrich, Heine, & Norenzayan, 2010), reliance on dichotomous thinking is alluring (Peng & Nisbett, 1999). Although many may try to avoid saying that differences in some behavior are due to either nature *or* nurture—because one cannot deny that it is both, of course—a common pitfall is to think that the behavior might be due *more* to nature or to nurture. Yet, this is just a weaker form of dichotomous thinking and does not address the complex way in which nature and nurture constantly work together to contribute to the rich variation seen across human populations. In actuality,

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culture often interacts with biological factors to change the way biological predispositions are phenotypically expressed in the way people think, feel, and behave.

The inextricable link between culture and biology means that questions of cultural differences are also biological questions, just as questions of human biology are often cultural. Yet, until recently, there was no theoretical and methodological paradigm to explore this link. Cultural neuroscience research has made notable progress to demonstrate how biological processes, including patterns of neural activation for instance, may play a role in the observed psychological differences between cultures, thus addressing a piece that was perhaps missing from earlier cultural psychological studies. These findings of culture-specific neural activation patterns are then interpreted alongside the cultural meaning behind such patterns. Ultimately, the goal of cultural neuroscience is to address how the culturally shaped mind is housed in a brain built by biological processes in the body, demonstrating that these biological processes cannot run effectively without meaningful inputs from the socio-cultural world (see Heejung Kim & Sasaki, 2014, for a more extensive review).

In this review, we discuss foundational and recent research on the interplay between culture and biology in three domains. First, we review evidence relevant to culture and genes, including gene–environment and gene–culture interactions. Second, we cover research on physiological processes, particularly neuroendocrine and immune responses, in different cultures. Third, we review cultural neuroscience research on how neural processes may relate to cultural differences in psychological outcomes. In discussing this research, we also highlight challenges in the field, emerging theoretical and methodological advances, and implications for cultural psychology more broadly.

## Culture and Genes

With the completion of the Human Genome Project (HGP-read) just more than a decade ago and the recent 2016 launch of its extension, Human Genome Project–Write (HGP-Write; [engineeringbiologycenter.org](http://engineeringbiologycenter.org)), which aims to “write” the human genome synthetically a decade from now (Boeke et al., 2016), scientists’ fascination with genes is far from over. There is a good deal that remains unknown about genes, particularly when it comes to their influence on complex psychological traits and behaviors. Given that genes are often taken to represent “nature,” it is especially important to understand the way genes interact with “nurture”—the surrounding environment or cultural context—to make advances in research on human psychology.

### *Gene–Environment Interactions*

According to research on gene–environment interactions ( $G \times E$ ), variation in traits and behaviors is most often the result of an interaction between genetic and environmental influences. Being in the same environment may predict different outcomes depending on variation in genes, and likewise, having the same genetic predisposition may predict different outcomes depending on variation in the environment. A clear example of this  $G \times E$  effect comes from research by Caspi and colleagues. In their study, they found that among people with two short (s) alleles of the serotonin transporter polymorphism (5-HTTLPR), a previously identified genetic risk factor for stress reactivity (e.g., Hariri et al., 2002, 2005), experiencing a greater number of stressful events was associated with higher depression, whereas for people with either one or two long (l) alleles, this association was much weaker, and in some cases, non-existent (Caspi et al., 2003; see Karg, Burmeister, Shedden, & Sen, 2011, Miller, Wankerl, Stalder, Kirschbaum, & Alexander, 2013, and Murphy et al., 2013, for recent meta-analyses).

Epigenetic processes underlying  $G \times E$  effects occur via crucial experiences throughout the life span (see Meaney, 2010, for review), and there are bidirectional influences across different

levels of analysis, from genetic and neural activity to behavior and the environment (Gottlieb, 2007). For instance, maternal behavior in rats, such as licking and grooming, is linked to differences in DNA methylation in offspring early in life and into adulthood, and these methylation differences in offspring can be experimentally reversed by cross-fostering with mothers (Weaver et al., 2004). In humans, perceptions of parental rejection predict increased DNA methylation patterns in whole-genome analyses (Naumova et al., 2016). There is also evidence that more traumatic life experiences are linked to epigenetic differences. In a study of postmortem hippocampi of suicide victims, a neuron-specific glucocorticoid receptor (NR3C1) promoter showed epigenetic differences in glucocorticoid receptor expression and cytosine methylation depending on victims' history of child abuse (McGowan et al., 2009).

Findings such as these demonstrate that psychological outcomes are not the result of nature *or* nurture, and furthermore, they are not the result of simply adding partial contributions of nature and nurture to come up with a total of 100% influence. It is more accurate to say that nature and nurture each contribute 100% to the equation, and importantly, they *interact* to produce variation in traits or behaviors. The nature of this interaction is crucial in that one cannot understand the overall effects of genes or the environment as separate from the interaction itself. To borrow an example from Frans de Waal (2001),<sup>1</sup> to ask whether differences in sound from a drum come from either characteristics of the drummer or the drum itself may be slightly misguided. Although any changes in timbre between an expert and a novice drummer playing on the same small drum can be attributed solely to their differences in drumming experience, this interpretation ignores the fact that features of the drum—its size, for instance—are crucial for a complete understanding of how these different drummers produced different sounds. Indeed, hearing both drummers play on a small drum, one very sensitive to touch, may expose any differences in the drummers' techniques, whereas a larger drum may dull the differences in the sounds they produce. Similarly, a  $G \times E$  effect may demonstrate that an environmental stimulus has a striking influence, but only for people with one particular genotype and not the other.

To explain  $G \times E$  effects, some researchers have theorized that having certain genetic variants indicates greater sensitivity to environmental inputs, “for better *and* for worse,” such that some people may be more genetically susceptible to be influenced not only by more harmful environments but also by more beneficial ones (Belsky, Bakermans-Kranenburg, & van IJzendoorn, 2007; Belsky et al., 2009). This *differential susceptibility hypothesis* predicts that in one environment, a genotype may seem “risky,” whereas in another environment, the opposite may be true. As an example of  $G \times E$  and test of differential susceptibility, Sasaki and colleagues (2013) examined whether a dopamine receptor gene (DRD4) interacts with experimentally primed religious salience to influence prosocial behavior. In this study, undergraduate participants were implicitly primed with a set of religion-relevant words or a set of neutral words and were then given the chance to behave prosocially by donating their time to various environmental organizations on the university campus. Results showed that the religion prime increased prosocial behavior, but only for people with 2- or 7-repeat alleles of DRD4, which have been linked to environmental sensitivity (Bakermans-Kranenburg & van IJzendoorn, 2011; biochemical and functional relation between DRD4 2- and 7-repeat alleles: Reist et al. 2007). For people without 2- or 7-repeat alleles of DRD4, the religion prime had no significant effect on their prosocial behavior. This research experimentally demonstrates the role of environmental cues—religious salience—in moderating the association between a gene and behavior. Put differently, these findings show that individuals with different genotypes vary in how directly responsive they are to environmental cues.

### *The Gene–Culture Interaction Framework*

Building on  $G \times E$  research, the gene–*culture* interaction framework is formulated to understand how the cultural context, as a form of environment, affects the association between genes and

psychological outcomes. The gene–culture interaction model considers the cultural environment as social groups with shared experiences—such as national or regional culture, religion, and social class—that shape specific meaning systems. Although the basic idea of environmental susceptibility is shared by both the  $G \times E$  and gene–culture interaction models, assumptions about the environment in these models differ. The  $G \times E$  model tends to focus on outcomes of varied degrees of functionality, such as psychopathology. In contrast, the gene–culture interaction model does not consider culture-specific behaviors and psychological functions in more versus less adaptive terms because it is assumed that divergences across cultures are the result of each group’s adaptation to their context-specific challenges and goals.

There is evidence from a developmental perspective that cultures can differ in their responses to particular challenges and that culture may continue to shape individuals in different ways over time. For example, the cultural value of emotion regulation and general calmness among Cameroonian Nso people may affect how infants behave when they are confronted by a stranger. The majority of Nso infants show no physiological or behavioral indicators of stress in this situation, whereas the more typical, “secure” response in Western middle-class contexts is for the infant to show signs of stress with a stranger and calmness with the mother (Otto, 2008, as cited in Keller & Otto, 2009). This process of cultural shaping begins early in life and continues across the life span. In fact, there is evidence that epigenetic differences in monozygotic twins increase throughout the course of development (Fraga et al., 2005), which has implications for processes of enculturation. It is likely that psychological traits are manifested in different behaviors depending on the demands of the surrounding culture, consistent with the assumptions of the gene–culture interaction model.

The basic idea of the gene–culture interaction perspective is that genetic influences shape psychological and behavioral predispositions, and cultural influences shape how these predispositions are manifested in the form of social behaviors and psychological outcomes. The model predicts that particular genotypes of environmental susceptibility genes predispose the carriers to respond more strongly to environmental input. Thus, when these carriers live in different cultural contexts with divergent values, expectations, and norms, they are expected to manifest those specific patterns more strongly than those who do not carry the same genotypes (Heejung Kim & Sasaki, 2012, 2014). Consequently, the model predicts that those carrying these environmental susceptibility genes may show the most pronounced cross-cultural differences and could at times even show opposite behavioral outcomes in different cultures.

There is a rapidly accumulating body of empirical evidence that supports the gene–culture interaction model. A typical methodological approach used in gene–culture interaction studies is to take two groups of participants from different cultural contexts (e.g., Americans and Koreans) and examine how cultural membership affects the association between a particular gene and behaviors that are empirically known to differ in those cultural contexts (e.g., level of emotional expressivity). Studies often also include a bicultural group (e.g., Korean American) that shares ethnicity and thus has similar allelic frequencies with one group (i.e., Koreans) but shares cultural experiences with another group (i.e., mainstream European Americans) as a way to distinguish the specific role of culture (e.g., Heejung Kim et al., 2011). This triangulation method has been used to rule out whether a gene–culture interaction could be attributed to covaried allelic frequencies of other unmeasured genes rather than cultural experiences.

Using this approach, researchers have found that culture moderates how a range of target genes predicts specific social behaviors and psychological tendencies. For example, the oxytocin receptor polymorphism (OXTR rs53576) that is known to predict socio-emotional sensitivity is associated with a different set of social behaviors in the United States and Korea. In the United States, where emotional expression is encouraged, carrying an environmentally susceptible (G) allele of OXTR increases the likelihood of the carrier being more emotionally open (Heejung Kim et al., 2011; LeClair, Janušonis, & Kim, 2014) and willing to seek emotional support under

stress (Heejung Kim, Sherman, Sasaki, et al., 2010a). In contrast, in Korea, where emotional restraint is encouraged, carrying the G allele increases the likelihood of emotion suppression (Heejung Kim et al., 2011) and a hesitation to seek emotional support in response to stress (Heejung Kim, Sherman, Sasaki, et al., 2010a). OXTR also seems to moderate the association between interdependence values at the individual difference level and empathy, such that the link is considerably stronger among G allele carriers than non-carriers (Luo et al., 2015). This empirical finding makes a novel contribution to pre-existing explanations of cultural differences in emotion regulation. Cross-cultural studies have demonstrated that there are varying norms for expressing versus suppressing emotions (Matsumoto, Yoo, Nakagawa, & 37 Members of the multinational study of cultural display rules, 2008), and this gene–culture interaction study suggests that one reason certain people regulate their emotions according to cultural norms is that they are biologically susceptible to be sensitive to the socio-emotional cues in a culture (Heejung Kim et al., 2011).

A similar pattern of results emerged with other genes besides OXTR. In a study comparing Japanese and Americans, those with an environmental susceptibility genotype (s/s) of 5-HTTLPR seem to have greater vigilance for facial expressions that change from positive to neutral, but only in a Japanese cultural context, in which social approval and disapproval matter more (Ishii, Kim, Sasaki, Shinada, & Kusumi, 2014). Moreover, another study reported that DRD4 moderates cultural differences in more general social orientation (Kitayama et al., 2014). Results of this study showed that individuals with environmentally susceptible alleles of DRD4 (i.e., 2- or 7-repeat alleles) tend to report a more independent social orientation in the United States, but a more interdependent social orientation in Japan. Taken together, these findings across different genes and psychological and behavioral outcomes support the notion that certain genotypes may endow people with greater predispositions to be influenced by cultural values, expectations, and norms.

The idea that genes predispose people to be more or less susceptible to cultural influence has implications for well-being and social adjustment. It is well established that the way particular psychological experiences lead to better or worse well-being outcomes depends greatly on cultural contexts (e.g., Kitayama, Mesquita, & Karasawa, 2006; Suh, 2002), and research suggests that these socio-cultural factors may interact with genes to influence one's well-being in a number of ways. First, certain cultural practices may discourage the psychological manifestation of a genetic predisposition. For example, researchers have argued that the cultural orientation of collectivism emerged as a way to protect its population's high genetic risk of depression (Chiao & Blizinsky, 2010). Consistent with this idea, a meta-analysis shows that the strength of the link between DRD4 variation and attention deficit hyperactivity disorder (ADHD) varies across nations such that the link is considerably stronger among some groups, such as European Caucasians and South Americans, than among other groups, such as Middle Easterners (Nikolaidis & Gray, 2010). Another study showed that Koreans who are more genetically sensitive to socio-emotional cues (i.e., G/G genotype of OXTR) experienced increased psychological well-being with greater religiosity, whereas European Americans showed a negative relationship (Sasaki, Kim, & Xu, 2011), perhaps because religiosity benefited well-being for those who are genetically predisposed to be socially sensitive but only in cultural contexts in which religiosity provides greater opportunities for social affiliation (Sasaki & Kim, 2011).

Second, cultural influence may foster potentially beneficial or costly psychological tendencies for individuals. For example, collectivistic cultures tend to value behaviors that could benefit social relations over behaviors that may promote individuals' well-being compared with individualistic cultures, which tend to prioritize individual goals (Triandis, 1989). Thus, people who carry environmentally susceptible genotypes are likely to embody culturally prescribed actions that may be personally costly or beneficial, depending on the cultural context. LeClair, Sasaki, Ishii, Shinada, and Kim (2016) found that carriers of the G/G genotype of OXTR rs53576, which is theorized to promote social affiliation and consequently, psychological resources (Saphire-Bernstein, Way, Kim,

Sherman, & Taylor, 2011), reported less loneliness than non-carriers in the United States, but people with this same genotype reported similar levels of loneliness as non-carriers in Japan. Moreover, this gene–culture interaction was mediated by avoidant attachment style, indicating that the social caution and reservation fostered in Japanese culture (e.g., Hashimoto, Mojaverian, & Kim, 2012) may be somewhat costly to individuals within this culturally normative pattern of relationship, curtailing the potential benefit of a social affiliative predisposition endowed by the G/G genotype.

Interestingly, higher levels of endogenous plasma oxytocin seem to predict successful socio-cultural adjustment among migrants in Canada (Gouin, Pournajafi-Nazarloo, & Carter, 2015). Those people who have higher levels of plasma oxytocin were initially lonelier at the beginning of their migration than those with lower levels of oxytocin, but after 5 months in a new culture, their reported loneliness decreased noticeably. More notably, those with higher levels of oxytocin increased their social relationship satisfaction and perceived social support relatively quickly over the course of 5 months, but among those with lower levels of oxytocin, social adjustment outcomes did not change. Although this is not a genetic study, it raises an interesting question about the roles that oxytocin-related genes may play in acculturation processes.

This finding suggests that the context of acculturation may provide highly valuable opportunities for researchers to investigate the process of cultural adaptability and how genes may affect such a tendency. Cultural susceptibility genes, such as OXTR, DRD4, or 5-HTTLPR, may influence acculturation outcomes among immigrants, and the exact nature of this influence probably depends on one's cultural and personal environment. However, it is also possible that greater genetic susceptibility to cultural cues, especially when a new culture fosters behaviors promoting individuals' well-being, could be beneficial because it is likely to readily increase cultural fit, which may in turn increase one's well-being. Sharing similar emotional experiences and worldviews tends to facilitate social contact and close relationships (Anderson, Keltner, & John, 2003; De Leersnyder, Mesquita, Kim, Eom, & Choi, 2014). Thus, increasing or decreasing the tendency to engage in culturally normative social behaviors is likely to have an impact on one's sense of cultural fit. At the same time, migration is a potentially stressful process, and thus, those people who are more susceptible to negative impacts of stressors, such as s allele carriers of 5-HTTLPR, may be more vulnerable to acculturative stress. Indeed, one study shows that among immigrants from a country with a higher population frequency of s allele carriers, their life satisfaction tends to decrease over time compared with those from a country with a lower frequency of s allele carriers (Kashima, Kent, & Kashima, 2015). Considering genes together with immigration patterns has important implications for theories of acculturation. Current bidimensional models of acculturation delineate two independent cultural identifications, that of heritage and mainstream culture (Berry, 1997; Ryder, Alden, & Paulhus, 2000), yet an interesting implication based on the Kashima et al. (2015) finding is that acculturation to the mainstream culture may vary depending on genotype frequencies in one's heritage culture. In other words, heritage and mainstream cultural identification may not be entirely independent for people depending on genotype distributions in different regions. Indeed, migration and acculturation are particularly relevant processes within which genes and culture work together to shape social behaviors.

Recently, there have been advances in understanding potential neural mechanisms underlying gene–culture interactions. For instance, Ma and colleagues (2014) found that people with the l/l genotype of 5-HTTLPR showed a positive relationship between self-reported level of interdependence and neural activation in the social brain network, including the medial prefrontal cortex, bilateral middle frontal cortex, and bilateral insula, when thinking about mental attributes of one's mother. However, this relationship between interdependence and activation in these regions did not hold for people with the s/s genotype. A study focusing on OXTR found that the association between interdependence and a neural response to others' suffering in the insula, amygdala, and superior temporal gyrus was stronger for carriers of the OXTR G/G genotype than the A/A

genotype (Luo et al., 2015). Investigations such as these that integrate across multiple methods and levels of mechanisms represent the cutting edge of cultural neuroscience.

### *Theoretical Issues in Socio-Cultural Approaches to Genetics*

Gene–environment and gene–culture interaction approaches can provide researchers with a useful way to articulate the mutual nature of genetic and environmental influence, and yet, understandings of the psychological and social mechanisms of gene–environment and gene–culture interactions are limited for a couple of reasons. First, although there have been numerous findings demonstrating that some environmental stimulus predicts different outcomes depending on whether a person has one or another genotype, what the field lacks is a satisfying mechanistic explanation at the level of psychology for why these interaction effects occur. Second, the meaning of the “environment” in  $G \times E$  is not clear. Which aspects of the environment are relevant for interacting with which genes to then influence thoughts and behaviors? The “environment” is a potentially unbounded term.

*Differential susceptibility and the motivational setting hypothesis.* The *differential susceptibility hypothesis* (Belsky et al., 2007) made important progress in the field by demonstrating that genetic susceptibility was not a risk factor, but rather, could bring about both positive and negative outcomes depending on the nature of the environment. Differential susceptibility put the focus on flexibility or malleability of particular genotypes rather than on risk or vulnerability. The significance of this insight cannot be understated. The differential susceptibility hypothesis predicts that people with certain genetic predispositions may be sensitive to the environment. However, it does not specify what psychological mechanisms underlie this sensitivity and which aspects of the environment are particularly impactful.

Another possibility, first set forth by Hyunji Kim, Nasiri, and Sasaki (in press), is the motivational setting hypothesis, which may offer insights for the psychological mechanisms of gene–environment and gene–culture interaction effects. According to this hypothesis, people seem “sensitive” to certain environmental inputs because they are focused on particular goals within psychological domains (e.g., anxiety, reward, and sociality). Sensitivity to the environment may exist at the level of perception and cognition, but the reason for this is ultimately motivational. For example, a person focused on avoiding anxiety will be more sensitive to aspects of the environment that are potentially threatening. The person would not necessarily be more sensitive to her environment in general, but rather would show sensitivity primarily to those aspects relevant to her goal of avoiding anxiety. Importantly, the meaning of environmental factors considered “potentially threatening” depends on the socio-cultural context, and thus, a cultural psychological perspective is necessary for a clear understanding of when and why sensitivity to certain aspects of the environment occurs. The motivational setting hypothesis also predicts that people have different settings as a default and in various contexts depending on different motivations. Even without an acute environmental stimulus seeming to elicit a response, a person will show a particular tendency as a baseline to reflect her underlying goal and default assumptions about the environment in general, and this baseline is likely set by interactions between genes and the environment that occur earlier in one’s developmental life history (Hyunji Kim & Sasaki, in press). The motivational setting hypothesis is consistent with research on person-by-situation interactions or “personality profiles” that show a predictable behavioral tendency depending on the situation (Mischel & Shoda, 1995).

The motivational setting hypothesis may be useful from a theoretical standpoint because it attempts to delineate which aspects of the environment are relevant for  $G \times E$  effects, and given that culture is a crucial component of the social environment, this hypothesis applies to instances of gene–culture interactions as well. To put it simply, the motivational setting hypothesis highlights



domain-relevant aspects of the environment because certain genotypes are linked to motivational settings in those particular domains. Importantly, the cultural context provides necessary information about what is meaningful in each domain. Whereas the differential susceptibility hypothesis does not specify which aspects of the environment may be relevant, the motivational setting hypothesis emphasizes that the aspect of the environment must be relevant to an underlying motivation. By focusing on motivation, this hypothesis also attempts to uncover some of the psychological mechanisms through which gene–environment interactions occur, contributing to an understanding of the complex mechanisms that allow people with different genetic predispositions to perceive, interpret, and respond to information in the socio-cultural environment.

*Culture as a meaningful form of environment in  $G \times E$ .* The second issue, regarding the specific meaning of the environment in  $G \times E$ , may be addressed by looking more closely at evidence of gene–culture interactions. The gene–culture interaction model predicts that culture, as a specific form of environment involving shared norms, interacts with genetic predispositions to predict different outcomes (Heejung Kim & Sasaki, 2014; Heejung Kim, Sherman, Taylor, et al., 2010). Although *culture* is a similarly unbounded term, one aspect of culture is fairly clear, and that is the role of culture in human meaning making. Culture provides a framework of meaning that guides people’s interpretations of objects and events. Thus, the moderating role of culture suggests that subjective interpretations of meaning making may be at the psychological core of  $G \times E$  effects. Just as there was a call for bringing meaning into psychology after the cognitive revolution (Bruner, 1990; Geertz, 1973), there may be a need for meaning in  $G \times E$  theorizing.

The differential susceptibility hypothesis does not fully account for a number of findings in  $G \times E$  studies, including research on gene–culture interactions. Regarding the issue of which aspects of the environment are relevant for  $G \times E$  effects, the answer must consider cultural interpretations of stimuli in the environment. One example comes from a gene–culture study described earlier (Ishii et al., 2014) showing that having two *s* alleles (*s/s* vs. *s/l* or *l/l*) of 5-HTTLPR was associated with being quicker to notice the disappearance of smiles, but only among people with a Japanese cultural background. This evidence of a gene–culture interaction is consistent with findings that people from Japan tend to have a greater concern for social approval (Suh, Diener, Oishi, & Triandis, 1998) and are more likely to experience social anxiety (Norasakkunkit & Kalick, 2002) compared with people from North America. Therefore, we can reason that as an environmental stimulus, the disappearance of a smile can be interpreted as a social threat and consequently, cause for increase anxiety, but only in a culture where social anxiety is high and vigilance for signs of disapproval is a shared norm.

The differential susceptibility hypothesis does not account for the meaning that is so central to cultural psychology because at first blush, the disappearance of a smile may seem like a uniformly negative environmental stimulus that should evoke a negative response. However, it is difficult to label this stimulus “negative” because there are cultural meanings tied to this label. In a culture such as North America, where social anxiety is not as high and there is relatively less concern over social approval, people may not hold the same meaning when they see a disappearing smile. Consistent with the motivational setting hypothesis, people with different genotypes of 5-HTTLPR may vary in their motivation to avoid anxiety. People with *s/s* (vs. *s/l* or *l/l*) genotypes may be more vigilant toward potential threats, or sources of anxiety. In one culture, a disappearing smile could be threatening for people with *s/s* genotypes, whereas in another culture, that same interpretation may not necessarily apply. This is what cultural psychology can add to  $G \times E$  research—meaningful explanations of  $G \times E$  influence at the level of psychology.

### *Methodological Issues in Socio-Cultural Approaches to Genetics*

Advances in the area of culture and genetics come with a number of unique challenges. A common method in gene–culture interaction research is the use of at least two different ethnic groups

as proxies for culture, and depending on the specific gene or set of genes examined in a study, the distribution of genotypes within each ethnic group may differ. For instance, in the case of 5-HTTLPR, l alleles are more common than s alleles in European populations, but it is the s allele, rather than the l allele, that is more common in East Asian populations. In fact, some researchers have argued that different frequencies of genetic polymorphisms across groups may be linked to certain cultural values, such as collectivism, via processes of gene–culture coevolution (Chiao & Blizinsky, 2010). It is important to note, however, that a population with a high frequency of susceptibility genotypes for one gene will not necessarily have high frequencies of susceptibility genotypes for other genes. Although the s/s genotype of 5-HTTLPR is considered a susceptibility genotype and is more common in East Asian than in European populations, the G/G genotype of OXTR, which is also considered a susceptibility genotype, is relatively less common in East Asian than European populations. Thus, one open question is how these various environmental susceptibility genes combine to contribute to susceptibility to different environmental factors.

One way to address the issue of differing genotype distributions between ethnic groups is to use a multi-gene approach. By creating an index of genetic susceptibility using an additive model (i.e., more environmental susceptibility genotypes indicate greater environmental susceptibility), one study found that this index was associated with a wider range of predicted psychological outcomes than using each individual gene alone (LeClair et al., 2014). Combining multiple genes into an index also normalized the distribution of susceptibility versus non-susceptibility genotypes across groups. Other studies have used a multi-gene approach to address the problem of predicting complex outcomes from a single gene (e.g., Stice, Yokum, Burger, Epstein, & Smolen, 2012), an issue that applies broadly to genetic association and  $G \times E$  studies (Munafò & Flint, 2009, 2011).

Another challenge that arises from gene–culture interaction research is that ethnic groups are often used to indicate “culture,” but as discussed above, ethnic groups can differ in their frequency of alleles across multiple genes. In a study with two ethnic groups representing different cultures, the candidate gene may be interacting with another gene or set of genes that covary with ethnicity, and not necessarily with cultural background. Therefore, it is possible that investigations of gene–culture interactions may actually be demonstrating gene–gene interactions.

This culture–ethnicity confound issue can be addressed in a couple of ways. First, studies can include a third ethnic group that differs in ethnicity from but shares the cultural context with Culture 1, and differs in cultural context from but shares ethnicity with Culture 2, as discussed earlier. Second, studies can utilize priming methods to causally manipulate the cultural value or norm of interest. Some research has manipulated religious salience to demonstrate that its causal effect on behavior is moderated by genes (Sasaki et al., 2013; Sasaki, Mojaverian, & Kim, 2015). Future research in this area may explore whether other primes, such as those manipulating self-construal (e.g., Gardner, Gabriel, & Lee, 1999), interact with genes in ways that parallel  $G \times C$  with cultural groups.

## Culture and Physiological Processes

Genes influence psychological processes by communication through neurotransmitters, triggering hormonal and immune responses. Thus, consideration of neuroendocrinology and the immune system in the context of cultural influence is of importance. In this section, we briefly review research on how culture influences neuroendocrine and immune responses to social situations and how neurotransmitters and hormones moderate culture-specific behaviors.

The way individuals respond to seemingly identical situations depends on how they interpret the situation. Culturally shared meaning systems provide varied frames to make an interpretation (Bruner, 1990), and different interpretations lead to divergent psychological and behavioral

responses (e.g., Cohen, Nisbett, Bowdle, & Schwarz, 1996; Heejung Kim, 2002). Biological responses are no exception. Research finds cultural differences in neuroendocrine and immune reactions to an array of intrapersonal and interpersonal tasks (e.g., Cohen et al., 1996; Heejung Kim, 2008; Stephens, Townsend, Markus, & Phillips, 2012; Taylor, Welch, Kim, & Sherman, 2007).

For example, previous studies have demonstrated that explicitly seeking and providing social support indicate good relationships (Chen, Kim, Sherman, & Hashimoto, 2015) and bring greater psychological benefits among European Americans than Asians and Asian Americans (Heejung Kim, Sherman, & Taylor, 2008). Building on this finding, Taylor et al. (2007) investigated outcomes of seeking different types of social support, focusing on cortisol response to an acute lab stressor. This study showed that experimentally instructing participants to explicitly seek social support increased cortisol responses (i.e., higher biological stress) to the lab stressor among Asian Americans, but such an increase was not found among European Americans. Extending this finding to a more chronic and long-term relationship context, another study examined proinflammatory cytokines in relation to individuals' perception of social support availability in their social network (Chiang, Saphire-Bernstein, Kim, Sherman, & Taylor, 2013). Cytokines are a part of an immune response that is adaptive in the short term but can have long-term negative impacts such as elevated chronic inflammation (Ridker, Rifai, Stampfer, & Hennekens, 2000), and thus, they are an important biomarker of health. Specifically looking at the proinflammatory cytokine interleukin-6 (IL-6), this study found that among European Americans, having more available social support predicted lower levels of IL-6, indicating lower inflammatory activity, whereas among Asian Americans, this relationship was not significant.

This pattern of results is also found in relation to more basic intrapersonal processes. Cultural differences in cortisol responses are found as a result of verbalizing thoughts (Heejung Kim, 2008) and facing cultural norms mismatched with one's own (Stephens et al., 2012). Moreover, even a well-established association in Western psychology, such as the link between negative emotions and health outcomes (e.g., Kubzansky & Kawachi, 2000), seems to vary across cultures. A study using large, nationally representative data sets (i.e., Midlife Development in the United States—a national longitudinal study of health and well-being [MIDUS]—a national longitudinal study of health and well-being—and Midlife Development in Japan [MIDJA]) found that experiencing a higher degree of negative emotions is associated with higher IL-6 (i.e., higher inflammatory activity) among Americans, but is not associated with the same outcome among the Japanese (Miyamoto et al., 2013). Taken together, these studies suggest that people from East Asian and mainstream American cultures define adaptive relationships and situations differently, and this difference may lead to culture-specific psychological and biological consequences of social interactions. These studies show that the biological functions that were examined mostly corroborate behavioral findings and provide a greater understanding of how socio-cultural experiences get into the mind through our biology.

Neuroendocrinology raises the question of not only how our biological systems respond to environmental stimuli, but also how they moderate the process of socio-cultural influences themselves. Most of the evidence at this point comes from research on the effects of oxytocin. Oxytocin, a peptide produced in the hypothalamus that functions as both neurotransmitter and hormone (Carter, 2014), has been the focus of much investigation, in part because it may be experimentally manipulated safely (MacDonald et al., 2011). This psychopharmacological approach, using experimental administration of intra-nasal oxytocin spray, allows testing of the causal roles of oxytocin suggested by genetic research.

A wide range of prosocial tendencies, such as social bonds, trust, and cooperation, have been associated with oxytocin, examined as both plasma oxytocin (e.g., Feldman, Weller, Zagoory-Sharon, & Levine, 2007) and exogenously administered oxytocin (e.g., Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005) among animals and humans (see Carter, 2014, for review). More recent analysis revealed, however, that these uniform experimental effects and simple

associations are weak (Nave, Camerer, & McCullough, 2015), thus challenging the notion that oxytocin simply promotes prosociality. This analysis highlights the importance of social contexts in understanding how oxytocin works. Research shows that oxytocin, in fact, may increase sensitivity to important social and emotional cues, such as the ability to accurately attribute the emotions and mental states of others (e.g., Domes, Heinrichs, Michel, Berger, & Herpertz, 2007), to distinguish in- and out-group membership (De Dreu et al., 2010), and to activate dominant relational schema (Bartz et al., 2010). Oxytocin can also increase the tendency to be selectively responsive to desirable feedback in updating one's beliefs and, thus, is proposed as a molecular substrate for optimistic belief updating, perhaps allowing people to adapt to different social environments (Ma et al., 2016).

Applying these findings to an understanding of cultural influence, a recent study experimentally administered oxytocin to a group of American and Japanese male college students and measured their behaviors indicative of social trust (Eom et al., 2016). Previous research established that there is lower generalized trust in Japan than in the United States (Yamagishi & Yamagishi, 1994). Based on previous gene-culture interaction findings, we predicted that oxytocin would magnify cultural differences by activating culturally dominant relationship schemas. The results demonstrated that Americans increased trust-related behaviors, such as entrusting one's money to a stranger in an economic game, in the oxytocin administration condition compared with the placebo condition, replicating previous studies on oxytocin and trust. However, interestingly, the Japanese participants showed the opposite tendency, displaying decreased trust in the oxytocin condition compared with the placebo condition. This study shows that, first, the effects of oxytocin differ across cultures, and second, oxytocin seems to cause people to behave in a more culturally expected manner. This second point, in particular, begins to inform biological mechanisms underlying cultural influences, such as norms about trust (Yamagishi & Yamagishi, 1994). Although there have been very limited psychopharmacological examinations of the interplay of culture and biology, it is clearly a very promising and central next step in cultural neuroscience research.

## Culture and the Brain

Early studies in cultural neuroscience focused primarily on patterns of neural activity across cultural groups. Rather than relying solely on reported beliefs and observed behaviors, for the first time, researchers could see what a cultural difference might look like in the brain. An increasing flow of functional magnetic resonance imaging (fMRI)<sup>2</sup> and electroencephalography (EEG) studies began mirroring well-known behavioral findings in cultural psychology, and an important message from this new field of cultural neuroscience was that questions of culture are also questions of biology, and crucially, the brain. Although many of these studies have been conducted only within the last decade, they form the foundation of cultural neuroscience and still represent the most active area of research within this field.

It is perhaps no surprise that one of the earliest and most highly cited cultural neuroscience articles (Zhu, Zhang, Fan, & Han, 2007) is based on independence versus interdependence across cultures, a pair of self-construals made famous in Markus and Kitayama's seminal *Psychological Bulletin* article in 1991. In their article, they describe the independent self as one that tends to be more separate from others, acting according to internal desires and traits. The interdependent self, however, tends to be more connected to others, incorporating relationship concerns into one's own actions (Markus & Kitayama, 1991). This phenomenon of the self as separated from versus connected to others was corroborated by research by Zhu and colleagues (2007), which asked participants to make judgments about the self, one's mother, or a familiar but non-close other while measuring activation in the medial prefrontal cortex (MPFC), an area previously associated with judgments about the self versus others (Kelley et al., 2002). Their results showed

that, for Western participants, MPFC activity increased only when making judgments about the self. However, for Chinese participants, “the representation of Chinese mother cannot be distinguished from the representation of their selves, in terms of MPFC” (Zhu et al., 2007, p. 1314)—a finding that very nicely affirmed the concept of overlapping selves from Markus and Kitayama’s (1991) theorizing just more than 15 years prior.

Studies such as these opened the door to many new investigations, including some aimed at deeper issues surrounding cultural influence and learning. In a recent EEG study, researchers addressed the question of how people detect right versus wrong ways to act in their own culture (Mu, Kitayama, Han, & Gelfand, 2015). Specifically, they tested whether there would be cultural differences in responses to social norm violations as measured by the N400 component (event-related potential negative deflection around 400 ms), a neural indicator of semantic incongruity (Kutas & Hillyard, 1980). Results showed that Chinese participants, who are from “tight” cultures relatively more concerned about norm violations, had a clear N400 effect in frontal and temporal regions in response to strong norm violations (vs. the appropriate norm condition); however, this effect did not hold for U.S. participants, who are from more “loose” cultures. Interestingly, these cultural differences emerged in response to violations of social norms in particular, and not in response to non-social semantic violations (Mu et al., 2015). The specificity of these results suggests that there may be important differences between tight and loose cultures in the way they process social norm-relevant information, but not necessarily information more broadly. This EEG study is consistent with research showing that tight cultures have higher constraints on the behaviors considered appropriate in everyday situations compared with loose cultures (Gelfand et al., 2011). Thus, detecting norm violations of various degrees may be a crucial ability for creating and maintaining shared beliefs and behaviors across cultures, and these findings demonstrate a neural mechanism through which people engage in these processes.

Across many cultural neuroscience studies, previously discovered cultural psychological effects have been reflected in patterns of brain activity (e.g., Hedden, Ketay, Aron, Markus, & Gabrieli, 2008; Varnum, Na, Murata, & Kitayama, 2012), with some studies integrating cultural priming methods to demonstrate causal effects of cultural influence (e.g., Chiao et al., 2009; Sui & Han, 2007). With increasing interest in the brain and its underlying neural mechanisms, scientific reductionism may be of growing concern to some researchers, especially in cultural psychology, where socially shaped, contextually driven cultural meanings are so central to the field. However, as many cultural neuroscience studies themselves demonstrate, meaning is actually at the core of these studies.

For instance, participants in one EEG investigation showed a stronger N400 response to incongruous versus congruous personal traits, but this effect occurred only among European Americans, who are more likely to spontaneously infer personal traits on the basis of observed behavior. East Asians are less likely to show a spontaneous trait inference effect, and likewise, they did not exhibit the same N400 effect when faced with incongruous trait information (Na & Kitayama, 2011). A related study found that Japanese females who were more interdependent (vs. independent) showed greater N400 activation in response to words spoken in a tone that was incongruent with their meaning (Ishii, Kobayashi, & Kitayama, 2010). In addition, an fMRI study demonstrated that American participants showed activation in the caudate nucleus and MPFC in response to dominant body displays, whereas Japanese participants showed this same activation pattern when viewing the opposite (i.e., submissive) type of body display (Freeman, Rule, Adams, & Ambady, 2009). Across all these studies, the broad pattern of findings is consistent: People show different responses at the level of neural activity depending on what is meaningful and reinforced in their culture, whether it be traits spontaneously inferred from behaviors, vocal tones that match or mismatch word meanings, or bodily postures that communicate dominance versus submission.

One of the strongest uses of neuroscience techniques, however, may be to elucidate psychological processes that would otherwise be difficult to observe. One such instance of this comes from an investigation of culture and numerical processing, including number representation, numerical addition, and quantity comparison (Tang et al., 2006). As participants performed these tasks, English speakers (relative to Chinese speakers) generally showed greater activation in the left perisylvian cortices, including the Broca and Wernicke areas—regions highly relevant to language processing. However, Chinese speakers (relative to English speakers) showed stronger activation in different brain regions compared with English speakers performing the same tasks. During an addition task, for instance, Chinese speakers showed stronger premotor association, and during a comparison task, they showed stronger connections between the visual cortex and supplementary motor area, suggesting greater visuospatial processing. Intriguingly, Chinese and English speakers did not differ in behavioral measures of accuracy or reaction time for the task (Tang et al., 2006). Although they were producing the same behavioral output, people from these different cultures seemed to be using different psychological processes to solve the same problem, and thus, the fMRI data in this case were crucial for highlighting a cultural difference in underlying psychological processes. Previous research without the use of fMRI came to a similar conclusion as Tang et al. (2006). Heejung Kim (2002) found that having participants talk aloud during an abstract reasoning task led to weaker performance for Asian Americans (compared with European Americans), suggesting that they may rely less on language processing when thinking through the problems. This research theorized that the Western assumption about talking and thinking being closely connected is not shared in East Asian philosophical thought. Because the Heejung Kim (2002) study demonstrated cultural differences using behavioral measures, it is likely that there would also be cultural differences in brain activation during this task, extending the cultural neuroscience findings from Tang et al. (2006) beyond numerical processing to abstract reasoning.

An important take-away point from neuroscience findings overall is that meaningful differences at the level of psychology suggest there are underlying differences in brain activation<sup>3</sup>—a point that may have been overlooked in the past. Findings such as those from the “overlapping self–mother representation in the brain” cultural neuroscience study (Zhu et al., 2007), for example, importantly remind the field that this surprising point perhaps should not have been surprising.

### *Theoretical Implications and Future Questions*

The present review aims to provide a summary of the current status of cultural neuroscience in an effort to connect previous parallel investigations of cultural and biological underpinnings of human behaviors, and in so doing, to offer a theoretical framework to look at how they jointly function. With this goal, there are a number of different ways in which cultural and cross-cultural psychology may benefit from findings in cultural neuroscience. One is to recognize the constituent role of culture in biological processes. Clearly, a wide range of biological factors, from genetic associations to neural responses in a lab situation, vary across cultures. Moreover, these variations are by and large explainable given values, assumptions, and norms shared in different cultures. In that sense, these findings simply underscore and extend the already well-established notion that culture fundamentally influences psychology and behavior by providing different meaning systems within which individuals may engage their social environment.

Another way to benefit is to consider these empirical findings as initial evidence to understand more complex biological mechanisms of cultural influence. Humans, along with all other non-human organisms, are biological beings whose thoughts, feelings, and behaviors necessarily involve biological processes. Given the importance of sociality for humans, there have to be biological pathways of socio-cultural influence. Integrating a gene–culture interaction perspective with psychopharmacological studies may ultimately help researchers to more fully understand

these pathways of influence. For example, existing findings suggest that certain neurotransmitter systems, such as dopamine and serotonin systems along with other neuromodulators, such as oxytocin, may underlie cultural influence. Fluctuations in signaling through these pathways across and within individuals are associated with varying degrees to which people are influenced by culturally dominant worldviews and norms.

Moreover, these studies may help us understand why different people might respond to cultural information in divergent ways and then show different downstream behavioral outcomes. Within any cultural group, there is a significant degree of heterogeneity in how much each individual conforms to the normative set of behaviors. Of course, these variations are outcomes of a multitude of personal, familial, and social factors. Gene–culture interaction findings suggest that genes may be one of these factors. In all studies to date, culture-specific behaviors are mostly carried out by those with environmental susceptibility genotypes, illustrating the point that not all members of a society are influenced by culture to the same extent. Diversity in individual traits within a social group is one of the keys to successful adaptation (Buss, 2009). Individual differences in the susceptibility to cultural influences are thus to be expected, and future research should address the issue of heterogeneity of cultural influence more directly.<sup>4</sup>

Many practical concerns in society can benefit from this assumption of mutual cultural and biological influence. For instance, the newly minted HGP-Write project has the broad goal of understanding “the blueprint for life” (<http://engineeringbiologycenter.org/>) and also aims to address challenges around the globe, including health care and environmental issues. An important implication from research on gene–culture interactions is that projects such as HGP-Write may require an understanding of not only biological factors but also cultural competency to ultimately achieve their goals.

The gene–culture interaction perspective in cultural neuroscience also provides a theory for understanding which aspects of the environment are potentially meaningful to people and why. Individual difference research that has been more common in mainstream genetics research may implicitly ignore more macro socio-cultural processes that change the way individuals think and behave. Similarly, some cultural research may unintentionally overlook individual differences. Cultural neuroscience sets out to understand the interplay of genes and culture, and the underlying neural and physiological mechanisms connecting the two, encouraging researchers across various areas of expertise to think about why individual differences are manifested in different ways across cultures. Advances in this relatively young field may have far-reaching implications for research in behavioral genetics, psychophysiology, personality and individual differences, cultural and cross-cultural psychology, and beyond.

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### **Notes**

1. And his example was modified from Kummer (1971).
2. There are also studies that examine structural magnetic resonance imaging (MRI), but given that functional magnetic resonance imaging (fMRI) and electroencephalography (EEG) are more commonly studied in cultural neuroscience, we focus on these two methods in this review.
3. If differences are observed in behavior but not observed in neural activation, that means current neural measures are not sensitive enough to detect the differences found in behavior.

4. However, we should note that so far, there is no evidence that the same set of individuals may be more susceptible to all kinds of cultural influences. In research by Na et al. (2010) demonstrating that cultural differences are not reducible to individual differences, they argue that it is unlikely for the same individuals to be culturally normative across all domains (e.g., self-representation, cognitive tendencies, emotional expressivity, etc.). Instead, certain individuals may be more culturally normative in one domain, whereas a different set of individuals may be more culturally normative in another.

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